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Citation for published version:

López-Cortegano, E, Carpena-Catoira, C, Carvajal-Rodríguez, A & Rolán-Alvarez, E 2020, 'Mate choice based on body size similarity in sexually dimorphic populations causes strong sexual selection', *Animal Behaviour*, vol. 160, 19-00334R, pp. 69-78. <https://doi.org/10.1016/j.anbehav.2019.12.005>

Digital Object Identifier (DOI):
[10.1016/j.anbehav.2019.12.005](https://doi.org/10.1016/j.anbehav.2019.12.005)

Link:
[Link to publication record in Edinburgh Research Explorer](#)

Document Version:
Peer reviewed version

Published In:
Animal Behaviour

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**Mate choice based on body size similarity in sexually
dimorphic populations causes strong sexual selection**

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RUNNING TITLE: Mate choice and sexual size dimorphism

**KEYWORDS: assortative mating; computer simulations; gaussian mating preference
function; intersexual selection; intrasexual selection**

24 **Abstract**

25 Traditionally it has been suggested that sexual selection can cause sexual size
26 dimorphism (SSD). However, a recent review in gastropods shows that SSD itself can
27 also cause sexual selection (Ng et al. 2019). This may be the case if mate choice exist,
28 with males preferring to mate with females similar in body size but somewhat larger
29 than themselves ([female-biased preference](#)). This verbal explanation is formally
30 investigated here by computer simulations using a Gaussian mating preference
31 function. Parameters of that function are also estimated from empirical data. Our
32 results suggest that sexual selection (estimated as selection differential) is strong when
33 mate choice is high and exerted by only one of the sexes, being influenced by SSD and
34 the magnitude of the female-biased preference. All these factors cause a negative
35 relationship between SSD and the (sexual) selection differential, similar to the one
36 observed in the previous review on gastropods. Empirical estimates of the male mate
37 choice from wild-captured mating pairs of different gastropod species confirm that
38 male mate-choice is biased towards females slightly larger than themselves. Our
39 results also illustrate that if mate choice is truly involved in determining SSD, present-
40 day sexual selection cannot be used to estimate the past magnitude of mate choice, as
41 SSD influences present day patterns of sexual selection.

42 INTRODUCTION

43 Sexual size dimorphism (SSD) is a widespread but complex phenomenon. In birds and
44 mammals, males are usually larger than females, but the opposite trend exists in
45 several invertebrate groups (reviewed in [Andersson, 1994](#); [Blanckenhorn, 2005](#);
46 [Fairbairn, Blanckenhorn, & Székely, 2007](#); [Ng et al. 2019](#)). The current consensus is that
47 males and females can adapt differently to maximize their reproductive efforts, but
48 different mechanisms have been proposed to explain observed patterns of SSD
49 ([Andersson, 1994](#); [Blanckenhorn, 2005](#); [Fairbairn et al., 2007](#); [Hirst, & Kiørboe, 2014](#);
50 [Rohner, Reder, Esperk, Lüpold, & Blanckenhorn, 2018](#); [Kappeler, Nunn, Vining, &](#)
51 [Goodman, 2019](#)). It has been suggested, for example, that sexual selection for body
52 size due to either mate competition or mate choice may differentially affect males and
53 females ([Berry, & Shine, 1980](#); [Székely, & Lislevand, 2007](#); [Rohner, Blanckenhorn, &](#)
54 [Puniamoorthy, 2016](#); see further examples in [Fairbairn et al. 2007](#)). These hypotheses,
55 however, assume that SSD is genetic in origin and caused by sexual selection (i.e. mate
56 choice or mate competition). Note that from an evolutionary perspective, sexual
57 selection is a process (a mechanism or a cause) that leads to different present-day
58 patterns, but in the present generation, from a biological perspective, sexual selection
59 can itself be caused by different mechanisms, such as mate choice and mate
60 competition ([Rolán-Alvarez, & Caballero, 2000](#); [Carvajal-Rodríguez, 2019](#)).

61 In gastropods, as in other invertebrates, there is typically female-biased SSD
62 (i.e. females are larger than males; reviewed in [Ng et al., 2019](#)), as well as sexual
63 selection favouring larger females due to male mate choice (reviewed in [Rolán-Alvarez,](#)
64 [Austin, & Boulding, 2015a](#); [Ng et al., 2019](#)). Females are usually passive, while males
65 exert mate choice by preferentially following certain female mucus trails, although

66 certain contributions by females during copulation cannot be excluded (Ng et al., 2019;
67 Rolán-Alvarez et al., 2015a). Males probably prefer larger females, as they are typically
68 more fecund, although there may be trade-offs, such as increasing the probability of
69 competition from larger males or even anatomical problems with copulation if the
70 difference in body size is too large. Therefore, the evolution of a mating preference
71 bias (e.g. males of size S preferring to mate with females of size $S+B$, with B being the
72 magnitude of the bias; see Figure 1 from Ng et al., 2019) could be a reasonable
73 evolutionary compromise among these forces. A negative correlation between sexual
74 selection (estimated by a linear sexual selection differential) and SSD was observed
75 across and within species of gastropods (Ng et al., 2019): a SSD whereby females were
76 larger than males led to sexual selection favouring smaller females (i.e. a negative
77 selection coefficient on female size), whereas an SSD whereby males were larger than
78 females led to sexual selection favouring larger females (i.e. a positive selection
79 coefficient on female size). By way of explanation, Ng and co-workers (2019) suggested
80 that a pre-existing SSD combined with certain mating preference (as the biological
81 cause of sexual selection), including a positive size bias (males preferring females
82 larger than themselves, would determine the strength of sexual selection (i.e. sexual
83 selection would be a consequence of mate choice + dimorphism). A novelty of this
84 explanation is that in previous studies sexual selection was considered the cause of
85 SSD (see examples in Berry, & Shine, 1980; Székely, & Lislevand, 2007; Rohner et al.,
86 2016). Therefore, when SSD already exists in a species with a certain mating
87 preference, a negative relationship between SSD and sexual selection can be expected
88 (Ng et al., 2019), i.e. in species with larger females, smaller females have a competitive
89 advantage. While these expectations have been outlined verbally, the expected

90 outcomes of this hypothesis under a range of pre-existing values of SSD, bias and mate
91 choice conditions remain unclear.

92 In order to better understand the relationship between mate choice and SSD,
93 we used computer simulations and re-analysis of published data to achieve three
94 major objectives: 1) to study the mechanism of action of mate choice and how it is
95 influenced by SSD, as well as other behaviours (preference bias, mate cost etc.); 2) to
96 estimate parameters of the mate choice function using experimental data from several
97 marine snail species and 3) to investigate whether the theoretical (point 1) and
98 empirical data (point 2) support the hypothesis of Ng et al. (2019) where a pre-existing
99 SSD plus certain male preference for females slightly larger than themselves can
100 explain observed trends in sexual selection.

