

# Multi-model inference of non-random mating from an information theoretic approach

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## ABSTRACT

Non-random mating has a significant impact on the evolution of organisms. Here, I developed a modelling framework for discrete traits (with any number of phenotypes) to explore different models connecting the non-random mating causes (mate competition and/or mate choice) and their consequences (sexual selection and/or assortative mating).

I derived the formulae for the maximum likelihood estimates of each model and used information criteria to perform multi-model inference. Simulation results showed a good performance of both model selection and parameter estimation. The methodology was applied to ecotypes data of the marine gastropod *Littorina saxatilis* from Galicia (Spain), to show that the mating pattern is better described by models with two parameters that involve both mate choice and competition, generating positive assortative mating plus female sexual selection. As far as I know, this is the first standardized methodology for model selection and multi-model inference of mating parameters for discrete traits. The advantages of this framework include the ability of setting up models from which the parameters connect causes, as mate competition and mate choice, with their outcome in the form of data patterns of sexual selection and assortative mating. For some models, the parameters may have a double effect i.e. they produce sexual selection and assortative mating, while for others there are separated parameters for one kind of pattern or another. From an empirical point of view, it is much easier to study patterns than processes and, for this reason, the causal mechanisms of sexual selection are not so well known as the patterns they produce. The goal of the present work is to propose a new tool that helps to distinguish among different alternative processes behind the observed mating pattern.

The full methodology was implemented in a software called InfoMating (available at <http://acraaj.webs6.uvigo.es/InfoMating/Infomating.htm>).

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## 1. Introduction

The concept of sexual selection is a key piece of modern evolutionary theory as it explains a great range of evolutionary patterns and diversity. Darwin (1871) originally defined sexual selection as competition between individuals of one sex to achieve matings with the other sex. Yet Darwin distinguished two general biological mechanisms of sexual selection: mate competition and mate choice (see Ng et al., 2019 and references therein). However, the concept of sexual selection has been controversial since its very beginning (reviewed in Andersson, 1994; Parker, 2014; Parker and Pizzari, 2015; Prum, 2012) and there is still disagreement on its actual definition (Fitze and Galliard, 2011), and even, its role as a key component of modern evolutionary biology has been challenged (Parker and Pizzari, 2015; Roughgarden et al., 2006; but see Shuker, 2010).

In this work, I adhere to the definition used in population genetics, where sexual selection is caused by processes of mate competition that may produce intrasexual selection, and/or processes of mate choice that may produce intersexual selection Casares et al., 1998; Endler, 1986; Lewontin et al., 1968; Ng et al., 2019; Rolán-Alvarez and Caballero, 2000.

The process of mate competition refers in the broad sense to access to matings by courtship, intrasexual aggression and/or competition for limited breeding resources (Andersson, 1994; Kokko et al., 2012; Wacker and Amundsen, 2014). These processes may generate a pattern of sexual selection (a change in frequencies of the trait under study) in the sex that competes (intrasexual selection Ng et al., 2019).

The process of mate choice occurs whenever the effects of traits expressed in one sex leads to non-random allocation of reproductive investment with members of the opposite sex (Edward, 2015). Choice may be mediated by phenotypic (sensorial or behavioural) properties that affect the propensity of individuals to mate with certain phenotypes (Jennions and Petrie, 1997). The

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observed pattern driven by mate choice can be a change in trait frequency in the other sex (intersexual selection) and/or a pattern of trait correlation between mates (assortative mating).

In sum, the evolutionary consequences of mate competition and mate choice are sexual selection and assortative mating. When the traits under study are discrete, the patterns of sexual selection and assortative mating are defined in terms of change in the phenotype frequencies, so that sexual selection corresponds to the observed difference in gene or phenotype frequencies in mated individuals with respect to population frequencies (Hartl and Clark, 1997; Rolán-Alvarez and Caballero, 2000). Similarly, assortative mating corresponds to the observed deviation from random mating within matings (Rolán-Alvarez and Caballero, 2000 and references therein).

Still, the relationships among these concepts are complex and can be approached from different perspectives (for extended details and alternative definitions the reader may consult Alonzo and Servedio, 2019; Arnold and Wade, 1984; Edward, 2015; Estévez et al., 2018; Futuyma and Kirkpatrick, 2017; Ng et al., 2019; Rolán-Alvarez and Caballero, 2000; Rolan-Alvarez et al., 2015b; Rosenthal, 2017).

In a previous work (Carvajal-Rodríguez, 2018b), the processes of mate competition and mate choice were modelled for discrete traits by means of the parameters  $m_{ij}$ , that represent the mutual mating propensity between a female of type  $i$  and a male  $j$ . Therefore, if A-type females prefer A-type males, this mate choice is modelled as a higher mutual mating propensity between these types as compared with the mutual mating propensity of the A females with other male types ( $m_{AA} > m_{AB}$ ). On the other hand, if B-type males mate more often than other males whatever the female, this mate competition is modelled by a higher marginal mating propensity of B-type males (see below).

