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Do metrics of sexual selection conform to Bateman's principles in a wind-pollinated plant ?

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1 **Abstract**

2 Bateman's principles posit that male fitness varies more, and relies more on mate acquisition, than
3 female fitness. While Bateman's principles should apply to any organism producing gametes of
4 variable sizes, their application to plants is potentially complicated by the high levels of polyandry
5 suspected for plants, and by variation in the spatial distribution of prospective mates. Here we
6 quantify the intensity of sexual selection by classical Bateman metrics using two common gardens
7 of the wind-pollinated dioecious *Mercurialis annua*. Consistent with Bateman's principles, males
8 displayed significantly positive Bateman gradients (a regression of fitness on mate number),
9 whereas the reproductive success of females was independent of their ability to access mates. A
10 large part of male fitness was explained by their mate number, which in turn was associated with
11 males' abilities to disperse pollen. Our results suggest that sexual selection can act in plant species
12 in much the same way as in many animals, increasing the number of mates through traits that
13 promote pollen dispersal.

14

15 **Introduction**

16 Darwin [1] introduced the notion of sexual selection, recognizing the tendency of males to compete
17 for access to females, and of females to choose their male partners. Bateman (1948) helpfully
18 developed this notion in three basic principles [2] that can be examined by estimating individuals'
19 reproductive and mating success, defined respectively as the number of offspring produced and the
20 number of mates. Bateman's principles [2] state that males should exhibit stronger variance than
21 females in (1) reproductive success and (2) mating success, and that (3) reproductive success should
22 depend on mating success in males more than in females. Noting the higher cost of producing
23 female *versus* male gametes (i.e. anisogamy), Bateman reasoned that males' reproductive success
24 should be limited by their mating and fertilization success rather than by investment in each gamete.
25 In contrast, females' reproductive success should depend on their ability to produce viable ovules
26 rather than to have them fertilized [2]. Numerous studies have tested Bateman's principles in
27 animals and, despite some disagreement [3,4], their utility and generality are widely accepted [5].
28 Male reproductive success relied on mates more than that of females in many animals, as expected
29 by Bateman (1948). Variance in reproductive success also tends to be larger for males than females
30 [6,7], particularly when females care for their young after fertilization, or when males express more
31 elaborated traits [8,9]. Counter-examples have been found where both sexes are similarly energy-
32 limited or mate-limited [10], or in the case of sex-role reversals or female-biased sex-ratios [5,11].
33 In contrast to animals, the application of Bateman's principles to plants has been limited [12],
34 despite wide acceptance of the role of sexual selection in plant evolution [13,14,15,16].

35

36 Sexual selection in plants likely occurs through between-male competition to fertilize a limited pool
37 of ovules, and may consequently affect the evolution of traits involved in pollen production, export
38 and competitiveness [13-15]. Such potentially sexually selected traits include: large flowers and
39 floral displays that enhance pollinator attraction [15,17-19]; increased pollen production [20,21];
40 male flowering phenology that tracks that of females [22]; vegetative architectures that enhance
41 pollen dispersal [21]; evolution of horn weapons that prevent the attachment of pollen-bearing
42 structure from additional males [23]; and high pollen-grain performance [24]. Floral strategies that
43 affect the distribution of pollen on pollinators' bodies could also be under sexual selection [25].
44 While botanists have commonly described plant female and male functions as limited respectively
45 by access to resources and pollinator visits [26], we still know little about the relationship between a
46 plant's mate and its reproductive success (but see [12] for an example in a bryophyte species).

47
48 The paucity of attempts to estimate Bateman gradients in plants may be attributable to difficulties in
49 its use, including those that apply generally, and those specific to plants. It is indeed typically
50 difficult to estimate mating success directly. In animals, only a few studies have actually counted
51 mating events, and a proxy for mating success is typically assessed using genetically-based
52 paternity assignment in a small subset of the total progeny produced [27]. The number of
53 individuals in the population that share at least one offspring with a given focal individual is
54 classically estimated using output of paternity assignments [5]. This estimate is thus a genetically-
55 based proxy for mating success rather than a direct estimate of mating success itself (hereafter
56 termed mating success proxy). Pollen tracking is possible but remains logistically difficult [25,28]
57 so that such a proxy remains a useful substitute for evaluating Bateman's principles.

58
59 The mating and growth habits of plants pose additional specific challenges to the evaluation of
60 Bateman's principles. First, plants are often assumed to be highly polyandrous [29], resulting in
61 potentially extremely high mate numbers. Given that genetic assays are made on a finite number of
62 seeds per plant, mates with small contributions to total reproductive success will likely be missed by
63 a genetically-based proxy. This could lead to underestimation of variance in mating success and a
64 potential bias towards more positive male Bateman gradients because both the reproductive and the
65 mating success of males are estimated using the same genetic data [27]. Moreover, a genetically-
66 based proxy registers mating success only if a male's paternity share exceeds a certain detection
67 threshold (typically determined by the number of seeds sampled per female). This may be a
68 problem when polyandry is high and when most males have a small share in paternity – a situation
69 often perceived as common in plants [29]. If, on the other hand, male contributions are very
70 unequal, focusing on major pollen donors poses less of a problem.

71

72 Second, plants are modular, and different flowers on a plant represent separate arenas for
73 competition between pollen donors. Arnold's [30] original definition of plant mating was centered
74 on access to mates. However, studies of plant reproduction have rather defined it as the realized
75 access by an individual to flowers or ovules rather than to mates [15], similar to those of
76 reproduction in aquatic animals with external fertilization [31]. In cases where pollen export from
77 different flowers is largely independent, mating success at the flower level might be a more relevant
78 variable for sexual selection than that at the plant level, but it is also conceivable that plant's traits
79 [e.g., 17,21,32] may influence mating success at the plant level, rendering estimates of mate number
80 at the plant level potentially profitable.

81

82 Plant size and plant architecture provide good examples of traits that may influence pollen
83 production and/or its dispersal distance, and that therefore might be selected, either through
84 fecundity selection or sexual selection. On the one hand, fecundity selection may select for larger
85 plants that enjoy larger pools of resources to allocate them to gamete production; this has been
86 termed a 'budget effect' of plant traits [33]. High pollen production may also allow the competitive
87 exclusion of pollen from other males, for instance, by saturating stigmas with pollen [33]. On the
88 other hand, sexual selection may occur through the placement of flowers on elongated branches or
89 inflorescences that favour pollen dispersal, especially in wind-pollinated plants; this has been
90 termed a 'direct effect' of plant traits [21,33]. Analogous ideas have been proposed for animals with
91 a sessile life-form and external fertilization, e.g., in broadcast spawners, in which increased sperm
92 speed and longevity allowed greater siring success over a larger spatial area [34]. Interestingly, the
93 positive male Bateman gradient found in at the gametophytic stage of a moss species was achieved
94 through increased clonal growth, and therefore increased individual spatial range [12].