101

102

103 **MATERIALS AND METHODS**

104 *The model of mate choice*

105 From a population genetics point of view, deviations from random mating can be
106 disentangled into two different patterns, namely sexual selection and assortative
107 mating effects (Merrel, 1950; Knoppin, 1985; Gavrilets, 2004). Assortative mating is
108 the correlation between the values of a trait across members of mated pairs (Jiang,
109 Bolnick, & Kirkpatrick, 2013). On the other hand, sexual selection can be defined as the
110 observed change in gene or phenotype frequencies in mated individuals as a
111 consequence of differences in mating and/or fertilization success, which might
112 contribute to trait evolution (Hartl, & Clark, 1997). Two main mechanisms can

113 contribute to sexual selection and assortative mating: mate competition (also called
114 mate propensity) and mate choice (Merrell, 1950; Lewontin, Kirk, & Crow, 1968). Mate
115 competition is the intrinsic tendency of one phenotype to mate more or less efficiently
116 than the others (Merrel, 1950; Lewontin et al., 1968; Knoppin, 1985), while mate
117 choice is the behavioural propensity of individuals to prefer mates with certain
118 phenotypes (Basolo, 1998; Roff, 2015; reviewed in Edward, 2015).

119 Mate choice can be formulated theoretically in different ways (see examples in
120 Gavrilets, 2004; Edward, 2015; Kopp et al., 2017), but some of the most powerful tools
121 are the Gaussian mating preference functions (GMPF), which have been used
122 extensively in theoretical work (Lande, 1981; Gavrilets, 2004; reviewed in Carvajal-
123 Rodriguez, & Rolán-Alvarez, 2014). In this context, mating preference is considered to
124 be synonymous with mate choice (Basolo, 1998; Roff, 2015; reviewed in Edward,
125 2015). GMPF are used to simulate mate choice by similarity-based rules (i.e. choosing
126 mates with similar or dissimilar variants of a trait; Lande, 1981) and calculate the
127 probability of mating occurring with any potential partner encounter (Gavrilets, 2004)
128 using the difference between the female (Z_f) and male (Z_m) phenotypes (e.g. body size)
129 as the main criterion. These GMPF must be formulated by separate positive or
130 negative functions, corresponding to a preference for similar or dissimilar mates
131 (reviewed in Carvajal-Rodríguez, & Rolán-Alvarez, 2014), respectively, although here
132 we will focus on a positive function for mate choice based on size (FND function,
133 Carvajal-Rodríguez, 2018). Mate choice was investigated only in the context of male
134 choice, as this is the mechanism preferred by marine gastropod species (Rolán-Alvarez
135 et al., 2015a; Ng et al., 2019). The positive FND function used (FND_{MALE}) is a

136 modification of the original one (Carvajal-Rodríguez, & Rolán-Alvarez, 2014), which
137 includes a bias (B) parameter:

$$138 \quad FND_{\text{MALE}} = e^{\frac{-C^2(D-B)^2}{s^2 D_{\text{max}}^2}} \quad [1]$$

139 D is the difference in body size between female and male phenotypes ($Z_f - Z_m$) in a
140 mating pair, B is the bias (the deviation of the preferred female size from that of the
141 male making the choice), D_{max} is the maximum difference between female and male
142 phenotypes within the population (i.e. $\max(Z_f - Z_m)$), C is the mate choice parameter
143 (ranging from 0 to 1, with 0 being equivalent to random mating and 1 to maximum
144 positive assortative mating) and s^2 is the variance of the mating function for the
145 choosiest specimen (Bolnick, 2004), used here as a constant for *a priori* tuning of the
146 strength of mating preference (here for FND we used 0.1, i.e. a moderate to low
147 strength; see Carvajal-Rodríguez, & Rolán-alvarez, 2014). This strategy guarantees a
148 high correlation between the *a priori* C parameter given in the simulations and the *a*
149 *posteriori* Pearson r coefficient in simulated mating pairs (see below).

150

151 ***Estimating assortative mating, sexual selection and sexual size dimorphism***

152 The strength of assortative mating is typically estimated in a set of wild-captured or
153 simulated mating pairs by means of Pearson correlation coefficients (r coefficient;
154 Jiang et al., 2013). Although using r coefficients to estimate the strength of assortative
155 mating in wild populations with complex structures may present potential biases

156 (Rolán-Alvarez et al., 2015b), here it is justified as our simulated populations have no
157 further structuring or complications (see below).

158 The strength of sexual selection has been estimated by different
159 methodologies, and it can be a rather contentious issue depending on the definition of
160 sexual selection (reviewed in Henshaw et al. 2016). However, we estimate sexual
161 selection within the same generation as the classical standardized selection differential
162 (SS; Henshaw, Kahn, & Fritzsche, 2016) following the Arnold and Wade (1984) strategy:

$$163 \quad SS = \frac{(Z_{MATED} - Z_{POPULATION})}{Z_{POPULATION}} \quad [2]$$

164 where Z_{MATED} is the mean size of mated specimens, and $Z_{POPULATION}$ is the mean size in
165 the population. Sexual selection differentials (SS) were estimated for each sex
166 separately. Finally, the SSD was estimated as the expected value of D (i.e. the
167 population mean female size minus the mean male size; Ng et al., 2019).

168

169 ***The simulated scenarios***

170 We carried out simulations using an in-house C++ program (see Data Availability
171 statement below) in order to quantify the magnitude of sexual selection under
172 different scenarios including different SSD, bias and mate choice parameters, as well as
173 differences in the number of potential mates evaluated (see below).

174 For all cases considered, a population of size 1000 was generated with 500
175 males and 500 females. Male body sizes were always sampled from a normal
176 distribution $N(\mu=0, \sigma=1)$, while female body sizes were sampled from normal
177 distributions with means ranging from -1 to 1 in steps of 0.5 (to generate five

178 alternative levels of dimorphism), and standard deviations of $\sigma=1$. In every case,
179 individual phenotypes (Z) were rescaled so that the simulated range of values were
180 between 0 to 1 following previous theoretical studies using GMPF (Carvajal-Rodriguez,
181 & Rolán-Alvarez, 2014) using the following expression:

$$182 \quad Z'_i = D_{max} \frac{Z_i - Z_{min}}{Z_{max} - Z_{min}} \quad [3]$$

183 where $D_{max} = 1$. The bias parameter was also scaled accordingly, as

$$184 \quad B' = B \frac{D_{max}}{Z_{max} - Z_{min}} \quad [4]$$

185 Male evaluation of the female phenotype was simulated by means of the
186 positive FND preference function described above. Males accept or reject female
187 mating partners with a probability relative to the maximum possible preference and
188 always proportional to FND. A total of 30 or 100 mating pairs were evaluated per
189 scenario. Because the formation of mating pairs depends on male preference, we
190 simulated the formation of mating pairs by taking a random sample of male individuals
191 (30 or 100) and allowing each male to meet females sequentially (up to all 500 in the
192 population) in random order until a mating pair was formed. Thus, different males
193 could potentially mate with the same female, and not all males mated (e.g. a male
194 could fail to mate after 500 female encounters), although most did.