By modelling the mating process as a differential mutual mating propensity among different types of mating pairs, it is possible to express the difference in mating phenotypes as the information gained due to non-random mating (Carvajal-Rodríguez, 2018b). This information gain is described in terms of the symmetric Kullback–Leibler divergence (Kullback, 1997). Describing random mating as the zero information model allows expressing the patterns obtained from mate choice and competition in terms of the information captured in the mutual mating propensity models.

Thus, the mating information-based framework provides a formal approach for developing a set of hypotheses about the causes (mate competition and mate choice) and their consequences (sexual selection and assortative mating). In addition, data-based evidence can be used for ranking each hypothesis and perform multi-model-based inference (Aho et al., 2014; Burnham et al., 2011; Link and Barker, 2006).

In the following sections I proceed as follows:

1- Given the population frequencies for some discrete trait I define the saturated mating model in terms of the mutual mating propensity parameters. Once the saturated model is defined I obtain the three necessary and sufficient conditions for random mating. Afterwards, by relaxing these conditions it is possible to generate models for which differential marginal mating propensity may produce female or male sexual selection without assortative mating, or on the contrary, models for which some mutual mating propensities represent mate choice that may produce assortative mating and frequency dependent sexual selection. I obtain the maximum likelihood estimates for the parameters of these models.

2- Relying on the previous section, it is possible to generate several mutual mating propensity models and apply information criteria for selecting the best candidate ones and estimating the mating parameter values based on the most supported models. I developed a software called InfoMating to do so.

3- Finally, I demonstrate the methodology by analysing simulated and real data.

## 2. Mutual mating propensity models

Consider a female trait with  $k_1$  different phenotypes and a male trait with  $k_2$  phenotypes, the total number of possible mating phenotypes is  $K = k_1 \times k_2$ . Let a sample have  $n'$  matings from which  $n'_{ij}$  correspond to  $i$ -type females that mated with  $j$ -type males so that  $\sum_i \sum_j n'_{ij} = n'$  with  $1 \leq i \leq k_1$  and  $1 \leq j \leq k_2$ . If the probability of the mating  $i \times j$  is  $q'_{ij}$ , then the logarithm of the multinomial likelihood function of the sample is

$$\ln L = C + \sum_{i=1}^{k_1} \sum_{j=1}^{k_2} n'_{ij} \ln(q'_{ij})$$

where  $C$  is the logarithm of the multinomial coefficient which is constant given the data. As it is well-known, the maximum likelihood estimator of the multinomial probability of the mating  $i \times j$  is  $n'_{ij}/n'$ .

### 2.1. Saturated non-random mating model $M_{sat}$

Let the population under study have  $n_{1i}$  females of type  $i$  from a total of  $n_1$  females and  $n_{2j}$  males of type  $j$  from a total of  $n_2$  males. Therefore, the population frequency of females of type  $i$  is  $p_{1i} = n_{1i}/n_1$  and the population frequency of males of type  $j$  is  $p_{2j} = n_{2j}/n_2$ .

The mating probability between types  $i$  and  $j$  can be expressed as  $q'_{ij} = m_{ij}q_{ij}$  (Carvajal-Rodríguez, 2018b) where  $q_{ij}$  is the product of the female and male population frequencies of each type ( $q_{ij} = p_{1i} \times p_{2j}$ ) and  $m_{ij} = m'_{ij}/M$ , where  $m'_{ij}$  is the mutual mating propensity for pair combination  $(i, j)$ , i.e. the expected number of matings given an encounter between females of type  $i$  and males of type  $j$ , and  $M$  is the mean mutual mating propensity across all mating combinations  $M = \sum_{i,j} q_{ij}m'_{ij}$ , so that  $\sum q'_{ij} = 1$ .

Under this multinomial model, the log-likelihood of the sample is

$$\ln L_{sat} = C + \sum_{i=1}^{k_1} \sum_{j=1}^{k_2} n'_{ij} \ln(m_{ij}q_{ij}) \quad (1)$$

This model is saturated ( $M_{sat}$ ) because it has as many parameters as independent mating-class frequencies,  $P_{sat} = K - 1$ . The female and male population frequencies,  $p_1$  and  $p_2$ , are either known or they need to be estimated from the data. Therefore, for model comparison, the population frequencies can be ignored when counting the number of parameters involved in each model.

The maximum likelihood estimate (MLE) of  $m_{ij}$  is  $(n'_{ij}/n')/q_{ij} = PTI_{i,j}$  where  $PTI_{i,j}$  is the pair total index i.e. the observed frequency of the mating class  $(i, j)$  divided by its expected frequency under random mating (Rolán-Alvarez and Caballero, 2000).

In this work I am interested in the estimation of the mutual mating propensity parameters (hereafter mutual-propensity parameters) for various competition and mate choice models. From that point of view, it is convenient to express the maximum likelihood estimator in a different way which I call  $\lambda$ -notation.