95

96 Because plants are sessile, mating patterns are likely to be strongly affected by spatial location of
97 individual plants and their prospective mates, and thus by density. For instance, males that
98 effectively sire seeds over multiple females may reap benefits associated with reduced local mate
99 (or local pollen) competition (because its pollen grains should compete less intensively with one
100 another; [35]) and local resource competition (because the seeds it sires are less likely to compete
101 with one another both for resources supplied by the female and for resources from the environment
102 during establishment; [33]). By contrast, dispersing pollen over greater distances may come at a
103 cost of pollen dilution, with a correspondingly lower paternity share on female mates nearby.
104 Analysis of Bateman gradients and variance partitioning at the scale of nearby males *versus* more
105 distantly related mates may therefore illuminate how selection operates on pollen production, pollen

106 dispersal and the resulting relationship between mate number and paternity share in a spatial
107 context.

108

109 Here, we consider the utility of Bateman gradients for understanding how sexual selection might
110 operate in a wind-pollinated herb. We conducted paternity analyses based on microsatellite data on
111 the outcome of mating in two semi-natural common gardens of the dioecious plant *Mercurialis*
112 *annua* that represent extremes in the range of plant densities found in natural populations. We tested
113 Bateman's predictions by calculating: (1) the opportunity for selection capturing variance in
114 reproductive success, (2) the opportunity for sexual selection expressed by variance in mating
115 success, and (3) the strength of sexual selection estimated using Bateman gradients quantified as the
116 slope of a regression of reproductive success on mating success. Because variance in reproductive
117 success may vary across stages of the life cycle, we decomposed variance in male reproductive
118 success into an ability (1) to access mates, (2) to secure paternity on their mates, and (3) to mate
119 with females with more ovule [36]. We specifically investigated 'direct' and 'budget' effects,
120 assessed by pollen production and dispersal on all fitness components. Because the two common
121 gardens differed in terms of their pot density, we used computer simulations of plant mating in a
122 spatial context to test the hypothesis that the effect of plant density on sexual selection might
123 depend on the scale of pollen dispersal. We tested the hypotheses that larger pollen dispersal
124 distances and, to a lesser extent, higher pollen production could give males greater access to more
125 mates. Finally, we adopted a paired design whereby males and females were grown together in a pot
126 to test the hypothesis that selection for mate acquisition ought to be stronger for access to
127 prospective mates placed further than the immediate surroundings of a focal plant.

128

129 **Material and methods**

130 Study species

131 *Mercurialis annua* is a wind-pollinated annual herb inhabiting disturbed habitats in western Europe
132 and around the Mediterranean Basin [37]. Populations vary in their sexual system across the
133 species' range, from dioecy, through androdioecy to monoecy [37]. Here, we focused on dioecious
134 populations. Males produce green staminate flowers held on erect inflorescence stalks
135 ('peduncles'), whereas females produce green dehiscent sessile capsules in their leaf axils. In
136 both sexes, flowering begins several weeks after seeds germinate and continues over a period of
137 three to four months [37].

138

139 Experimental design

140 Our study is based on a recently published dataset that estimated male fitness through marker-
141 assisted paternity analyses in two common gardens [21]. Seeds were collected from 35 populations
142 located in northern Spain that were bulked and grown for three generations in a common garden in
143 Lausanne. Male and female fitness components were assessed after mating in two common gardens
144 at varying densities and equal sex-ratios in Montpellier. A peculiarity of the design is that males and
145 females were grown in pairs, allowing us to compare male strategies that were successful at siring
146 ovules locally versus over longer distances.

147

148 In each garden, female-male pairs were transplanted into pots that were assigned randomly to a
149 position in a 10x10 grid. Pots in both gardens were initially established at a low density of 1.0 m
150 between pots. When plants had begun producing male and female flowers, we moved their pots to
151 establish two contrasting densities. In one garden, pots were moved such that the new pot spacing
152 measured 20 cm, while in the other garden pots were maintained at the same spacing. We
153 constrained plants from both gardens to grow at the same low-density initially because, we wished
154 to minimize variance in plant architectural traits that might be affected by a plastic response of
155 shade avoidance classical of high-density population [21]. Plants in both gardens were allowed to
156 continue mating for an additional four weeks, so that all seeds sampled at the end of the experiment
157 had been fertilized under the conditions after pots had been moved (in *M. annua*, seeds are
158 dispersed about two weeks after fertilization, so that seeds sired prior to the change in imposed
159 densities were not sampled). Note that our design does not allow a statistical comparison between
160 densities; we explored the effect of density specifically by means of computer simulations (see
161 below).

162

163 In both gardens, leaves of all adults were sampled at the end of the experiment and preserved in
164 silica gel for later DNA extraction and genotyping. All seeds of all 100 females were harvested in
165 both gardens by drying vegetative parts, threshing and winnowing seeds from the samples. Seeds
166 were then counted for each female using an automatic seed counter (Elmor C3; Elmor Angewandte
167 Elektronik, Schwyz, Switzerland). On each male, inflorescences were harvested, dried and weighed
168 to estimate inflorescence weight, which is known to provide a reliable estimate of pollen production
169 [37]. To characterize male dispersal abilities, we extracted individual mean dispersal distances of
170 pollen from previous inferences [21], in which genotype and spatial data were used in a spatially
171 explicit model of pollen dispersal kernels with a negative exponential power function.

172

173 *Paternity assignment: estimation of reproductive and mating success*

174 A paternity analysis was performed in each garden separately, based on the genotyping of all adults
175 and 651 and 621 offspring in the low- and high-density gardens, respectively [21]. Genotyping was
176 performed on eight microsatellites [38]. The two paternity analyses were performed using CERVUS
177 version 2.0 [39], allowing for a maximum of four mismatches and accounting for a 0.7% error rate
178 in genotyping. This error rate was calculated as a mean across markers, for both gardens combined,
179 of the overall proportion of offspring whose genotype did not match that of their mother. We
180 assigned paternity based on a 95% confidence (strict) criterion [39]. In the low- and high-density
181 gardens respectively, 96 and 93 males were assigned as the father of at least one seed, four and
182 seven males were not, and none of the males were excluded from the analysis because of a failure in
183 genotyping.

184

185 In females, reproductive success RS_f was estimated as the number of seeds. We calculated male
186 reproductive success RS_m as the sum over all female partners of the product between the proportion
187 of the female's seeds sired by the focal male (estimated best father) and the RS_f of the female
188 partner. Our proxy for mating success for females and males (MS_f and MS_m , respectively) was
189 calculated as the number of genetic partners (i.e., the number of individuals in the population that
190 share at least one offspring with a given focal individual). This measure is an estimate of effective
191 mating success given that the probability of detection of a mate is proportional to the number of
192 seeds effectively sired.

193

194 The germination probability for seeds of a given mother was calculated based on an average of 10.8
195 (± 2.29 SD) and 11.3 (± 2.72 SD) seeds sown per female for the low- and high-density gardens,
196 respectively [21]. In females, the number of mates necessarily depends on seed germination rates,
197 since mate number was determined by evaluating paternities of seedlings resulting from the
198 germination trial. For the purpose of consistency between sexes, we presented results using RS_m
199 estimated without weighting the number of seeds by germination probability in both sexes.
200 However, our results were robust when RS_m was estimated by weighting RS_f by seed germination
201 probabilities, accounting for a more integrative measure of male fitness. Distance to the center of
202 each garden did not affect either mating nor reproductive success.