195 Simulations were carried out for choice parameter values ranging from 0 to 1 in
196 steps of 0.1 (i.e. from random mating where $C=0$ to complete positive assortative
197 mating where $C=1$). Three values of bias were also considered: 0 (no bias), 0.25 and 0.5
198 (i.e. a deviation of male preference equal to half the males mean body size; see
199 scenarios used in Figure 1). A total of 1000 replicates were run for each of these cases.

200 In order to check the stability of the former patterns, we also considered mate cost
201 (*sensu* [Gavrilets, 2004](#)) by limiting the maximum number of female encounters to 1, 10
202 or 100 (i.e. allowing each male to access only a reduced sample from the population
203 pool of 500 females). The results of our model were validated using a different pipeline
204 involving C++ software to simulate the populations, followed by the use of MateSim
205 ver 0.7 software ([Carvajal-Rodríguez, 2018](#)) to generate mating pairs (see
206 Supplementary Figure S1).

207

208 ***Inferring processes from real data***

209 Ng et al. (2019) suggest that most gastropods use some kind of similarity-based mating
210 preference function (such as GMPF), which includes a positive bias (i.e. males prefer
211 females of a similar to somewhat larger size). Such an explanation was supported by a
212 strong negative correlation between the female sexual selection differential and the
213 SSD (r coefficient=-0.77, P value=0.001; from [Ng et al., 2019](#)), i.e. in species with a
214 larger SSD (females larger than males), selection will favour the smallest females. In
215 order to further examine this explanation, we reviewed experimental data from the
216 former study (Table 1) and ran several simulations to reveal the relationship between
217 SSD and sexual selection under empirically estimated bias and choice. To do so, we
218 first needed to estimate the parameters of the FND function. C was estimated as the
219 C_{rough} coefficient following Fernández-Meirama et al. (2017a), and B as the difference
220 between the average mated female size and the average mated male size ($B_{\text{estimated}}$).
221 Since the correlation between the simulated average bias and the empirical estimates
222 was very high (r coefficient=0.78; P value < 0.001), we considered the $B_{\text{estimated}}$ a good

223 proxy for real bias. Simulations were validated by comparing their results to empirical
224 data from Ng et al. (2019) (see Table 1 and online Supplementary Figure S2).

225

226 ***Data availability***

227 The code used for simulations is available in a WEB repository (link after MS
228 acceptance), and the empirical data from gastropods is publicly accessible from Dryad
229 (<https://doi.org/10.5061/dryad.h214h8t>).

230

231 **RESULTS**

232

233 ***Mate choice and assortative mating***

234 The Pearson correlation coefficients between body sizes of males and females in
235 mating pairs (phenotypic correlation; $corZ$) had a strong and positive (>0.9)
236 relationship with mate choice (C) in all scenarios tested (see Figure 2 and
237 supplementary Figure S3). Therefore, the value of $corZ$ among simulated mating pairs
238 can be considered a good proxy for mate choice (C) in our scenarios.

239

240 ***Effects of mate choice, SSD and bias on sexual selection***

241 Observed patterns of sexual selection depended on the combination and degree of
242 mate choice, SSD and bias (Figure 3). As expected, sexual selection only affected
243 female size because when $C > 0$ the distribution of mated females moved towards that
244 of males, according to their phenotype and preference, as illustrated in Figure S4.
245 Second, when sexual selection occurred, it was positively correlated with mate choice

246 values (C). Additionally, sexual selection showed a negative association with SSD. In
247 summary, when SSD is male-biased, female sexual selection typically favours the
248 largest female, while the contrary is expected when SSD is female-biased, depending
249 on the particular values of B and SSD. It is worth noting that such a negative
250 association with SSD could be considered as a U-shape fitness relationship if the sexual
251 size differential is given in absolute values.

252 Mate cost when males choose (which limits the number of mating attempts per
253 male) produced similar results to those above for FND_{MALE} without costs. Therefore,
254 when cost increased (<100 attempts), the male sexual selection differential increased
255 in absolute value, whereas the female sexual selection differential decreased (Figure
256 4), producing a pattern similar to that observed when both sexes were allowed to
257 choose (not shown). This occurred because several males did not mate as they were
258 unable to find a suitable female before reaching their limit of attempts, leading to
259 differences in mating success among males.

260

261

262 ***Inferring processes from empirical data***

263 The experimental data reviewed by Ng and co-workers (2019), as well as the
264 corresponding estimators of C_{rough} and bias ($B_{\text{estimated}}$), are presented in Table 1. These
265 data were used to estimate female sexual selection within the same generation
266 through simulations. Thus, we could check whether theoretical expectations produced
267 the same sexual selection-SSD relationship observed in the former review. The results
268 of the simulations showed a strong and negative relationship (mean r coefficient=-

269 0.99; p value < 0.001; see Figure 5), which was reduced somewhat when individual
270 replicates were performed and the results averaged (mean r coefficient= -0.89; 95%
271 Confidence interval: -0.9657 and -0.7677).

272

273 **DISCUSSION**

274 The causes of sexual size dimorphism (SSD) are complex and may differ from one taxon
275 to another, so the search for general explanations has been difficult (reviewed in
276 [Shine, 1989](#); [Andersson, 1994](#); [Blanckenhorn, 2005](#); [Fairbairn et al., 2007](#); [Ng et al.,](#)
277 [2019](#)). Perhaps one of the most discussed relationships is the possibility that sexual
278 selection could contribute to the pattern of SSD by favouring distinct sizes in each sex
279 (for example [Berry, & Shine, 1980](#); [Rohner et al., 2016](#); but see [Kappeler et al., 2019](#)). A
280 typical argument used to propose such a relationship is based on the correlation
281 between sexual selection and SSD ([Blanckenhorn, 2005](#)). Sexual selection, however,
282 can be caused by mate competition, mate choice or both mechanisms simultaneously,
283 but it is unknown whether the mechanism causing it is relevant for explaining patterns
284 of SSD. When mate competition is supposedly driving SSD, the interpretation is
285 straightforward in principle (e.g. [Berry, & Shine, 1980](#); [Székely, Lislevand, & Figuerola,](#)
286 [2007](#); [Rohner et al., 2016](#)). For example, males are larger than females in many
287 vertebrate species, and in many cases this could be caused by male competition during
288 mating and the relationship between body size and mating success (see several cases
289 reviewed in [Blanckenhorn, 2005](#); [Fairbairn et al., 2007](#)). However, when mate choice
290 drives sexual selection, the situation is more complex; according to our results, mate

291 choice can produce varying levels of sexual selection depending on other factors,
292 including the level of SSD itself (Figure 3).

293 In a recent review, Ng and co-workers (2019) found a strong and negative
294 relationship between female sexual selection based on size and SSD, but contrary to
295 other claims, they suggested that the SSD could influence the observed patterns in
296 sexual selection rather than the other way around. They proposed a biological
297 mechanism which could explain such a relationship: male mate choice under a
298 similarity-based mechanism plus a certain positive bias (i.e. males preferring females
299 with a similar or somewhat larger body size). Here we tried first to formalize such a
300 mechanism with a new FND function (see Equation 1) and later by computer
301 simulations in order to theoretically understand the relationship of SSD with different
302 factors that may affect sexual selection, and secondly to simulate the empirical cases
303 previously studied to confirm that the Ng et al (2019) hypothesis will produce the
304 expected experimental pattern found.

