

1 TITLE: No support for intra-nor inter-locus sexual conflict over mating latency and copulation duration in a
2 polyandrous fruit fly
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20 Author Contributions: JMC designed, carried out, and collected the data for Population 2. JLS designed,
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23 supplementary material. JMC and JLS wrote and edited the paper.

24 Conflict of Interest: The authors declare no conflict of interest.
25

26 Abstract

27 The total strength of sexual selection on males depends on the relationship between various
28 components of pre- and post-copulatory fitness. Misalignment between male and female interests
29 creates inter-locus sexual conflict, where the fitness of one sex is increased at the expense of the other.
30 Although rarely considered, mating behaviours can also be genetically correlated between males and
31 females, creating intra-locus sexual conflict, where beneficial alleles in one sex are costly when
32 expressed in the other sex. How inter- and intra-locus sexual conflicts operate on the expression of
33 mating behaviours remains little understood. Here, we study male attractiveness, mating latency and
34 copulation duration in two populations of the polyandrous *Drosophila serrata*. Univariate analyses show
35 little genetic variance in mating latency, and that males, but not females, contribute to copulation
36 duration genetic variance. Further, multivariate analyses revealed little covariance between the studied
37 traits. However, analyses considering male and female contribution in a single framework supported
38 genetic contributions from both sexes for mating behaviours and complex patterns of between sexes
39 correlations. Finally, our study did not find any association between those mating behaviours and fitness
40 component, specifically (i) no phenotypic covariance between male attractiveness and mating latency
41 and, (ii) longer copulations did not result in the production of more offspring. With no detectable fitness
42 benefits in any sexes for shorter mating latency or longer copulation duration, our results do not
43 support the presence of inter- nor intra-locus sexual conflict for these mating traits.

44

45 Keywords: mating latency, copulation duration, quantitative genetics, indirect genetic effect, sexual
46 conflict, *drosophila serrata*, multivariate analyses, Cuticular HydroCarbons

47

48 Introduction

49 The total strength of sexual selection on males depends on the relationship between various
50 components of pre- and post-copulatory fitness (Collet et al., 2014). Theoretical expectations of how
51 pre- and post-copulatory fitness covary, however, are unsettled. On the one hand, the phenotype-linked
52 fertility hypothesis predicts that male ornaments reflect their fertility, and thus male pre- and post-
53 copulatory success are predicted to be positively correlated (Sheldon, 1994). On the other, trade-offs
54 may exist between pre- and post-copulatory traits, for example, mating success and sperm
55 competitiveness, resulting in a negative correlation between pre- and postcopulatory fitness (Parker &
56 Pizzari, 2010). The empirical data are also mixed: substantial experimental and observational studies
57 support both negative (e.g. Danielsson, 2001) and positive (e.g. Collet et al., 2012) phenotypic
58 correlations (See metaanalysis Mautz et al., 2013). Despite the interest in, and the large number of
59 phenotypic studies, there have been fewer to focus on the genetic covariances between pre- and post-
60 copulatory traits (but see Taylor et al., 2013, Hall et al., 2013). Genetic covariances, however, are the
61 currency for evolution, and in order to understand the evolution of copulatory traits in males, we must
62 understand how they genetically covary.

63 In addition to within-sex genetic covariances, correlations of homologous traits between the
64 sexes have an important role in determining the evolutionary trajectories of fitness-related and other
65 traits (e.g. Gosden et al., 2012, McGlothlin et al., 2019, Sztepanacz & Houle, 2019, Holman & Jacomb,
66 2017). When the largely shared genome of males and females is subject to divergent selection to sex-
67 specific phenotypes, intralocus sexual conflict can arise (Bonduriansky & Chenoweth, 2009). For
68 example, when the alleles that underlie traits which increase male reproductive fitness, such as
69 attractiveness, come at a cost when they are expressed in females, and vice versa. Sexual antagonism
70 can also arise when selection is sexually concordant, suggesting that it is an inevitable by-product of
71 species with separate sexes (Connallon & Clark, 2014). Intralocus sexual conflict results in a reduction of
72 population mean fitness because neither sex can reach their fitness optima. Although sexual conflict
73 may be resolved by the evolution of sexual dimorphism (Collet et al., 2016, Bonduriansky & Chenoweth,
74 2009), the pervasiveness of negative intersexual genetic correlations for fitness indicate that these
75 conflicts are often unresolved (Chippindale et al., 2001, Brommer et al., 2007, Foerster et al., 2007,
76 Kohorn, 1994, Cox & Calsbeek, 2009) .

77 Another form of sexual conflict, interlocus sexual conflict, can arise from the interactions between the
78 sexes, which increase the fitness of one sex at the expense of the other (Arnqvist & Rowe, 2005). These
79 interactions result in a coevolutionary arms race where adaptation of a trait in one sex results in
80 counteradaptation of the interacting trait in the other sex (Parker, 1979, Moore & Pizzari, 2005, Rowe et
81 al., 2005, Arnqvist & Rowe, 2005, Chapman et al., 2003, Clutton-Brock & Parker, 1995). Such
82 evolutionary arms races can lead to the rapid evolution of interacting traits. Historically, intra- and inter-
83 locus sexual conflict have been treated as separate evolutionary processes. More recently, however, the
84 potential for an interaction between intra- and inter-locus sexual conflict has been highlighted (Pennell
85 & Morrow, 2013). In particular, theory has shown that when reproductive traits are involved in both
86 intra- and inter- locus sexual conflict their interactions can lead males and females into a repeating cycle
87 of conflict escalation followed by resolution, preventing them from reaching a stable equilibrium
88 (Pennell et al., 2016).