203

204 Quantification of sexual selection

205 We quantified the strength of sexual selection separately for each sex, and assessed the extent of
206 differences between the sexes using: (i) the standardized variance in reproductive success, I , i.e., the
207 'opportunity for selection', (ii) the standardized variance in mating success, I_s , i.e., the 'opportunity
208 for sexual selection'; and (iii) the slope of a least-square regression of reproductive success against

209 mating success, β_{SS} , i.e., the ‘Bateman gradient’ [40]. These metrics quantify the maximum strength
210 of selection on offspring production (I), on selection on mating success (I_S), and the fitness gain for
211 one sex for mating with another individual (β_{SS}). To compare Bateman gradients (β_{SS}) between sexes
212 we standardized both mating and reproductive success proxies by dividing by their mean values
213 prior to β_{SS} estimation. Similarly, we standardized both the opportunity for selection (I) and for
214 sexual selection (I_S) by dividing the variance in both mating and reproductive success by the square
215 of their mean value.

216

217 Measurement errors on reproductive success typically differ between sexes [41]. Our estimate of
218 RS_f involved direct counts of seeds, whereas that of RS_m relied on estimates of paternity share of a
219 subset (typically $N=4.8$) of the seeds produced by each female, effectively introducing an additional
220 binomial error component for male compared to female components. Following [41], we computed
221 the expected additional error variance due to binomial errors in males and subtracted it from raw
222 variances to arrive at an estimate with a comparable contribution of measurement error in both
223 sexes, and to be able to compare variances between sexes.

224

225 Decomposition of male reproductive success

226 We decomposed RS_m into its different components by adapting previous methodology [42,43] to
227 study which fitness components contribute most to variance in male fitness (see Supplementary
228 Methods S1). RS_m was first decomposed into intra-pair and extra-pair components, and we obtained
229 a total of six components of variance: (I) the proxy for intra-pair mating success, (II) the paternity
230 share on intra-pair female partners, (III) the fecundities of intra-pair female partners, (IV) the proxy
231 for extra-pair mating success, (V) the paternity share on the extra-pair female partners, and (VI) the
232 fecundity of extra-pair female partners. All associated covariances were also assessed. As paternity
233 share and fecundity of female partners cannot be calculated when there are no female mates, we
234 considered only males with $MS>0$ to compute their variances and covariances (Supplementary
235 Methods S1); in the case of intra-pair components, males all had $MS=1$, so the covariances between
236 MS and paternity share or mate fecundity were undefined. We represented graphically the
237 proportion of variance in RS_m that is attributable to each of these six fitness components and their
238 covariances.

239

240 Statistical analyses

241 We estimated Bateman gradients (β_{SS}) by regressing reproductive success against the proxy for
242 mating success at the global, intra-pair and extra-pair scales. Following previous recommendation
243 [30,27], we compared the likelihood of linear and quadratic relationships between relative mating

244 success and relative reproductive success using likelihood ratio tests. Because quadratic
245 components were not significant, only linear regressions are reported. We examined the difference
246 in the strength of sexual selection between sexes by assessing the significance of the interaction
247 between the proxy for mating success and sex.

248

249 We estimated the linear relationship between the proxy for relative mating success and both mean
250 pollen dispersal distance and pollen weight (standardized within gardens) using bivariate regression
251 to account for their correlation. We regressed components of RS_m against pollen dispersal distance
252 and pollen weight using either linear models or generalized linear models, depending on the
253 distribution of the fitness component. Both intra-pair mating success and paternity share were
254 analysed using a binomial error distribution, and we accounted for a Poisson error distribution for
255 extra-pair mating success. Generalized linear mixed models were performed treating individuals as
256 random effects to correct for residual over-dispersion (when necessary). Correlations between
257 pollen dispersal distance and weight were examined using Pearson correlation tests. Significance of
258 all the effects described above was examined using likelihood ratio tests. We assessed confidence in
259 variance in RS_m , MS_m and in all components of RS_m by performing 10,000 bootstrap samples for all
260 statistics described in Supplementary Methods S1 (i.e., reproductive success, mating success,
261 paternity share, fecundity of mates). We further calculated and plotted 95% confidence intervals for
262 all components of reproductive success (I-XI) and compared the confidence intervals between
263 sexes. We used this bootstrap re-sampling to assess the significance of covariance between
264 components of male fitness by computing the p-value associated with a null covariance in the
265 bootstrap distribution. Finally, we performed bivariate linear regressions for all our fitness
266 components against both pollen dispersal distance and pollen weight to quantify the variance for
267 each fitness component explained by these two traits. All statistical analyses were performed using
268 the `lm`, `glm` and `glmer` functions in the `lme4` package [44] in R 3.2.2 [45].

269

270 Simulation model of pollen dispersal abilities

271 The effect of plant density on the intensity of sexual selection was investigated by modelling pollen
272 dispersal from male pollen donors to female recipients (see Supplementary Methods S2). Pollen
273 dispersal from each male donor was simulated using a negative exponential function. We calculated
274 simulated RS_m and MS_m , and resulting Bateman metrics, based on the males' contribution to the
275 pollen cloud of each female by simulating a sample of eight seeds per female. We compared
276 Bateman metrics calculated in three simulated spatial scenarios with: (1) no variance in pollen
277 dispersal between males; (2) among-male variance in pollen dispersal abilities with a long average
278 dispersal distance relative to inter-individual distances; and (3) among-male variance in pollen

279 dispersal with a short average pollen dispersal distance relative to inter-individual distances. These
280 three scenarios were simulated both under a regular grid (corresponding to our design) or a random
281 distribution of 100 males and 100 females in a squared population.

282

283 **Results**

284 Males and females differed in their Bateman metrics

285 Both the opportunity for selection (I) and the opportunity for sexual selection (I_S) were higher in
286 males than in females, regardless of plant density, and none of the bootstrap confidence intervals
287 overlapped between sexes (Table 1). In females, no significant relationship was found between the
288 proxies for mating and reproductive success (β_{SS}), whereas males displayed a significantly positive
289 Bateman gradient (Fig. 1). In both gardens, such differences were revealed by a significant
290 interaction between sex and the proxy for mating success (mating success x male at low-density:
291 $\beta_{SS}=1.52$, $df=1$, $p<0.0001$; at high-density: $\beta_{SS}=1.14$, $df=1$, $p<0.0001$; Fig. 1). In the low-density
292 garden, females displayed a marginally significant negative Bateman gradient (Fig. 1).
293 Reproductive success was positively related to the proxy for mating success at both at the intra- and
294 extra-pair scales (but with a marginally significant effect at the intra-pair scale in the low-density
295 garden; Fig. S1).