305

306 **Theoretical considerations about mate choice**

307 We tried to understand how mate choice (including C and B) affects sexual selection
308 and assortative mating under different scenarios by running a variety of simulations
309 (Figure 1). This approach is based on the assumption that our FND mating function
310 reasonably approximates what is happening in nature (see Fernández-Meirama et al.
311 2017a and below). In fact FND-like functions have been widely used to theoretically
312 model the evolutionary consequences of mate choice *in silico* (Dieckmann, & Doebeli,
313 1999; Edelaar, & Bolnick, 2012; Thibert-Plante, & Gavrillets, 2013; Carvajal-Rodriguez,

314 & Rolán-alvarez, 2014; but see Kopp et al., 2017). Our results are rather
315 straightforward with respect to assortative mating, being caused by the C parameter
316 (mate choice strength) and unaffected by bias or dimorphism, at least for the range of
317 values investigated here. Assortative mating is not easy to estimate directly in the
318 field, as it can be influenced by external factors such as the SCE (scale-of-choice effect
319 *sensu* Rolán-Alvarez et al., 2015b). Nevertheless, this complication does not affect our
320 simple computer scenarios in the absence of any complex population substructure.

321 The relationship between mate choice and sexual selection is more difficult to
322 infer, which may explain, in part, the difficulty of inferring processes from patterns in
323 this context. First, the strength of sexual selection depends on both C and B, and it is
324 also affected by the level of SSD. In fact, sexual selection differentials can change from
325 positive to negative depending on the level of SSD (Figure 3). In summary, any
326 similarity-based mechanism ($C > 0$) will not produce (linear) sexual selection effects
327 without bias or dimorphism, and when present, both bias and dimorphism strongly
328 influence patterns of sexual selection in a similar way. In fact, sexual selection may not
329 be observed, even when a similarity-based mate choice mechanism is present ($C > 0$),
330 if $B = SSD$ (Figure 3). Therefore, when detecting (linear) sexual selection in wild
331 populations (as in Ng et al., 2019), this suggests the possibility that either bias or
332 dimorphism could exist (Table 1).

333 Finally, and especially relevant, is that the effects of mate choice on sexual
334 selection could be importantly influenced by the expected number of available
335 attempts from the chooser (mating cost *sensu* Gavrillets, 2004). The cost of mating has
336 been considered to influence sexual selection by reducing the efficiency of mating

337 preference ([Pomiankowski, 1987](#)). Although this result is well known from a theoretical
338 perspective, we believe that it has not been given enough consideration when
339 discussing the causes of SSD. This effect makes it even more difficult to infer the
340 mechanisms responsible for sexual selection patterns, as the pattern may be
341 importantly influenced by direct cost or even by demographic or ecological conditions
342 that could indirectly affect the pattern of sexual selection measured. Note for instance,
343 that male sexual selection appeared when the mating cost was excessive, even when
344 mate choice was determined exclusively by males (Figure 4), which could be confused
345 with a scenario where both males and females choose their mates.

346

347 **Inferring mate choice from wild data**

348 The estimation of mate choice parameters from the wild is a huge, but necessary, task
349 ([Rosenthal, 2016](#)). Traditionally, most studies trying to estimate mate choice have used
350 laboratory-designed experiments (see for example [Knoppien, 1985](#); [Rosenthal, 2016](#)).
351 However, such an alternative is not always desirable, because it has been shown in
352 several model organisms that field estimates do not typically coincide with laboratory
353 estimates ([Coyne, Elwyn, & Rolán-Alvarez, 2005](#); [Adams, & Morse, 2014](#); [Câmara de](#)
354 [Aquino, & Joachim-Bravo, 2014](#); [Holveck, Gauthier, & Nieberding, 2015](#)). Here we have
355 used experimental data from mating pairs captured in the wild from 15 populations
356 belonging to 7 different species to estimate the mate choice parameters C (C_{rough}) and
357 B by using the FND function (Table 1). The utility of C_{rough} to estimate C has already
358 been studied by simulations ([Fernández-Meirama et al., 2017b](#)), and here we have
359 confirmed that our estimates of bias are proportional to empirical estimates of bias

360 and are perhaps valid as preliminary rough estimates as well. True validation, however,
361 would come from experimental laboratory studies that are capable of directly
362 estimating B and comparing these values to those in Table 1.

363 In addition, our simulations confirm the hypothesis suggesting a negative
364 relationship between SSD and the sexual selection differential (Ng et al., 2019) under
365 different levels of SSD and mate choice strengths, e.g. female sexual selection favours
366 large females for scenarios with male-biased dimorphism (Figure 3). When simulations
367 were run using the trait mean and variance, as well as the mate choice parameter of
368 the wild populations studied in Ng et al. (2019; see Table 1), we observed a similarly
369 strong and negative relationship between sexual selection and SSD (r coefficient = -
370 0.89; Figure 5). The empirical unstandardized relationship observed in natural
371 populations (r coefficient=-0.55 from data in Table 1) fell outside the confidence
372 interval of our simulations. However, a partial reduction in the strength of the
373 relationship in the empirical data is reasonable because sexual selection may be
374 affected by a variety of different external factors and sources of bias. For example, our
375 simulations are based on the assumption that the estimates of C and bias are precise.
376 Therefore, the overall high and negative correlation observed in both empirical data
377 and simulations do, in our opinion, support the claims of Ng and co-workers (2019)
378 that 1) the observed female sexual selection is a consequence of male mate choice on
379 populations with certain pre-existing dimorphism and 2) that the negative relationship
380 between SSD and SS suggests a preference-like similarity function common to
381 gastropods. In addition, our simulations also point to the existence of large variation in
382 the bias parameter between species (Table 1). This study emphasizes the relevance of
383 combining experimental data with simulations for comprehensive understanding.