89 The extent of between-sex pleiotropy (intra-locus) for traits that are also involved in inter-locus
90 sexual conflict is scarce, and in general, we lack a comprehensive study of traits that may experience
91 both intra- and inter-locus sexual conflict in a single framework. Copulatory traits are one class of traits
92 that may be genetically correlated between the sexes and also interact during mating, leading to the
93 potential for both intra- and inter- locus sexual conflict. Here, we used a quantitative genetic breeding
94 design to investigate the within and between sex heritabilities and correlations of copulatory traits in
95 *Drosophila serrata*. Specifically, we estimated the heritability of male attractiveness, male and female
96 mating latency and copulation duration, and the within and across- sex genetic correlations of these
97 traits. Furthermore, we investigated whether any of these traits predicted male and female fitness,
98 indicating the potential for sexual conflict.

99 The relationship between attractiveness and mating latency has been particularly well described
100 in *Drosophila melanogaster*, where males that carry the cuticular hydrocarbon (CHC) pheromone, 7-
101 tricosene, are more attractive (as measured by their mating rate), and mate faster, than males that do
102 not (Grillet et al., 2006). In one study, variation in mating latency was explained to a similar extent by
103 the genetic identity of both males and females, suggesting a role of both sexes in determining this
104 phenotype (Tennant et al., 2014). The relationship between male attractiveness and mating latency is
105 not universal, however. In *D. bunnanda*, males that were artificially selected to carry a more attractive
106 combination of cuticular hydrocarbons (as measured by their mating rate) did not mate faster than
107 males selected for a less attractive combination (McGuigan et al., 2008), and in *D. melanogaster*,

108 MacKay *et al* (2005) found that the genetic background of females was the best predictor of mating
109 latency. In *D. serrata*, male attractiveness has also been well described, where females have been shown
110 to prefer a particular combination of CHC contact pheromones in males (Chung *et al.*, 2014, Hine *et al.*,
111 2002, Hine *et al.*, 2011, Chenoweth & Blows, 2003). In a number of studies, these CHCs have consistently
112 predicted male mating success, explaining up to 46% of its variance (Rundle *et al.*, 2005). CHCs also
113 genetically covary between the sexes, and may experience intralocus sexual conflict (Gosden *et al.*,
114 2012). The relationship between male CHCs and mating latency, however, has not been established in
115 this species.

116 In many insects, once mating starts, a cocktail of proteins (Seminal fluid proteins, Sfps) are
117 transferred along with sperm during copulation (Poiani, 2006). These proteins trigger an array of
118 behavioural and physiological responses in females which increase male fitness, for example, decreasing
119 female receptivity to subsequent mating, stimulating egg laying, facilitating sperm storage, forming a
120 mating plug, and displacing sperm from other males (Chen *et al.*, 1988, Gioti *et al.*, 2012, Chapman &
121 Davies, 2004). These responses come at a cost to females, as Sfps reduce female lifespan and their
122 lifelong reproductive success (Wigby & Chapman, 2005, Fowler & Partridge, 1989). Mating in *D.*
123 *melanogaster* takes ~20 minutes, twice the time needed to transfer sperm alone (Gilchrist & Partridge,
124 2000), and mating duration has a genetic basis (Moehring & Mackay, 2004), and is phenotypically plastic
125 depending on the social environment (Rouse *et al.*, 2018). In a rare study investigating sex-specific
126 genetic contributions to copulation duration, Edward *et al.* (2014) found significant genetic variance for
127 copulation duration in both males and females *D. melanogaster*, although male's contribution was
128 higher than female's.

129 Copulations in *D. serrata* are markedly different. In a modest study of 31 individuals, median
130 mating duration was 4 minutes, with 157s recorded as the shortest mating duration that could lead to
131 progeny (Hoikkala *et al.*, 2000). Males in this species appear to transfer sperm in a single clump (J
132 Sztepanacz *pers observation*), suggesting that longer copulation durations would not equate to more
133 sperm transferred. Whether males also transfer seminal fluid proteins that affect female physiology or
134 behaviours is unknown. Hoikkala *et al* (2000) observed a weak and non-significant negative relationship
135 between copulation duration and the number of progeny produced by females, suggesting that Sfps
136 may not have a large role in this species.

137 In this study we estimated the phenotypic and genetic correlations between male
138 attractiveness, mating latency, duration, and productivity, in two independent data sets from the same

139 species. Each data set was a large quantitative genetic breeding design with 80 sires and phenotypes on
140 over 3,000 flies measured in each experiment. These independently replicated data provide
141 unprecedented power to identify the genetic basis of copulatory behaviours and their effects on fitness.

142

143 Materials and methods

144 Experimental and Breeding Design

145 The data that we analyse here come from two independent populations and experiments in *D. serrata*
146 performed under similar conditions. The data from Population 1 allows us to estimate the heritabilities
147 for and genetic correlations between male attractiveness, mating latency, and mating duration. The data
148 from Population 2 allows us to estimate the phenotypic correlations between male attractiveness and
149 mating latency, and heritabilities for and genetic correlations between male and female mating latency
150 and duration, and their cross-sex genetic correlations. Further, this experiment measured productivity of
151 the resulting matings, allowing us to directly estimate the relationship between mating behaviour and
152 fitness. Therefore, the combination of these two experiments enable us to track the outcomes of mating
153 interactions from pre- to post-copulatory fitness.