296

297 Male mating success explained substantial variance in reproductive success

298 Our paternity analysis found an average of 4.97 and 4.62 male partners per female in the high- and
299 low-density gardens, respectively. Local male partners sired a proportion of 0.22 and 0.38 intra-
300 paired seeds at the high- and low-density gardens, respectively. Variance in access to mating
301 partners (component V) was a strong determinant of variance in RS_m in both gardens (Fig. 2); it was
302 the largest variance component in 92% and 100% of the bootstrap replicates in the low- or high-
303 density gardens, respectively. Securing paternity share at the extra-pair scale (VI) was a strong
304 determinant of variance in RS_m in both gardens (Fig. 2). In both gardens, but to a greater extent in
305 the low-density garden, some variance also emerged at the intra-pair scale, and this was not only
306 because female seed production varied among pots (III) but also because some males failed to
307 pollinate their associated female (I) and because their paternity share was variable when they did so
308 (II). The significantly positive covariance between intra-pair and extra-pair reproductive success
309 suggested that males that gained high reproductive output at the intra-pair scale also did so at the
310 extra-pair scale in both gardens (Fig. 2, XI). Still, in both gardens males with greater extra-pair
311 mating success also sired a larger proportion of ovules on their extra-pair partners, as revealed by
312 significant positive covariance between mating success and paternity share at the extra-pair scale
313 (Fig. 2, IX).

314

315 Increased pollen dispersal distance allowed males to gain more mates

316 We found that males dispersing their pollen further acquired more mates in both gardens (Table 2;
317 Fig. 3a). Pollen weight was not related to the proxy for male mating success in either garden (Table
318 2; Fig. 3b). Pollen weight and dispersal distance were correlated in the high-density garden ($r=0.35$,
319 $t=3.65$, $df=93$, $p=0.0004$), but not in the low-density garden ($r=0.16$, $t=1.64$, $df=98$, $p=0.11$).

320

321 In both gardens, increased pollen dispersal distance was positively associated with, and explained a
322 large proportion of, extra-pair mating success (Table 2; Fig. 2). Increased pollen dispersal
323 contributed to the positive associations found between intra-pair and extra-pair reproductive
324 success, while pollen weight tended to decrease this association in the low-density garden (Fig. 2).
325 In the low-density garden, increased pollen dispersal distance and pollen weight allowed males to
326 sire larger proportion of ovules on extra-pair or intra-pair mates, respectively (Table 2), but the
327 explanatory power of the latter regression was very low (Fig. 2). In the high-density garden,
328 increased pollen dispersal was associated with larger mating success at both scales, and with larger
329 paternity share on intra-pair females (Table 2).

330

331 Simulations revealed opposite effects of plant density on Bateman metrics, depending on pollen
332 dispersal abilities

333 With a simulated fixed ability to disperse pollen, we found that both I and I_s were larger at low than
334 at high density when plants were distributed randomly over space (Fig. S2d, e) but not when
335 simulating a regular grid (Fig. S2a, b). In neither of the simulated spatial conformations were
336 Bateman gradients (β_{ss}) affected by density in the case of a fixed ability of males to disperse their
337 pollen (Fig. S2c, f). When simulating among-male variation in pollen dispersal distance, the impact
338 of density on Bateman metrics depended on the distance of pollen dispersal relative to mean inter-
339 individual distances: (1) with simulated long pollen dispersal distances, all three sexual selection
340 metrics were larger at high compared to low density (Fig. 4; Fig. S2); (2) with simulated short
341 pollen dispersal, Bateman metrics were larger at low compared to high density (Fig. 4; Fig. S2).

342

343 **Discussion**

344 Our study used classical Bateman statistics to quantify sexual selection in a flowering plant [5].
345 Variances in reproductive and mating success proxies were larger in males of *M. annua* than in
346 females, confirming that both natural and sexual selection had a greater opportunity to operate on
347 males than on females, as is common in animals [5,7]. Previous work has obtained contrasted
348 results on this point; variance in plant mating success was larger in males than in females in

349 *Chamaelirium luteum* [46], while reported variances in reproductive success tended to indicate
350 larger ones in females compared to males [47-49]. In our study, in addition to a difference in
351 variance between the sexes, *M. annua* also conformed to the third Bateman principle: in both
352 gardens, only males (i.e., not females) gained fitness benefits from having many mates. Males
353 gained mates particularly through pollen dispersal over larger distances, rather than through pollen
354 production, a result that points to sexual rather than fecundity selection. These results complement
355 the body of work suggesting male-male competition as a selective force acting on several
356 reproductive and vegetative plant traits [15,17-24]. Sexual selection should therefore act primarily
357 on architectural traits that facilitate pollen dispersal in wind-pollinated plants [21,33] and, in insect-
358 pollinated plants, on floral traits attracting pollinators that travel further away or on traits that
359 promote more effective pollen deposition on pollinators [25].

360

361 Importantly, Bateman gradient estimates might be subject to a widely discussed statistical bias that
362 is inherent in genetic estimates of mating success [4,27]. In such analyses, mating events that result
363 in no, or few, fertilized eggs are necessarily ignored, so that variance in mating success may be
364 overestimated (i.e., many male mates may remain below the detection threshold). In the likely
365 scenario in which the male paternity share is strongly asymmetrical, our approach would allow the
366 identification of the most successful males despite the low number of seeds sampled. It is not easy
367 to identify an artificially induced variance in male mating success, but our positive Bateman
368 gradients are unlikely to emerge only from random variation in the representation of males in the
369 genotyped seeds.

370

371 Several features of our results indicate that they do capture true variance in the ability of males to
372 access mates, and are not just the result of sampling error. First, we observed spatial effects in
373 mating patterns. Specifically, (1) most males tended to sire a large proportion of seeds on their local
374 female, resulting in variance in the intra-pair paternity share; and (2) some males sired several of
375 the sampled seeds on extra-pair females, increasing variance in the extra-pair paternity share.
376 Second, males with many mates also showed a larger paternity share than expected at random.
377 Third, a strong spatial component emerged in mate acquisition, suggesting that males dispersing
378 their pollen over greater distances sired more seeds than expected by chance. Patterns of correlation
379 in paternity, similar to those presented here, have recently been taken as indicative of the extent of
380 sexual selection in plants [50], but they should ideally be estimated on the basis of more seeds
381 sampled per female. Both the spatial effects and the variation in paternity share revealed by our
382 approach suggest that males did differ from one another in their pollen efficiency, despite high
383 polyandry.

384

385 To what extent might we regard the positive effect of pollen dispersal on male mating as just a
386 consequence of wind-pollination dynamic? For a given male, spreading pollen over more mates
387 should reduce local mate and resource competition [33,35]. Nevertheless, the benefits of dispersing
388 pollen widely likely could come at the cost of diluting the concentration of pollen (and lowering
389 paternity share) per female. Yet we did not observe such trade-offs; if anything, males that dispersed
390 their pollen over greater distances tended to have a higher share in paternity on the local female (at
391 high density) or on distant females (at low density). This pattern suggests that males whose pollen
392 travels further also have correlated traits that increase their paternity success in spite of potential
393 pollen dilution. While the amount of pollen produced explained a small amount of the variance in
394 male reproductive success, traits involved in the competitive ability of pollen might be correlated
395 with pollen dispersal. This is reminiscent of many studies in animals where males in good condition
396 tend to perform well for several fitness components at the same time, overriding potential trade-offs
397 [51].