384

385 **General considerations about the evolution of sexual size dimorphism**

386 Sexual size dimorphism (SSD) is a general phenomenon, although, it probably doesn't
387 have any general explanation (Andersson, 1994; Blanckenhorn, 2005; Fairbairn et al.,
388 2007; Ng et al., 2019). When discussing the evolutionary significance of SSD, and
389 especially when discussing explanations for SSD based on sexual selection, one
390 assumption must be reconsidered: when sexual selection differs between sexes this
391 could be a causal explanation for SSD, which is reasonable when the cause of sexual
392 selection is mate competition. However, if the cause of sexual selection is mate choice,
393 it is very difficult to estimate it accurately together with any preference bias, and thus
394 it is also difficult to estimate the long-term consequences of mate choice, because
395 both dimorphism and bias influence present-day SSD. In fact, following the FND_{MALE}
396 function, the same magnitude on sexual selection estimates (with opposite signs) are
397 expected irrespective of varying bias or dimorphism. For example, the sexual selection
398 pattern with $B=0$ and $SSD=0.0$ is the same as with $B=0.5$ and $SSD=0.5$, and so it can be
399 observed for other combinations of values where the difference in B values equals the
400 differences in SSD (see Figure 3). From an evolutionary perspective, if we imagine a
401 case in which the SSD was caused by mate choice (due to a certain bias), in the long
402 term we would expect that the effects of sexual selection would be counter-balanced
403 by dimorphism until sexual selection becomes absent by reaching an equilibrium.
404 Therefore, the best model cases to study SSD caused by mate choice would be those
405 that apparently do not show sexual selection nowadays, contrary to what intuition
406 suggests. This study has focused on premating mate choice, but this mechanism works

407 identically (on theoretical grounds) to post-mating (i.e. gametic) mate choice and,
408 therefore, the former conclusions could immediately be extended to the latter.

409

410 **ACKNOWLEDGEMENTS**

411 We thank Mary Riádigos for administrative managing. We thank Drs. Sam
412 Crickenberger, Tin Yan Hui and two anonymous referees for improving later versions of
413 the manuscript. The analyses reported here were performed on the FinisTerra
414 machine provided by CESGA (Galicia Supercomputing Centre). This work was
415 supported by Xunta de Galicia (ED431C 2016-037), FONDOS FEDER (“Unha maneira de
416 facer Europa”) and the Ministerio de Economía, Industria y Competitividad (CGL2016-
417 75482-P). All authors declare to have no conflict of interest.

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Table 1. Mean (\pm SD) size of mated males and females, dimorphism and estimates of mating preference function parameters, of species and populations obtained from Ng et al (2019).

Species	Locality	N	Mated		Dimorphism	SS _{♀♀}	B	C _{rough}
			Males	Females				
<i>Echinolittorina malaccana</i>	Shek O	80	6.04 \pm 1.01	6.49 \pm 1.23	-0.15	0.93	0.45	0.53
	CDA1	102	8.65 \pm 0.88	9.01 \pm 0.98	0.28	0.55	0.36	0.599
	CDA2	456	8.44 \pm 1.38	9.23 \pm 1.45	0.42	0.7	0.79	0.469
<i>E. radiata</i>	CDA1	108	6.36 \pm 1.51	7.73 \pm 1.62	1.35	0.26	1.37	0.652
	CDA2	102	7.27 \pm 1.54	8.22 \pm 1.53	0.7	0.69	0.95	0.574
<i>E. vidua</i>	CD1	82	6.97 \pm 1.06	7.41 \pm 1.02	0.01	0.68	0.44	0.558
<i>Littoraria flava</i>	FLE	480	10.8 \pm 1.72	11.8 \pm 1.80	0	0.9	1	
<i>Littorina fabalis</i>	ABE1	190	6.98 \pm 0.67	7.60 \pm 0.78	0.28	0.64	0.62	0.412
	ABE2	292	6.63 \pm 0.81	7.42 \pm 0.97	0.71	0.37	0.79	0.761
<i>L. littorea</i>	LAN	88	19.5 \pm 2.05	19.2 \pm 2.87	-1.1	1.2	-0.3	0.375
<i>L. saxatilis</i> _{crab}	SAL1	44	11.5 \pm 1.21	12.0 \pm 1.17	0.7	0.9	0.5	0.48
	SAL2	46	11.2 \pm 1.39	12.1 \pm 1.77	0.5	1.2	0.9	0.21
	ANG	44	10.1 \pm 1.04	10.7 \pm 1.01	0.8	1.1	0.6	0.41
	LAN	96	10.6 \pm 1.31	10.8 \pm 1.54	-0.9	1.4	0.2	0.546
<i>L. saxatilis</i> _{wave}	SAL1	76	5.5 \pm 1.44	6.2 \pm 1.06	1	-0.9	0.7	0.45
	SAL2	76	4.7 \pm 0.91	5.6 \pm 1.05	0.6	-0.1	0.9	0.53

Dimorphism= population $Z_{\text{female}} - Z_{\text{male}}$; SS_{Ufemale} = mated $Z_{\text{female}} - \text{population } Z_{\text{female}}$; Bias= mated $Z_{\text{female}} - Z_{\text{male}}$. N is the sample size. Dimorphism and female sexual selection ($SS_{\text{♀♀}}$) are based on crude measurements (unstandardized; see standardized values in Ng et al. (2019). Bias (B) was estimated as the mated female mean size minus male mean size. C_{rough} is a mate choice estimate based on the one sex positive FND function (see Fernández-Meirama et al. 2017a).