154 *Population 1*

155 Experiments in population 1 were conducted on an outbred laboratory population of *D. serrata* (Rundle
156 et al., 2006) maintained at a large population size ($N > 2000$) under standard laboratory conditions. A half
157 sibling breeding design was carried out to estimate additive genetic variances and covariances in traits
158 of interest. The details of the breeding design are described in detail in Sztepanacz and Rundle (2012).
159 Briefly, eighty sires were each mated to three virgin dams, which were allowed to oviposit for 72h after
160 mating. Upon emergence of their offspring, male offspring were collected from these families using CO₂
161 anaesthesia and were held as virgins at a density of 6 flies per vial for 5-7 days prior to their use in
162 experimental assays. The breeding design was conducted in two blocks of 40 sires, spanning two
163 generations of the laboratory population, and resulted in 2941 individuals from 240 full- and half-sibling
164 families from 80 sires. Brothers from each family were used in either a (1) a competitive mating trial
165 where their cuticular hydrocarbons (CHCs) were subsequently extracted or (2) in a behavioural assay
166 which measured mating latency and duration.

167 The details of the binomial mate choice and CHC assay are described in detail in Sztepanacz and Rundle
168 (2012), where these data were first published. They found that male CHCs were under significant
169 directional sexual selection which explained 9.1% of the variance in male mating success. In order to
170 obtain an ‘attractiveness’ score for these males, here we applied the standardized sexual selection
171 gradient β , presented in their paper, to the individual pheromone profiles of each male (n=1979 males).

$$172 \text{ Attractiveness score} = \beta^T \text{CHC}_i \beta$$

173 Where β is the standardized sexual selection gradient, T denotes the transpose of the vector, and CHC_i
174 indicates the vector of 8 CHC traits for an individual.

175 To measure mating latency and duration a single male fly was introduced in a vial with a single female
176 which had the same genetic background as the male, but was fixed for a recessive orange-eye mutation.
177 The time it took before mating began was recorded as mating latency. Once mating started, copulation
178 duration was recorded as the time during which genital contact could be observed (n=962 males). If the
179 pair did not mate during the first two hours, the pair was discarded from the measure of mating latency
180 and copulation duration.

181 *Population 2*

182 Experiments in population 2 were conducted on an outbred laboratory population of *D. serrata*
183 described elsewhere (Hine et al., 2014), maintained with a large population (N>2000) under standard
184 laboratory conditions. First, we carried out a paternal half-sibling breeding design to estimate the
185 genetic variances and covariances between mating latency, duration, and productivity in males and
186 females. Eighty sires were each mated with three females and up to 10 female and 10 male virgin
187 offspring of each pair were collected using ice anaesthesia. Males and females were kept separately (up
188 to four males per vial, up to six females per vial) in vials containing 7mL of standard food, for four to six
189 days before mating trials. The day before the experiment, males and females from the breeding design
190 were transferred in an individual vial with fresh food. In total 1558 males and 1726 females, were
191 produced across three blocks from 80 sires and 220 dams. Males and females from each family were
192 used in (1) behavioural assays to measure mating latency and duration, and (2) had their productivity
193 subsequent measured.

194 On the day of the experiment, each focal female was put together with a virgin male from the same
195 population and time until mating started was recorded as mating latency. If the pair did not mate during
196 the first two hours, the pair was discarded from the measure of mating latency and copulation duration.

197 Once mating started, copulation duration was recorded as the time during which genitalia contact could
198 be observed. At the end of the mating, males were discarded, and females placed in individual 10mL
199 vials with standard food and without live yeast. We left females lay eggs for 24 hours, after which
200 females were discarded and offspring were left to develop. We chose 24h to capture the potential male
201 effect of mating on the number of eggs laid, that was shown to occur when sex peptide was injected
202 into female *D. melanogaster* (Aigaki et al., 1991). After offspring emergence, vials with adult offspring
203 were frozen at -20C and the number of adults that had emerged was counted as the measure of
204 productivity.

205 Males from the paternal half-sibs were tested in similar conditions. The day before mating trial, males
206 from the breeding design were isolated in a fresh vial with 10mL standard food. On the mating trial day,
207 each male was put together with a virgin female that was fed with *ad libitum* yeast. Mating latency and
208 copulation duration were recorded the same way as for females. Male productivity was also recorded as
209 the number of offspring that emerged from the vial of their female mate.

210 When recording productivity from the frozen vials, there was a few instances where the number of
211 offspring was impossible to individually count, as they emerged in the stopper. In a few vials, we
212 proceeded to careful visual inspection to estimate that around five flies must have been caught in the
213 stopper. Thus, five additional offspring were systematically added to the productivity obtained in
214 subsequent vials in which those emergence were encountered.

215 Finally, we measured whether attractive males mated faster. We randomly collected virgin males and
216 females at emergence from the population. Four to six days after collection, to guarantee sexual
217 maturity, two virgin males were put together with a virgin female. The time between the introduction of
218 the female in the vial with both males and the beginning of the mating was recorded as mating latency.
219 After copulation started, the mating pair was separated and the male who mated (chosen) and the other
220 male (rejected) had their CHCs extracted and assayed using gas chromatography following standard
221 procedure as in population 1 (Blows et al., 2004, Sztepanacz & Rundle, 2012). We then followed the
222 same method as in population 1 to obtain attractiveness scores; we determined the selection gradients
223 for male CHC profile by using the partial regression coefficients of the linear regression of standardized
224 mating success on the standardized log contrasts of CHCs peaks, and applied it to the individual
225 pheromone profile of each male.