398

399 Both a sex-specific cost of reproduction and pollen limitation might lead to sex differences in
400 Bateman metrics, two factors whose importance we did not evaluate. Females probably often incur
401 a larger cost of reproduction than males, but the reverse could be true for wind-pollinated herbs in
402 which males produce large amounts of pollen [52]. If so, the larger opportunity for selection
403 reported here for males might in part reflect among-male differences in a capacity to harvest
404 resources. In species with a larger female reproductive cost, among-female variation in resource
405 acquisition might dramatically increase variance in female reproductive success, which has
406 commonly been found in plants [15,47-49], regardless of sexual selection. In our experiment,
407 female reproductive success was independent of access to mates, but positive Bateman gradients in
408 females are nevertheless expected under pollen-limited conditions [53]. Pollen limitation is unlikely
409 to have been important in our experiment, in which females were close to a male in both gardens,
410 and is probably rarely important in natural populations of *M. annua*, which tend to be dense [54]. At
411 low density, pollen limitation might however be important in many species, as for sperm limitation
412 in broadcast spawners, where variance in female reproductive success is typically larger at lower
413 densities [31].

414

415 Our simulations similarly suggested that the intensity of sexual selection in plants may be density-
416 dependent, albeit constrained by the scale at which pollen is dispersed relative to the spatial
417 distribution of potential mates. Increased variance in both reproductive and mating success was
418 predicted with increasing distance between the sexes, because the skewness of pollen dispersal

419 kernels enhanced differences in the ability of males to disperse pollen successfully at lower density.
420 In a randomly arranged population, some males will by chance experience a more female-biased
421 neighborhood than others, as can happen in natural populations [55], and might thus enjoy both a
422 higher mating and a higher reproductive success. Such a stochastic effect of decreased density was
423 canceled in populations with a uniform distribution of plants, i.e., a regular grid in our experiment.

424
425 While plants may have little genetic control on their relative positions, our simulations also
426 indicated that sexual selection may have non-neutral density-dependent effects on traits involved in
427 pollen export. The opportunity for sexual selection increased at lower densities only when a few
428 males dispersed their pollen further than average males, thus obtaining disproportionate fitness
429 gains by mating with more mates (when most males dispersed their pollen over shorter distances
430 than the typical inter-individual distance). In contrast, the opportunity for sexual selection increased
431 at higher densities only when a few males dispersed more pollen in their immediate vicinity than
432 average males. In this case, local dispersal should be disproportionately favoured by concentrating
433 pollen on the closest females where they can outcompete other pollen donors. Sexual selection
434 might bring about the evolution of strategies (or plastic responses to variation in plant density) that
435 allow males to disperse most of their pollen either locally or far away, depending on the spatial
436 distribution of their prospective mates. These simulation results echo findings in broadcast
437 spawners, where sperm traits that increased competitive performance were favoured by selection at
438 high density, whereas sperm traits facilitating the localization of rare eggs were favoured at low
439 density [31,34].

440
441 By applying a mate-centred approach, and by decomposing male reproductive success into different
442 components, our study suggests that a capacity for enhanced pollen dispersal is associated with
443 larger success in accessing mates, which in turn is the main determinant of male fitness – a result
444 that might not always hold. Both our experimental results and our simulations revealed that the
445 spatial conformation of a population may significantly affect the strength and direction of sexual
446 selection. Bateman metrics and variance decomposition, initially developed to quantify how sexual
447 selection operates in animals, thus have the potential to capture this variation and to inform us on
448 selection on traits that affect the spatial dispersal of pollen.

449 450 **Acknowledgments**

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579 **Figure 1:** Sex-specific Bateman gradients in *M. annua* grown in two common gardens at (a) low
580 density and (b) high density.

581

582 **Figure 2:** Decomposition of the variance in RS_m at (a) low and (b) high density and explanatory
583 power of pollen weight, dispersal distance and their covariance. I: variance in intra-pair mating
584 success; II: variance due to the different reproductive outputs of the intra-paired female; III:
585 variance due to paternity share on intra-pair female partners; IV: covariance between II and III; V:
586 variance in extra-pair mating success; VI: variance due to the differences in reproductive success of
587 extra-pair females; VII: variance due to differences in paternity share of extra-paired females; VIII:
588 covariance between V and VI; IX: covariance between VI and VII; X: covariance between V and
589 VII; XI: covariance between reproductive success at the intra-pair and extra-pair scale.
590 Abbreviations: *MS*: mating success; *Pat*: paternity; *FRS*: reproductive success of the female
591 partners; *cov* : covariance. Confidence intervals (95%) were calculated on the basis of bootstrap re-
592 sampling of males. Significance of covariance terms was evaluated by computing the p-values
593 corresponding to a null covariance term in the bootstrap distribution (* $p < 0.05$).

594

595 **Figure 3:** Relationship between mating success and (a) mean pollen dispersal distances and (b)
596 pollen weight in *M. annua* grown at low density and at high density.

597

598 **Figure 4:** Effect of simulated low- and high-density (L vs. H) on the Bateman gradient when male
599 abilities to disperse pollen are variable. We implemented either a long or short mean dispersal
600 distance of pollen compared to typical distances between males and females (long and short,
601 respectively). Dots represent mean values, and error bars correspond to one standard deviation.

602

603 **Figure S1:** Male Bateman gradients inferred from 100 males using only extra-pair reproductive
604 success (blue, dashed line), only intra-pair reproductive success (orange, dashed line) or both
605 components of reproductive success (black, full line) at (a) low and (b) high density.

606

607 **Figure S2:** Results of simulations of the effect of plant density on the strength of sexual selection
608 for two spatial scenarios: a regular grid corresponding to our experimental design (a, b, c); and a
609 random distribution of males and females in blocks of the same size as in the regular grid (d, e, f).
610 Three metrics quantifying sexual selection were calculated: the opportunity for selection, I , (a, d),
611 the opportunity for sexual selection, I_s , (b, e) and Bateman gradients, β_{SS} , (c, f). In each of these
612 cases, we simulated three scenarios: (i) no variation in male abilities to disperse their pollen and a
613 medium dispersal distance of pollen of 5.25 m (medium and constant pollen dispersal kernels); (ii)

614 implementing a coefficient of variation of 90% around a mean dispersal distance of pollen for long
615 compared to typical distances between males and females (variable and long pollen dispersal
616 kernels); and (iii) implementing a coefficient of variation of 90% around a mean dispersal distance
617 of pollen for short compared to typical distances between males and females (variable and short
618 pollen dispersal kernels). In each simulation, we compared low- and high-density cases (L vs. H).
619 One hundred simulations were performed in each case; dots represent mean values for the metric,
620 while error bars represent one standard deviation around this mean value.