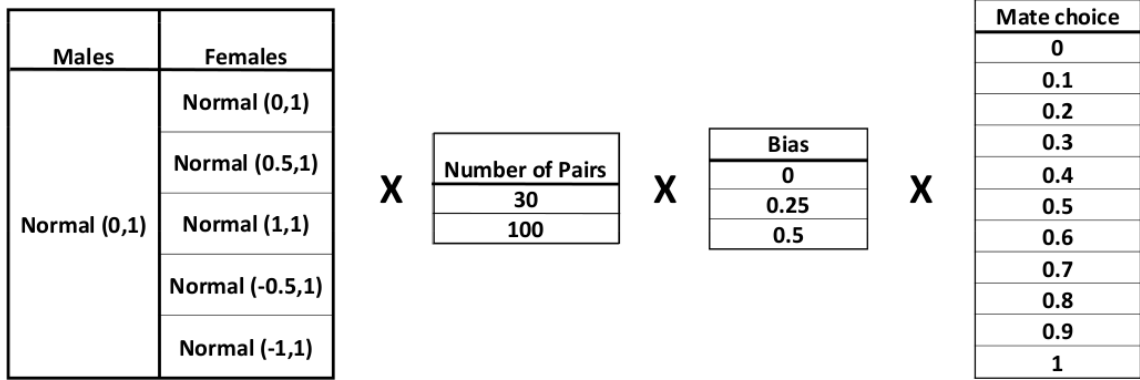


Figure 1

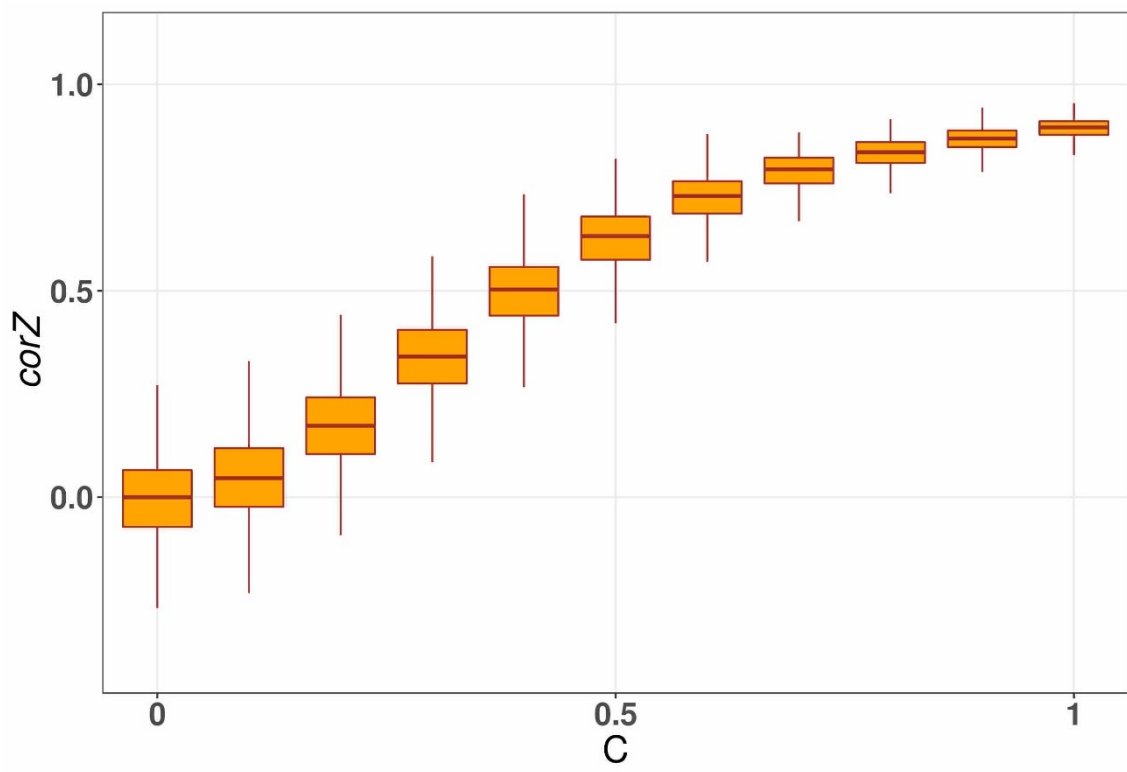


Figure 2

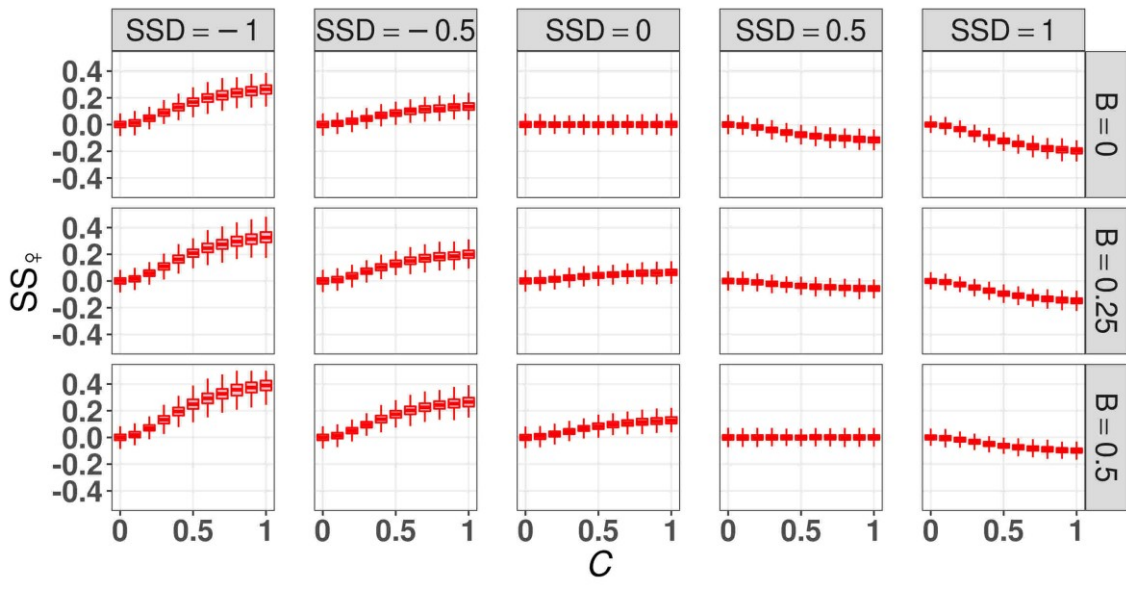


Figure 3

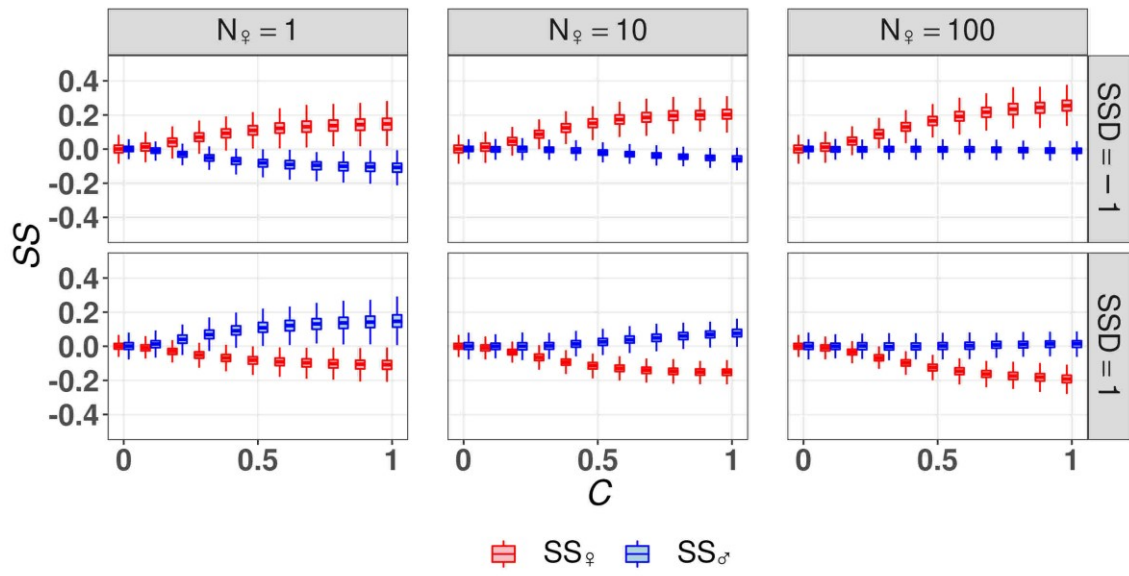


Figure 4

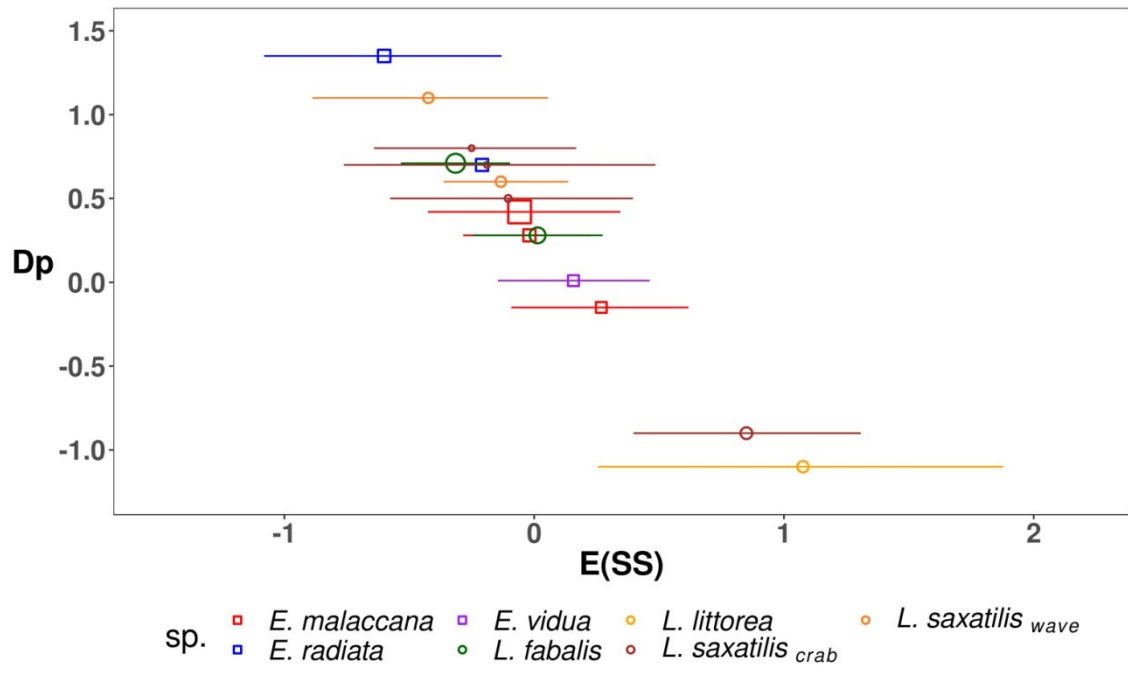


Figure 5

Tables and Figures Legends

Figure 1. Combination of scenarios used in simulations for the variables SSD, Number of mating pairs, Bias (B) and mate choice values (C).

Figure 2. Relationship between a priori mate choice (C) and a posteriori assortative mating among pairs (r coefficient, corZ) with no bias ($B=0$) or dimorphism (Dimorphism=0; see Figure S3 in online appendix for the same relationship in other scenarios). Pearson's correlation \pm SD = 0.91 ± 0.023 .

Figure 3: Sexual selection differentials for females ($SS_{\text{♀}}$) for the different levels of Bias (B, in rows) and sexual size dimorphism (SSD; in columns; range -1 to 1).

Figure 4. Sexual selection differentials for males ($SS_{\text{♂}}$; in blue) and females ($SS_{\text{♀}}$; in red) without bias ($B=0$) for two values of sexual size dimorphism (SSD) in rows. Different columns represent the mating cost (number of attempts a male can use before remaining unmated) to find a female partner (see text).

Figure 5. Relationship between expected female sexual selection $E(SS)$ and dimorphism (D_p) estimated from empirical population values through simulations. The shape of the points indicate the biological genus, and the colour the different species. The point size is proportional to the sample size of the real sample. Values of C and B were estimated from the mating data available in Ng et al (2019; see Table 1 and text). The relationship was qualitatively and quantitatively similar to the observed relationship obtained from empirical wild data (see Figure 3 from Ng et al., 2019).