226

227 Statistical analyses

228 *Quantitative genetic analyses in Populations 1 and 2: heritabilities and genetic covariances*

229 All models estimating quantitative genetic parameters in both populations were performed on
230 standardized (z-score) data using animal models (Lynch & Walsh, 1998, De Villemereuil, 2012) with the R
231 package MCMCglmm (Hadfield, 2010). In all models, blocks were entered as fixed effects and additive
232 genetic effects (using the pedigree information) were entered as random effects. In models that
233 included attractiveness in population 1, a supplementary *column* effect was added to account for the
234 use of two different gas chromatography columns for this experiment. Error distributions were
235 Gaussian. Number of iterations, burn in, and thinning intervals varied for each model, and they were set
236 to achieve convergence by using the Heidelberger and Welch test in the coda R package (Heidelberger &
237 Welch, 1981, Plummer et al., 2006) and a minimum effective sample of 1000 for all studied parameters.
238 All credible intervals are 89% (Makowski et al., 2019). Analyses of Population 1 and Population 2 were
239 performed independently.

240 First, univariate animal mixed models were performed on mating latency, copulation duration, and
241 attractiveness, in females and in males. Prior distributions were sets to inverse-Gamma, with
242 parameters $V=1$ and $\nu=0.002$. Heritabilities were calculated from the posterior distribution as the
243 median proportion of phenotypic variance explained by the animal factor. To confirm whether there
244 was additive genetic variance, we compared the Deviance Information Criterion (DIC) of these univariate
245 models to the DIC of models that did not include the ‘animal’ random effect. DIC are useful to select the
246 model which best describes the data (as for example the AIC), when the posterior distribution is well
247 summarized by its mean (Spiegelhalter et al., 2002, Gelman et al., 2014).

248 To investigate covariance between pre- and post-copulatory traits, and between the sexes, we ran
249 multivariate animal mixed models including the traits for which we tested genetic covariance with
250 MCMCglmm. Additive genetic variance-covariance G matrices were inferred from the median posterior
251 distribution of genetic variances and covariances of the animal effect. To test the extent of genetic
252 covariance, we compared the DIC of those models to the DIC of models in which the genetic covariance
253 was set to 0 (*idh*, off-diagonal of the G matrix =0).

254 *Phenotypic analyses in population 2: relationships between copulatory and fitness traits*

255 We used population 2 to investigate whether mating latency or copulation duration could predict the
256 measured components of pre- and post-copulatory fitness. First, we used the mate choice experiment to
257 see whether more attractive males mated faster. We tested whether the log transformed mating
258 latency could predict the attractiveness score with a linear model (lm in R-Core-Team, 2014) in males
259 that were successful at mating.

260 Further, we tested whether mating latency or copulation duration predicted the pair's productivity.
261 Because the dataset was obtained in the paternal half-sibs breeding design, we accounted for
262 relatedness between tested individuals with the following mixed model (Pinheiro et al., 2020):

$$263 \quad Y_{ijk} = \beta_0 + \beta_1 \text{block} + \beta_2 \text{trait} + b_{k(j(i))}$$

264 where Y_{ijk} is the standardized productivity of the k^{th} male, son of the j^{th} dam and i^{th} sire, *block* is to
265 account for the three blocks performed, *trait* either mating latency or copulation duration. b_{ijk} is an
266 observation (k)-level random effects nested in dams (j), themselves nested in sires (i). Statistical
267 significance for the *trait* effect was tested with Log-Likelihood ratio tests comparing two models where
268 the *trait* fixed effect was included or not.

269

270 Results

271 Heritability of attractiveness, mating latency, and mating duration

272 There was substantial phenotypic variation in male attractiveness scores in both populations, which had
273 a heritability of 0.31 in population 1 (estimated using REML, genetic effect vs. no genetic effect
274 $\Delta\text{AIC}=75.2$, Suppl Materials, MCMCglmm $\Delta\text{DIC}=1018$, Table 1). Mating occurred shortly after males and
275 females were put together in the vial. Over a quarter of the pairs mated in the first 5 minutes in
276 Population 1 and in the first 7 minutes in Population 2, however the distribution was skewed with a long
277 tail extending to 120min, which is when the experiment was stopped (Fig. 1). The median mating latency
278 in Population 1 was 10.2 minutes, and in Population 2 was 22.4 minutes (Fig. 1). We estimated the
279 heritability of mating latency using the observed variance standardised data, and using log-transformed
280 values. Overall, the estimates of heritability were similar, so we report the non-transformed values here
281 and heritability of log-latency in the supplementary material (Supplementary Table 2). Univariate

282 analyses in population 2 found no evidence for heritable variation in mating latency in males ($h^2=0.007$;
283 CI [0.000 ; 0.046]) nor in females ($h^2= 0.009$; CI [0.001 ; 0.050]). In population 1, however, there was
284 some evidence that latency was heritable in males ($h^2= 0.068$; CI [0.003 ; 0.175]) and evolvable ($e =$
285 1.3%). In *D. melanogaster*, single phenotypic observations of latency have been shown to be a highly
286 noisy measure (Hoffmann, 1999), which may explain why we were able to detect heritable variation in
287 one population but not the other.