Table 1 : Opportunity for selection (I) and opportunity for sexual selection (I_s) in males and females in the low-density and high-density gardens. Opportunity for selection and opportunity for sexual selection were standardized by dividing by the square mean reproductive success or mean mating success. The opportunity for selection in males was corrected for Binomial sampling errors in the measurement on paternity shares in each female (uncorrected values are indicated in parentheses). The 95% confidence intervals calculated on the basis of bootstrap replicates are provided in brackets.

	Low density		High density	
	Female	Male	Female	Male
I	0.28 [0.18-0.37]	0.53 (0.53) [0.40-0.69]	0.25 [0.19-0.31]	0.63 (0.63) [0.45-0.81]
I_s	0.12 [0.09-0.16]	0.26 [0.19-0.35]	0.11 [0.08-0.14]	0.43 [0.32-0.56]

Table 2 : Effect of pollen dispersal distance and pollen weight on several components of male reproductive success at the scale of intra-pair, extra-pair matings and on relative mating success at the global scale. Both pollen dispersal distances and pollen weight were standardized and analyzed in bivariate models. Mean and standard deviation are provided for each component of reproductive success. The significance of each component of the reproductive success of males was evaluated using likelihood ratio tests: $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Results with a p-value < 0.10 are highlighted in bold.

	INTRA PAIR			EXTRA PAIR			GLOBAL
	Mating success	Paternity share	Partner reproductive success	Mating success	Paternity share	Partner reproductive success	Relative mating success
Low density							
Mean (\pm SD)	0.82(\pm 0.39)	0.38(\pm 0.26)	121.45(\pm 64.08)	3.8(\pm 2.22)	0.16(\pm 0.03)	113.09(\pm 31.29)	
Pollen dispersal	$\beta = 0.45, p = 0.11$	$\beta = 0.12, p = 0.16$	$\beta = 3.91, p = 0.61$	$\beta = 1.11, p < \mathbf{0.0001}^{***}$	$\beta = 0.008, p = \mathbf{0.02}^*$	$\beta = 2.10, p = 0.52$	$\beta = 0.25, p < \mathbf{0.0001}^{***}$
Pollen weight	$\beta = 0.13, p = 0.65$	$\beta = 0.17, p = \mathbf{0.03}^*$	$\beta = -0.68, p = 0.93$	$\beta = -0.13, p = 0.69$	$\beta = -0.002, p = 0.47$	$\beta = 3.31, p = 0.31$	$\beta = -0.02, p = 0.59$
High density							
Mean (\pm SD)	0.64(\pm 0.48)	0.22(\pm 0.23)	93(\pm 44.14)	4.33(\pm 3.02)	0.17(\pm 0.04)	88.62(\pm 25.46)	
Pollen dispersal	$\beta = 1.23, p < \mathbf{0.0001}^{***}$	$\beta = 0.81, p < \mathbf{0.0001}^{***}$	$\beta = -0.004, p = 0.99$	$\beta = 1.67, p < \mathbf{0.0001}^{***}$	$\beta = 0.002, p = 0.72$	$\beta = 3.35, p = 0.26$	$\beta = 0.41, p < \mathbf{0.0001}^{***}$
Pollen weight	$\beta = -0.15, p = 0.60$	$\beta = 0.01, p = 0.91$	$\beta = -9.21, p = 0.09$	$\beta = 0.39, p = 0.10$	$\beta = 0.001, p = 0.86$	$\beta = 0.67, p = 0.82$	$\beta = 0.05, p = 0.37$

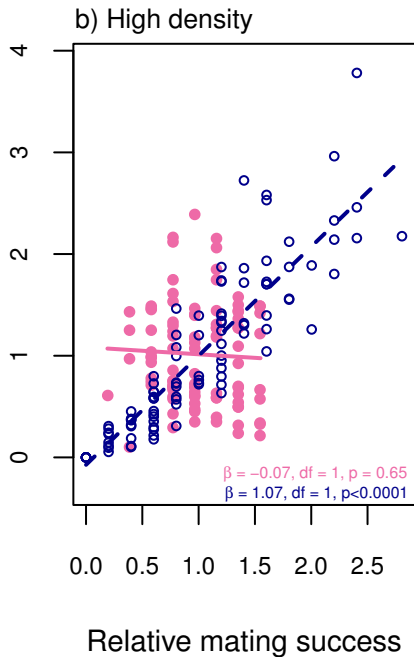
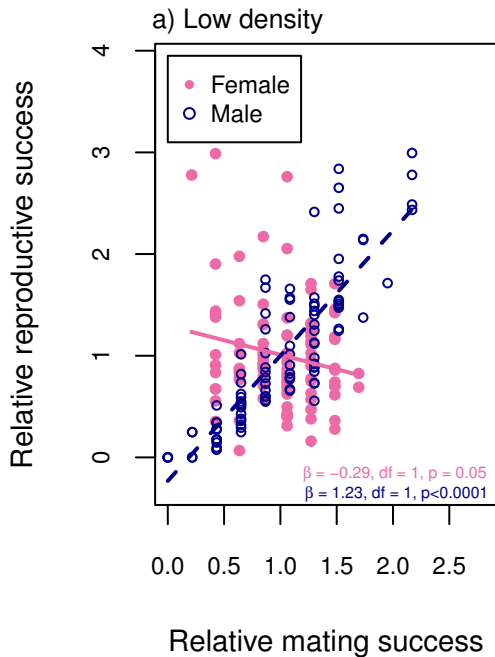
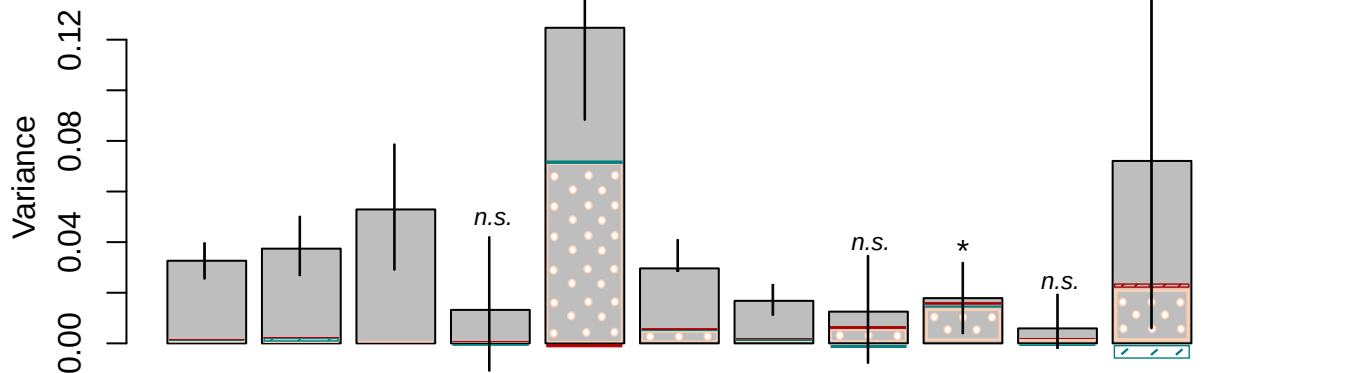