Figure A1. In order to validate the previous simulations, we repeated part of the former scenarios using the program MateSim (Carvajal-Rodríguez, 2018). We first used an in-house C++ software to produce samples of 500 males and females following the scenarios outlined in Figure 1. Every scenario was replicated 100 times. The software MateSim ver 0.7 was used to generate mating pairs from these samples. Phenotypes were rescaled as described above. MateSim uses the FND functions described above (FND_{MALE} is obtained with the tag `-onechoosy 1`). Sexual selection and assortative mating were measured as described above. Results were summarized and analyzed in R (R core team, 2019). The figure shows the difference in sexual selection (SS) between the new C++ program used in this MS and the simulations ran in SimMate for the different combinations of bias and dimorphism.

Figure A2. Relationship between bias estimated from simulations $E(B)$ and bias estimated from empirical data ($B_{\text{estimated}}$; Table 1). The values of C and bias were estimated from wild mating pair data available in Ng et al (2019; see text). The shape of the points indicate the biological genus, and the colour the different

species. The point size is proportional to the sample size of the real data. The dotted line represents the case $E(B) = B$.

Figure A3. Relationship between Pearson's r coefficient and mate choice strength (C) using FND_{MALE} with different combinations of sexual size dimorphism (SSD; in columns) and Bias (B ; in rows).

Figure A4. Body size distribution in males (Z_{σ} blue area), females ($Z_{\text{♀}}$ red area) and the mated females after being chosen by males using the FND_{MALE} function (red bars) in four different scenarios. Dimorphism was always 0.5.