288 Once mating started, the median copulation duration in Population 1 was 5.8 minutes and 4.6 minutes
289 in Population 2 (Fig. 2). This is consistent with the durations observed in *D. serrata* by Hoikkala et al
290 (2000), which ranged from 2.62 to 7.87 minutes with a median of 4 minutes. Copulation duration was
291 heritable in males from Population 1 with an estimated heritability of 0.15 and an evolvability of 1.5%,
292 suggesting that this trait has a genetic basis and can respond to selection (Table 1). In Population 2,
293 however, heritabilities were low in both sexes, although higher in males (male $h^2 = 0.043$ [0.002 ; 0.043];
294 female $h^2 = 0.005$ [0.000 ; 0.031]), with little statistical support (male Δ DIC = 6; female Δ DIC = -1, Table
295 1).

296 Relationships between copulatory traits

297 There was no genetic correlation between male attractiveness score and mating latency, with a credible
298 interval that overlapped zero (Bivariate model in Population 1: r_G : 0.11; [-0.17 ; 0.37]; Δ DIC = 21, Table
299 2). The genetic covariance matrix for male attractiveness, mating latency, and mating duration in
300 Population 1 is shown in Table 2. Overall, the genetic correlations were low between all traits with
301 confidence intervals of the estimates overlapping 0 and Δ DIC between models with and without genetic
302 covariance equal to -2.

303 Cross-sex relationships for interactive traits

304 In population 2 we were able to estimate both within-sex and across-sex genetic covariances for mating
305 latency and duration. The full genetic correlation matrix is shown in Table 3. Similar to population 1,
306 genetic correlations between latency and duration within each sex were modest with credible intervals
307 of the estimates overlapping 0. However, the overall G matrix contained some level of genetic
308 covariance, as Δ DIC between models with and without genetic covariance equal to 95.

309 Consistent with other studies that estimate cross-sex genetic covariance matrices (Gosden &
310 Chenoweth, 2014, Sztepanacz & Houle, 2019), we found that estimates of cross-sex cross-trait

311 correlations were asymmetric. The point estimate of the correlation between latency in males and
312 duration in females was negative ($r_G = -0.056$; $[-0.379 ; 0.283]$), while the correlation between latency in
313 females and duration in males was positive ($r_G = 0.094$; $[-0.260 ; 0.416]$). The confidence intervals of
314 these estimates were large and overlapping however, so we cannot say with confidence that they differ
315 from each other

316 Relationships between copulatory traits and fitness components

317 In population 2 we were able to determine the relationship between mating latency, copulation
318 duration, and two fitness components: male attractiveness (determined from mating success assays)
319 and productivity. There was no phenotypic relationship between male attractiveness and mating latency
320 (Population 2: $F_{1,199} = 0.83$, $p=0.36$, Fig. 3A) nor with the pair productivity ($F_{1,1781} = 0.14$, $p=0.71$, Fig. 3B).
321 Finally, copulation duration showed a tendency to be negatively associated with the pair productivity
322 ($F_{1,1754}=3.6$, $p=0.06$, Fig. 4).

323

324 Discussion

325 This study provides a unique overview of the fitness effects and genetic contributions of two widely
326 studied interactive traits, mating latency and copulation duration, in a species with higher polyandry and
327 shorter copulations than traditional *Drosophila* model systems. We found that, in *Drosophila serrata*, (i)
328 copulation duration was heritable in males in both population, (ii) multivariate analyses provided more
329 power to detect male and female contributions to interactive traits, and (iii) mating latency and
330 copulation duration did not predict the two measured fitness components, namely male attractiveness
331 and short-term productivity.

332 Quantitative genetic analyses showed that variation in copulation duration was heritable in males from
333 both populations. When only one of both sexes genetically contribute to an interactive trait, it limits the
334 opportunity for arm race, as adaptation would only respond to selection on one of the sexes (although
335 plastic behaviours may still enable conflictual interactions, Moore & Pizzari, 2005). However, female
336 genetic contribution to copulation duration is significantly higher than 0, as revealed by multivariate
337 analyses (Table 3), so the opportunity for conflict is not absent.

338 Male and female genetic contributions to copulation duration were very similar in this study than in *D.*
339 *melanogaster* ($h^2_{\text{female}} = 0.08 \pm 0.04$ in *D. melanogaster* vs $h^2_{\text{female}} = 0.08 \pm 0.05$ in *D. serrata*, and $h^2_{\text{male}} =$
340 0.13 ± 0.05 in *D. melanogaster* vs $h^2_{\text{male}} = 0.15 \pm 0.10$ and $h^2_{\text{male}} = 0.12 \pm 0.06$ in population 2 of *D.*
341 *serrata*). To obtain these results in *D. melanogaster*, Edward *et al.* (2014) also used a paternal half sibs,
342 but they mated pairs that both came from the breeding design in a full-factorial design. Thus, their
343 multivariate model incorporated both male and female genetic contributions, as did our second,
344 multivariate model. Sex-specific genetic contributions to copulation duration may thus be conserved
345 between species.

346 The differences in heritability estimates between univariate and multivariate models that incorporated
347 both sexes in population 2 were important, underscoring the value of incorporating both sexes' genetic
348 contributions in a single model when studying traits that can cause sexual conflict. However, we did not
349 find any significant pairwise correlations between pre- and post-copulatory traits, or across sexes. Other
350 studies of multivariate cross-sex genetic covariances between copulation behaviours are rare. Edward *et*
351 *al.* (2014), found support for within female genetic covariance for number of eggs laid before and after
352 mating in *D. melanogaster*, whilst Han *et al.* (2020) found support for inter sexual genetic correlation for
353 male mate guarding and female latency to mate in field crickets. Our comprehensive approach
354 considering several traits in both sexes in a single framework showed that the cross-sex G matrix carried
355 complex and statistically supported covariance between interactive traits and sexes.

