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

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Abstract

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

INTRODUCTION

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

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

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

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

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

MATERIALS AND METHODS

The model of mate choice

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

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

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

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

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

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

Estimating assortative mating, sexual selection and sexual size dimorphism

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

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

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

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

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

The simulated scenarios

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

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

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

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

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

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

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

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

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

Inferring processes from real data

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

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

Data availability

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

RESULTS

Mate choice and assortative mating

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

Effects of mate choice, SSD and bias on sexual selection

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

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

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

Inferring processes from empirical data

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

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

DISCUSSION

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

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

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

Theoretical considerations about mate choice

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

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

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

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

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

Inferring mate choice from wild data

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

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

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

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

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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_{female} - Z_{male} ; SS_{Ufemale} = mated Z_{female} - population Z_{female} ; Bias= mated Z_{female} - Z_{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_{f}) 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_{m} ; in blue) and females (SS_{f} ; 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 ($Z_{\text{♂}}$ 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