Appendix on Mate choice and sexual size dimorphism

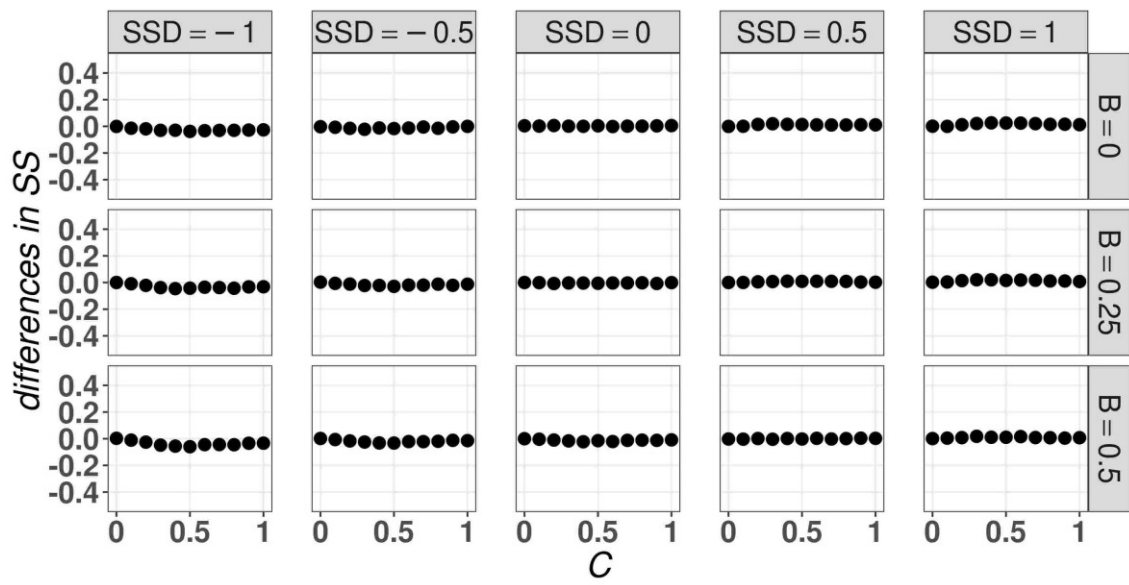


Figure A1

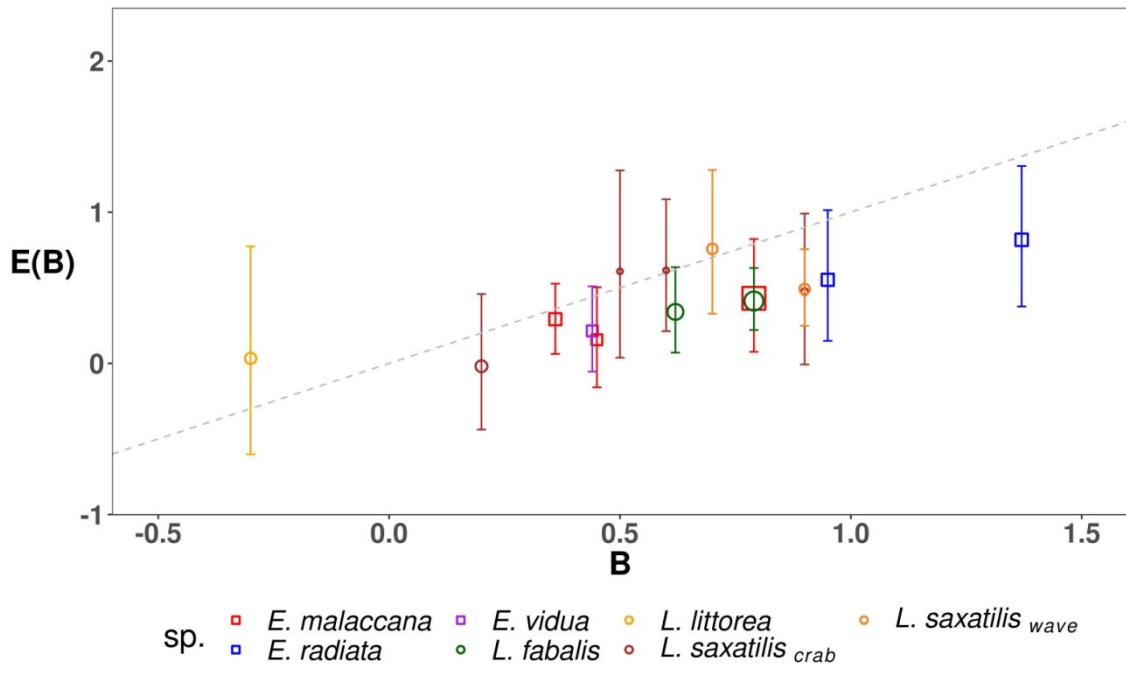


Figure A2

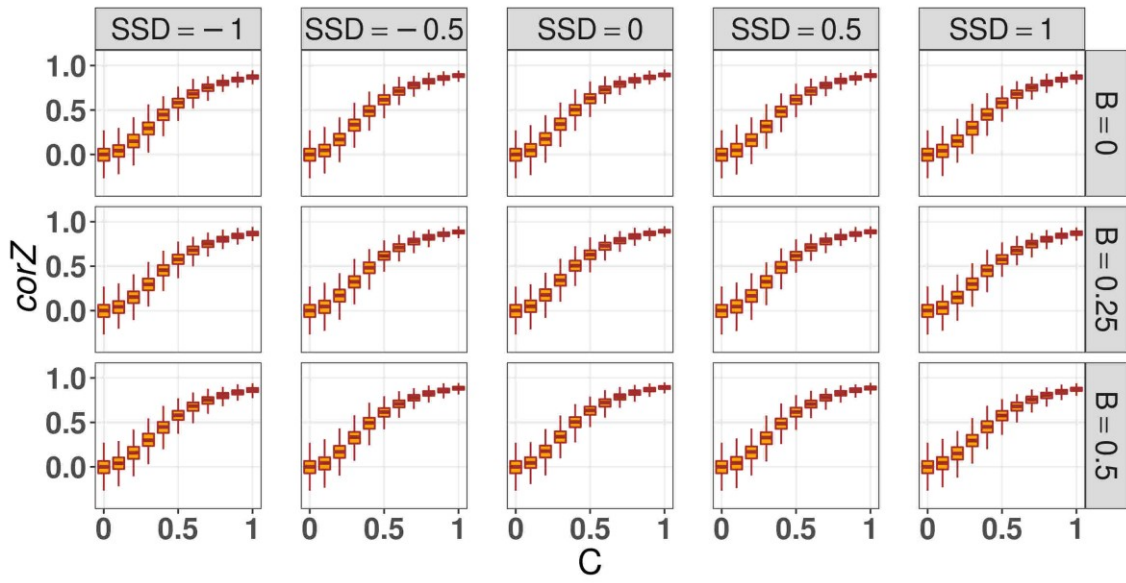


Figure A3

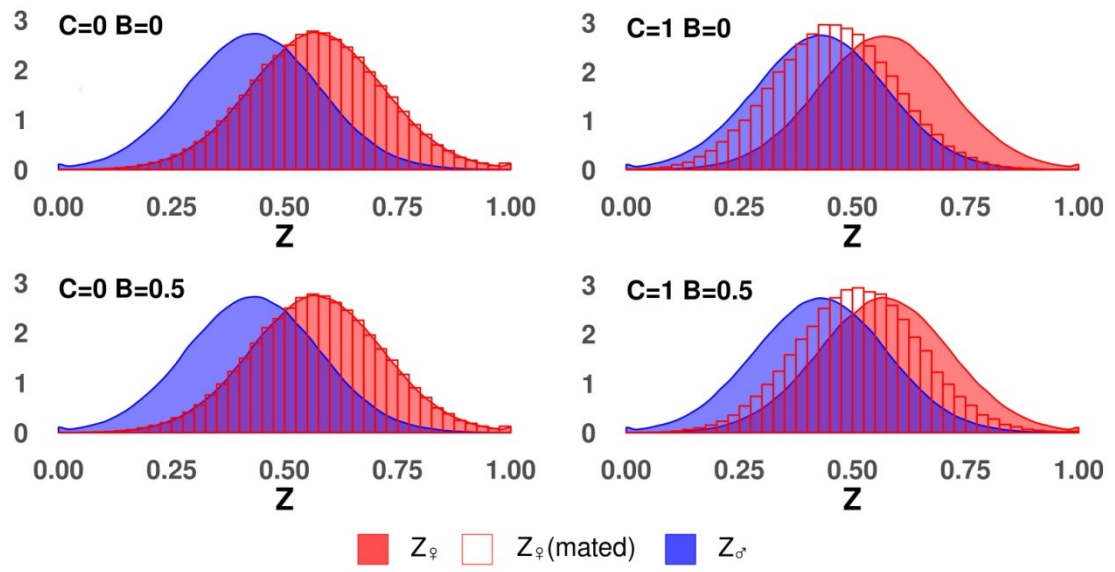


Figure A4