356 Male attractiveness was not correlated with mating latency at the phenotypic or genetic level in our
357 study. Consistent with this result, several experiments selecting for more attractive and more
358 competitive males have failed to detect a change in their mating latency. In *D. pseudoobscura*
359 (Bacigalupe *et al.*, 2008), *Callosobruchus maculatus* (Maklakov *et al.*, 2010), and even *D. melanogaster*
360 (Nandy *et al.*, 2013), males under male biased sex ratio, an experimental condition expected to favour
361 attractive males, did not have a different mating latency than males evolved under equal or female
362 biased sex ratios. In *D. bunnanda*, artificially selected attractive males also failed to mate faster
363 (McGuigan *et al.*, 2008), which the authors suggest was due to a lack of variation in attractiveness rather
364 than latency being a non-heritable trait in males. Mating latency may also vary with female
365 attractiveness, but we could not test this using our data. Mating latency could also be due to female
366 responsiveness and choosiness, however, the heritability of mating latency in females was as low as in
367 males. Finally, we may have failed to detect genetic contributions to our traits because of our
368 experimental protocol. Mating traits are notoriously difficult to capture in single assays. Hoffman (1999)

369 found that mating latency did not appear heritable after one mating trial, however when individuals
370 were tested several times for the same mating trait it was possible to detect non-zero heritability.
371 Although our experimental protocol created numerous repetitive measures within families (on average
372 28 sons tested per sire, 160 sires across populations), there was no repetition of individual measures
373 and environmental noise of single measures may have overwhelmed our ability to detect genetic
374 variation.

375 We did not find that longer matings resulted in more offspring. Indeed, our results showed a non-
376 significant trend that longer copulations resulted in fewer offspring produced, consistent with that
377 observed by Hoikkala et al (2000). In *D. melanogaster*, sperm transfer only takes half of the time of
378 copulation and the second half is used to transfer seminal fluid proteins (Gilchrist & Partridge, 2000).
379 Those proteins affect numerous female functions, in particular increase the number of eggs they lay and
380 reduce their receptivity to subsequent mating (Chen et al., 1988, Gioti et al., 2012). In *D. serrata*, sperm
381 are transferred in a single ball (Sztepanacz, pers. comm.), and little is known about Sfps transfer. Wing
382 song, however, has been shown to be an important component of copulatory courtship display, with
383 females discriminating against males that were not able to produce courtship song during copulation
384 (Hoikkala et al 2000.). Wing shape in male *D. serrata* is genetically variable (Sztepanacz & Blows, 2015),
385 and in other species there is weak evidence that shape variation may be associated with variation in
386 wing-song (Menezes et al., 2013, Snook et al., 2005). Whether *D. serrata* males with different wing
387 shapes produce different courtship songs, and whether song variation explains variation in copulation
388 duration is unknown. *D. serrata* males have also been shown to make active courtship and mounting
389 attempts after copulation (Hoikkala et al 2000.), which may keep the female unreceptive, preventing
390 further matings and sperm displacement (Alcock & Buchmann, 1985). Although relatively little is known
391 about male manipulation after mating, our results suggest that physiological effects of seminal fluid
392 proteins may be limited in this species.

393 Altogether, our comprehensive analyses of mating latency and copulation duration provide little support
394 for the hypothesis that these traits could be subject to intra- or inter-locus sexual conflict, as they were
395 not phenotypically or genetically associated with any pre- and copulatory components of fitness studied
396 here. We cannot rule out a lack of experimental power as a cause of low heritability estimates, however,
397 we analysed data from over 6000 flies and 160 sires, underscoring the difficulty in estimating
398 quantitative genetics parameters on behavioural traits. Multivariate cross-sex genetic analyses revealed

399 that complex patterns of between sexes correlations could set the scene for complex evolution for these
400 interactive traits.

401 Acknowledgements

402 JMC is very grateful to Jessica McCarroll and Grace Stanton for their valuable help in the laboratory, and
403 to Mark Blows for his excellent suggestions for the experimental design and to support this project. JLS
404 thanks Howard Rundle for supporting this work, and D. Arbuthnott, M. Delcourt, and K. MacLellan for
405 help in the lab. JMC's contributions to this work was funded by the Australian Research Council, and
406 JLS's contributions were funded by NSERC.

407

408 Figures

409 **Figure 1:** Distribution of mating latencies (in seconds) in population 1 and population 2. In population 2,
410 results are shown in two different colours according to whether they were measured in females or
411 males of the breeding design.

412 **Figure 2:** Productivity of mating pairs according to the duration of their copulation. Darker colours
413 appear when several datapoints overlap. The line corresponds to a regression line obtained with the
414 mixed models accounting for the individuals relatedness.

415 **Figure 3:** Mating latency (in seconds) as a predictor of male fitness: either **A:** male attractiveness or **B:**
416 productivity of a pair. **A:** Each datapoint represents a successful male's latency from introduction into a
417 vial with a virgin female to copulation, and their attractiveness index based on their CHCs profiles. The
418 line corresponds to a linear model ("lm" in R). **B:** Each datapoint represents a mating pair. Darker colours
419 appear when several datapoints overlap. The line corresponds to the regression line obtained using a
420 mixed model accounting for the replication due to relatedness between individuals.

421 **Figure 4:** Distribution of copulation durations (in units of seconds) in population 1 and population 2. In
422 population 2, results are shown in two different colours according to whether they were measured in
423 females or males of the breeding design.