Figure 1

a. Low density garden



b. High density garden

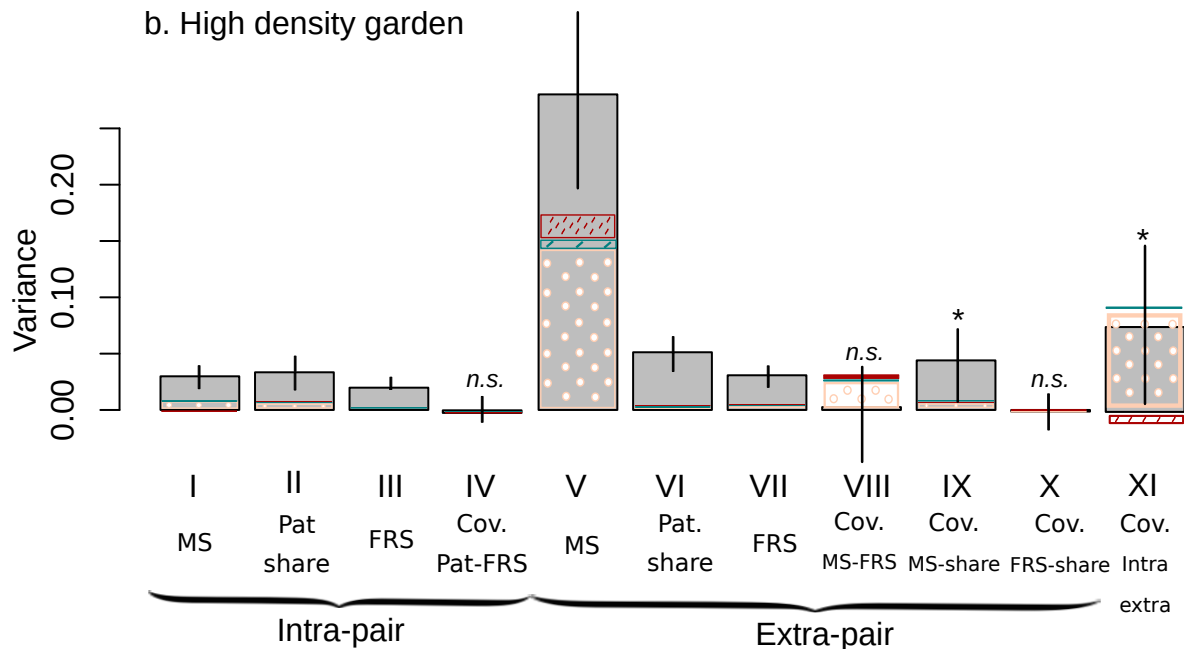


Figure 2

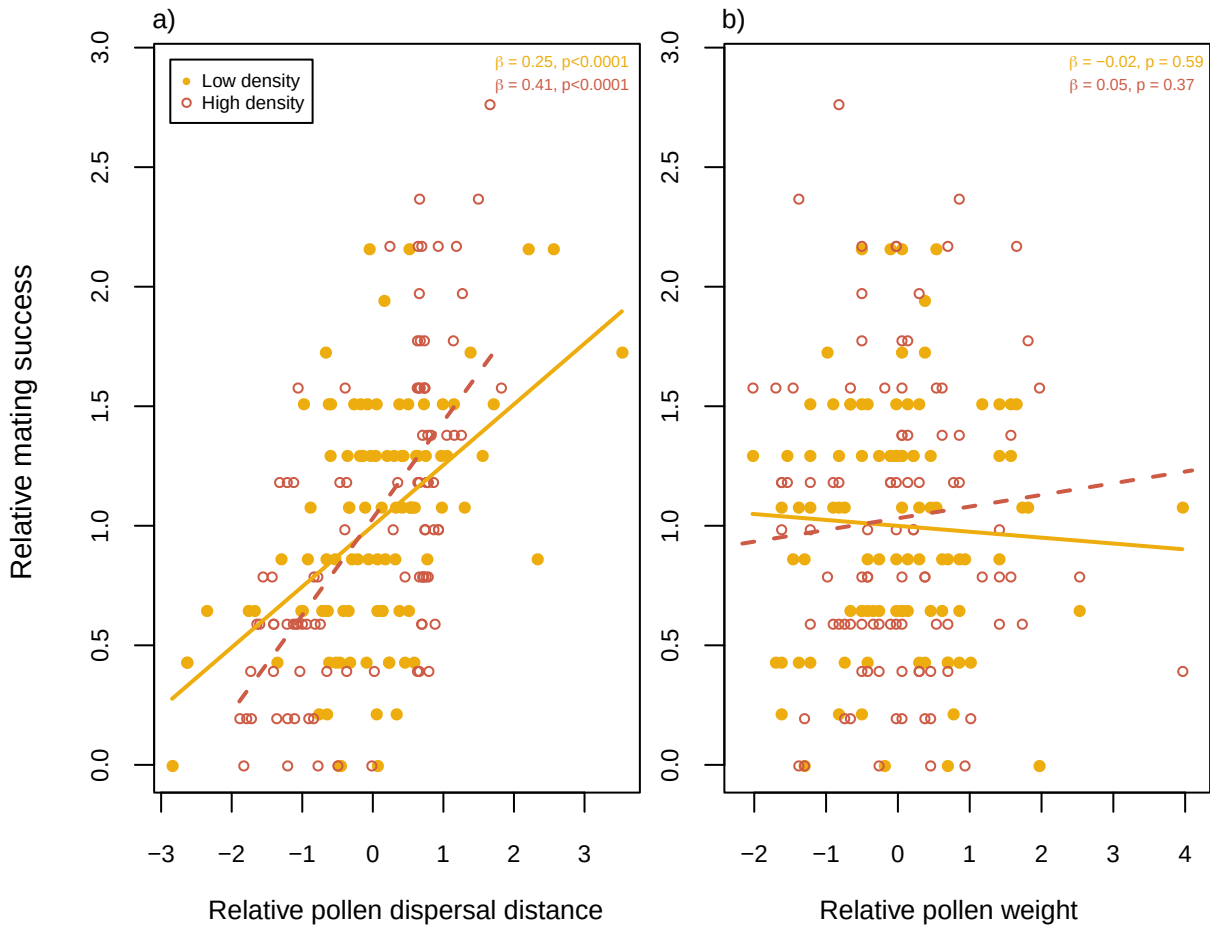


Figure 3