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TABLE 1: Summaries of univariate models. h^2 is the median narrow sense heritability, Eff. Samp. is the Effective Sample Size, DIC dif is the difference in the deviance Information Criterion between the null model and the tested models. Credible intervals are 89 %. *models for those estimates did not converged according to the Heidelberger and Welch test.

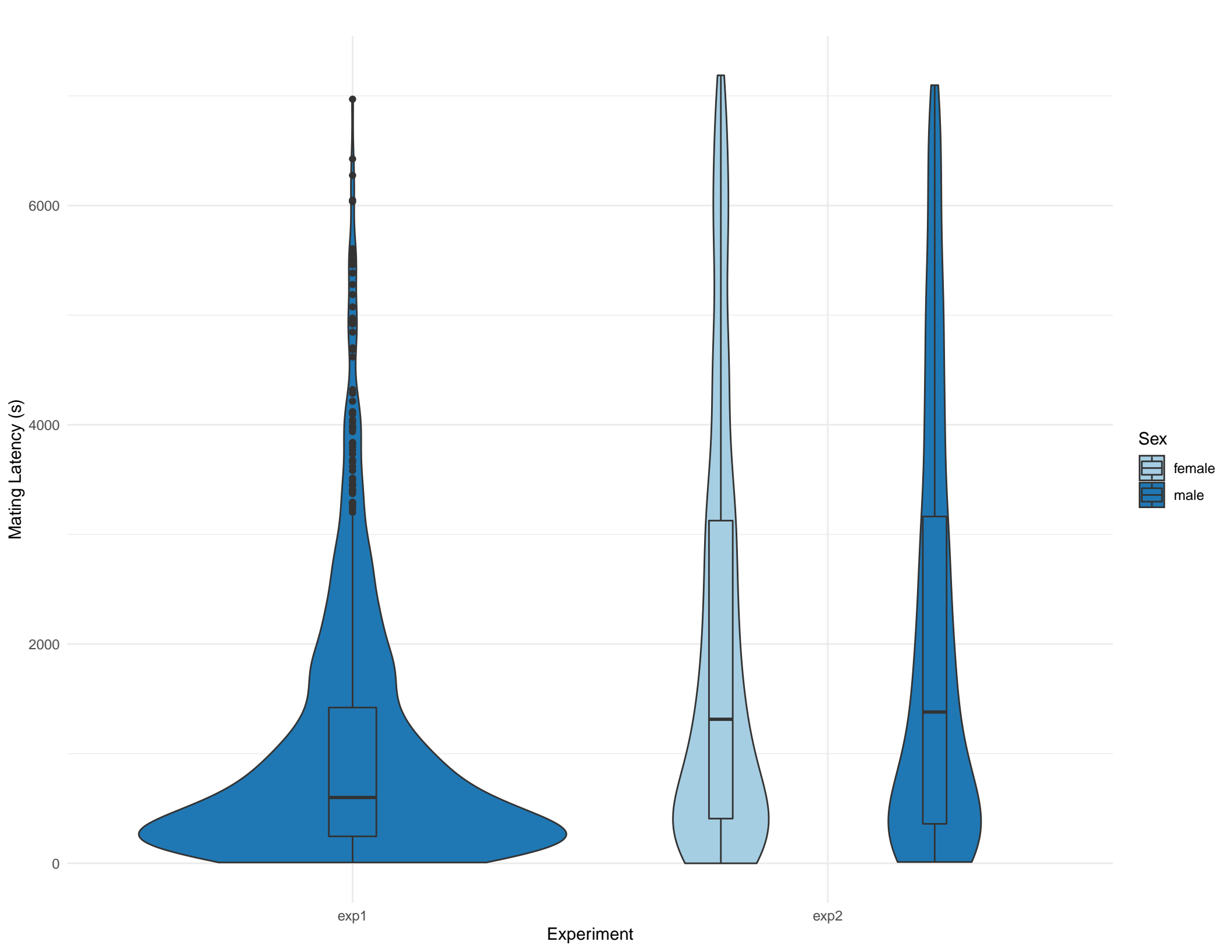
Population	Parameter	h^2	Credible interval	Eff. Samp.	DIC dif	evolvability (%)	Credible interval
1	Male Latency	0.068	[0.003 ; 0.175]	1871	10	1.3	[0.0 ; 26.0]
	Male Duration	0.153	[0.064 ; 0.257]	2737	35	1.5	[0.7 ; 2.6]
	Male attractiveness	0.678	[0.576 ; 0.787]	26397	1018		
2	Male Latency	0.007	[0.000 ; 0.046]	1138	-1	0.0*	[0.0 ; 2.1]*
	Male Duration	0.043	[0.002 ; 0.043]	1135	6	0.2	[0.0 ; 0.6]
	Female Latency	0.009	[0.001 ; 0.050]	1724	0	0.0*	[0.0 ; 2.5]*
	Female Duration	0.005	[0.000 ; 0.031]	1084	-1	0	[0.0 ; 0.2]

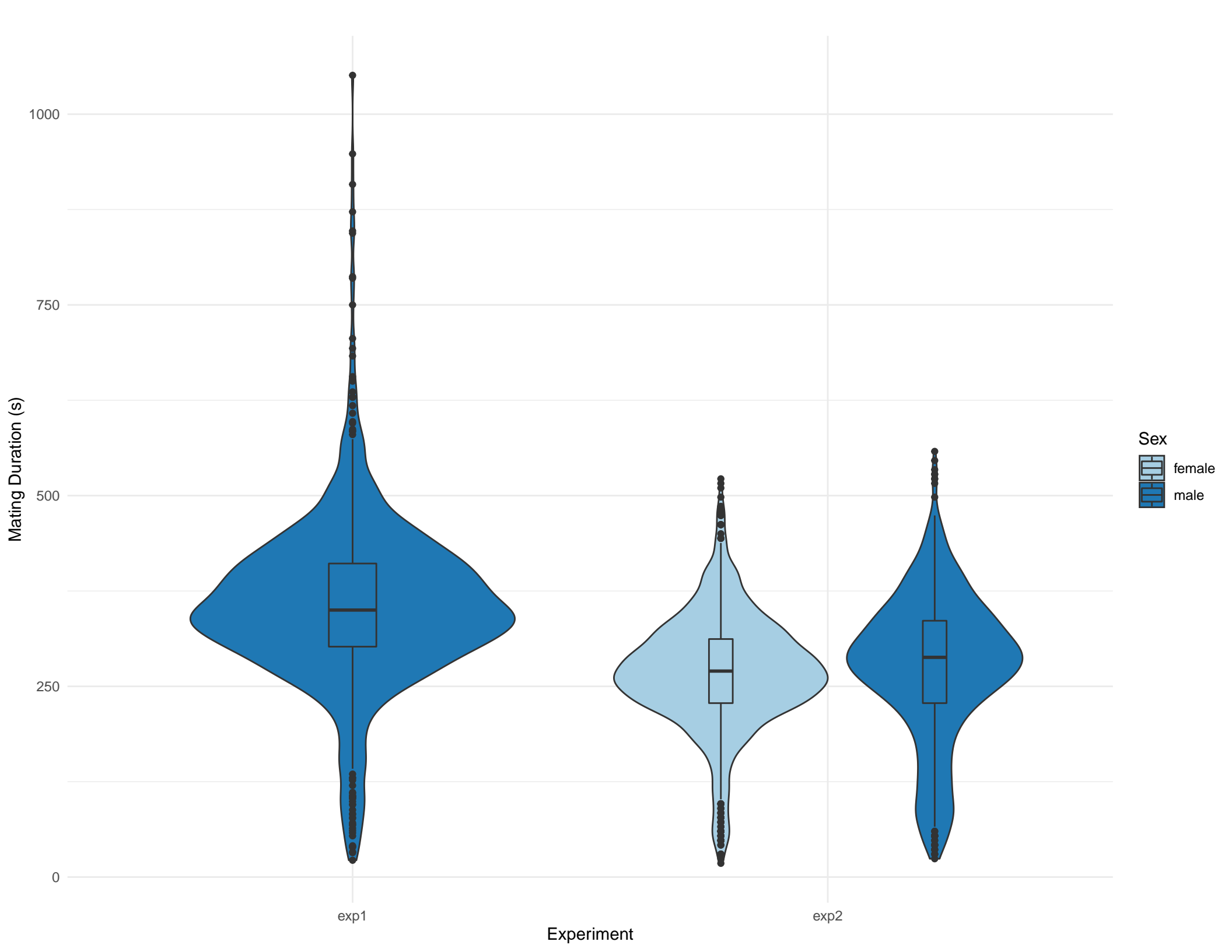
TABLE 2: The genetic variance-covariance matrix, G for male attractiveness, mating latency, and copulation duration in population 1. Heritabilities are in bold along the diagonal, covariances are below the diagonal, and correlations are in italic above the diagonal. 89% confidence interval for each value are in brackets.

	Attractiveness	Latency	Duration
Attractiveness	0.636 [0.553 ; 0.716]	<i>0.102 [-0.152 ; 0.347]</i>	<i>-0.059 [-0.281 ; 0.176]</i>
Latency	0.009 [-0.015 ; 0.035]	0.133 [0.076 ; 0.217]	<i>-0.062 [-0.421 ; 0.316]</i>
Duration	-0.006 [-0.032 ; 0.020]	-0.009 [-0.071 ; 0.050]	0.179 [0.104 ; 0.276]

TABLE 3: The genetic variance-covariance matrix, G_{fm} for latency and mating duration in population 2. Heritabilities are in bold along the diagonal, covariances are below the diagonal, and correlations are in italic above the diagonal. 89% confidence interval for each value are in brackets.

		Female		Male	
		Latency	Duration	Latency	Duration
Female	Latency	0.084 [0.051 ; 0.133]	<i>-0.081 [-0.392 ; 0.251]</i>	<i>0.111 [-0.239 ; 0.431]</i>	<i>0.094 [-0.260 ; 0.416]</i>
	Duration	-0.006 [-0.033 ; 0.020]	0.070 [0.044 ; 0.108]	<i>-0.056 [-0.379 ; 0.283]</i>	<i>-0.170 [-0.473 ; 0.171]</i>
Male	Latency	0.010 [-0.021 ; 0.043]	-0.004 [-0.033 ; 0.023]	0.087 [0.052 ; 0.142]	<i>-0.126 [-0.456 ; 0.239]</i>
	Duration	0.009 [-0.026 ; 0.045]	-0.014 [-0.049 ; 0.015]	-0.012 [-0.053 ; 0.024]	0.116 [0.069 ; 0.183]





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Male attractiveness

0.2

0.0

-0.2

0

2000

4000

6000

B

100

75

50

25

0

Productivity

0

2000

4000

6000

Mating latency