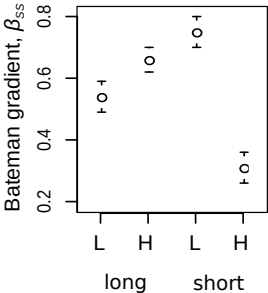


Figure 4

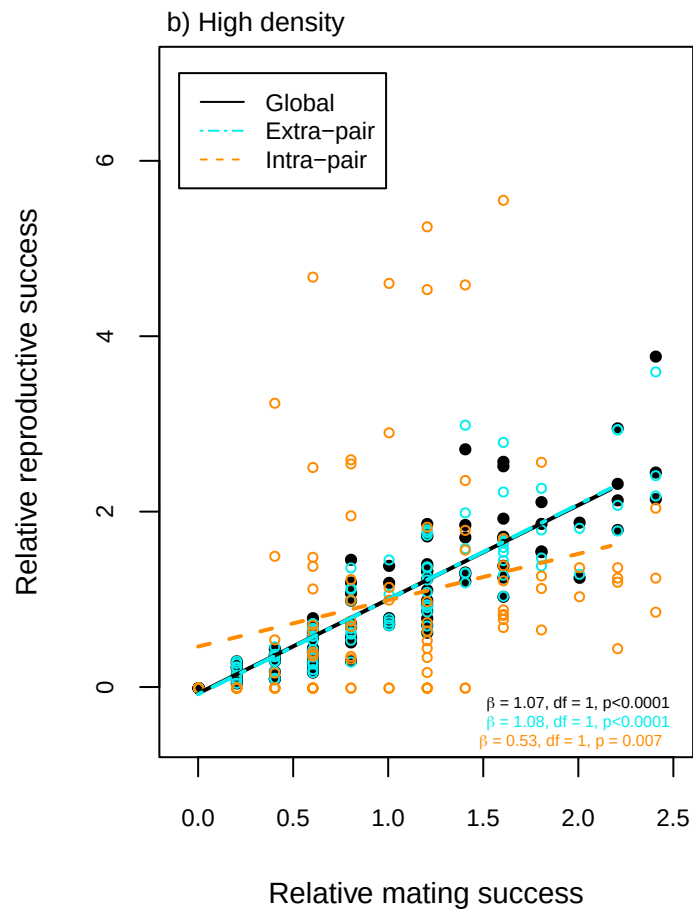
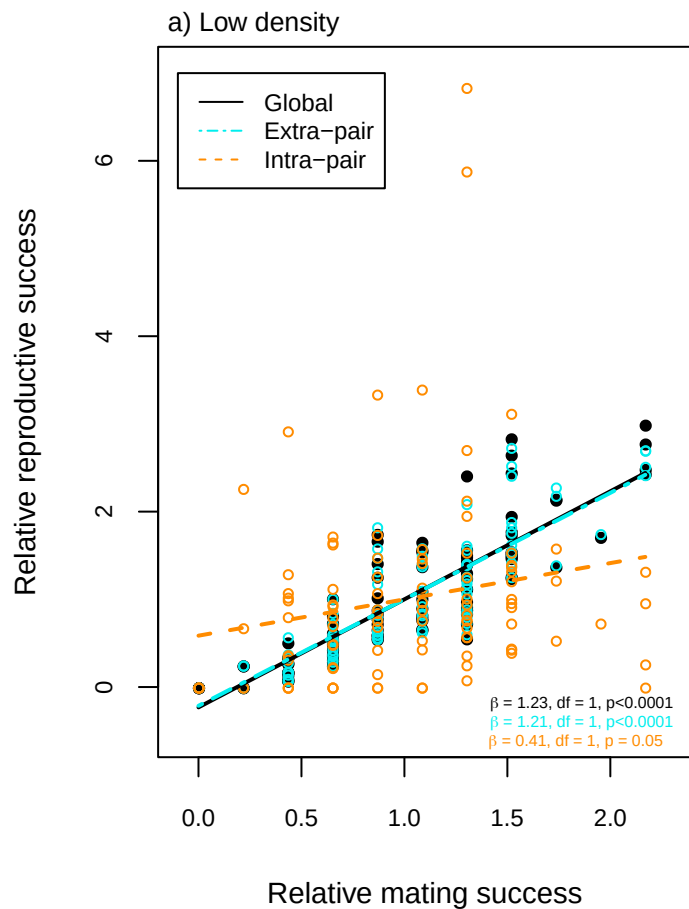


Figure S1

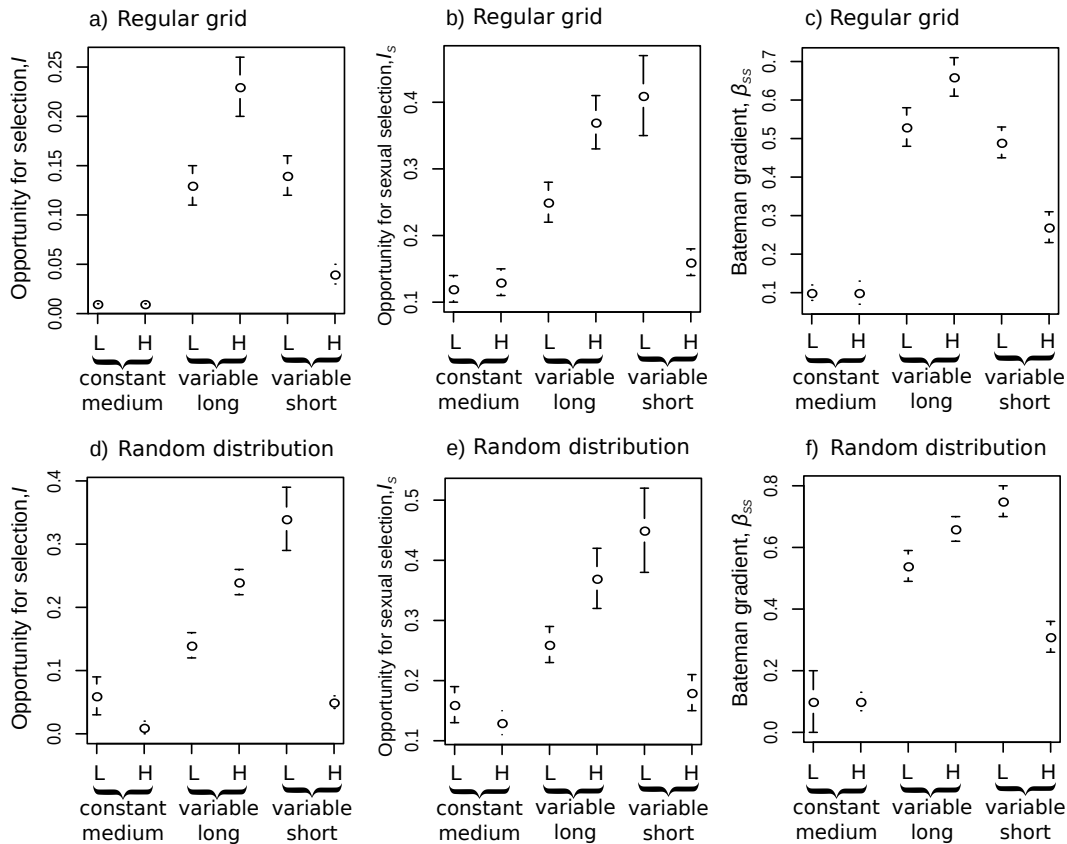


Figure S2