### 2.2. $\lambda$ -notation

Consider the non-normalized parameters  $m'_{ij}$  and recall that  $m_{ij} = m'_{ij}/M$ . The MLE of  $m'_{ij}$  under  $M_{sat}$  is simply  $M \times PTI_{i,j}$  i.e.  $M \times (n'_{ij}/n')/q_{ij}$  that can be conveniently rearranged as  $(n'_{ij}/q_{ij})/(n'/M)$ . Because the mating parameters are normalized, it is possible, without loss of generality, to set just one of the  $m'_{ij}$  to an arbitrary value of 1. Thus, if we set  $m'_{k_1k_2} = 1$  and note (details in

Appendix A) that in such case  $n'/M = n'_{k_1k_2}/q_{k_1k_2}$ . Therefore, the MLE of the parameters of the saturated model can be expressed as

$$\hat{m}'_{ij} = \frac{\lambda(m'_{ij})}{\lambda(1)}$$

where

$$\lambda(\theta) = \frac{\sum_{ij \in A} n'_{ij}}{\sum_{ij \in A} q_{ij}} \quad (2)$$

i.e., the function  $\lambda$  of a mating parameter  $\theta$  is the sum of the counts of all the mating classes in the set  $A = \{(i_1, j_1), \dots\}$  having mutual-propensity  $\theta$  divided by the sum of their expected frequencies under random mating.

Thus,  $\lambda(m'_{ij})$  expresses the sum of the observed matings with mutual-propensity  $m'_{ij}$  divided by the product of the population frequencies from each partner type. Similarly,  $\lambda(1)$  is simply  $\lambda(\theta = 1)$  i.e. it corresponds to the sum of the observed matings having unity mating parameter divided by the corresponding products of population frequencies.

As already mentioned, the most parameterized model is the saturated model that has  $K - 1$  parameters so, when divided by the mean mutual-propensity  $M$ , the estimates  $\lambda(m'_{ij})/(M\lambda(1))$  are the corresponding pair total indices (PTI<sub>ij</sub>, i.e. the observed frequency of the mating class  $(i, j)$  divided by its expected frequency under random mating).

The model  $M_{sat}$  is the most complex model that can be fitted to the available data. The principle of parsimony suggests to consider reduced special cases of this saturated model. Next, I computed the ML estimates of different classes of reduced models that require less parameters, beginning by the most reduced one which is the random mating model.

### 2.3. Random mating model $M_0$

The random model  $M_0$  corresponds to the simplest, most reduced model, which is nested within all others (it is a particular case of any other model) while it is not possible to derive any simplified version from it. When random mating occurs, the mating probability between types  $i$  and  $j$  is  $q'_{ij} = q_{ij} = p_{1i} \times p_{2j}$ . Under this model, the information would be zero (Carvajal-Rodríguez, 2018b). This zero-information model is a particular case of the saturated model when the mutual-propensities are equal for every mating phenotype. The number of independent mating parameters is  $P_0 = 0$ .

The log-likelihood of the sample of mating is

$$\ln L_0 = C + \sum_{i=1}^{k_1} \sum_{j=1}^{k_2} n'_{ij} \ln(q_{ij}) \quad (3)$$

Now, let us define the marginal propensity  $m_{Fem_i}$  for a female of type  $i$  as

$$m_{Fem_i} = \sum_{j=1}^{k_2} p_{2j} \frac{m'_{ij}}{M} = \sum_{j=1}^{k_2} p_{2j} m_{ij} \quad (4)$$

Similarly for a male of type  $j$

$$m_{Male_j} = \sum_{i=1}^{k_1} p_{1i} \frac{m'_{ij}}{M} = \sum_{i=1}^{k_1} p_{1i} m_{ij}$$

Then, the  $M_0$  model corresponds to  $M_{sat}$  subjected to the following restrictions (recall that  $k_1$  is the number of female types and  $k_2$  the number of the male types):

(i) Equal female marginals  $m_{Fem_i} = m_{Fem_j} \forall i, j \in k_1$  (5)

(ii) Equal male marginals:  $m_{Male_i} = m_{Male_j} \forall i, j \in k_2$

(iii) Multiplicativity:  $m_{ij} = m_{Fem_i} \times m_{Male_j} \forall i \in k_1$  and  $j \in k_2$

It is useful to express  $M_0$  in terms of these three restrictions because by relaxing some of them it is possible to define different classes of models. For example, a model with equal female marginal propensities and multiplicative mutual-propensities (conditions i and iii hold) but different male marginal propensities (relaxing ii), corresponds to a case with competition among males that may provoke a (intra)sexual selection pattern (see below).

Therefore, by relaxing some of the conditions in (5), it is possible to control the kind of causes that produce the different non-random mating patterns. In fact, there are three general classes of models that can be combined. The two first classes correspond to relaxing the first or second condition and involve mate competition in females or males, provoking female or male (intra)sexual selection, respectively. Provided that the third condition is maintained, these models cannot produce an assortative mating pattern (see below). The third class corresponds to relaxing the third condition and involves mate choice, which may provoke just assortative mating, or both assortative mating and sexual selection, the latter depending on the population phenotype frequencies (Fig. 1).

### 2.4. Mate competition models

These class of models correspond to relaxing the first and/or second conditions in  $M_0$  while maintaining the condition of multiplicativity (5)-iii. The maintenance of the third condition implies that the mutual-propensity of a mating pair  $(i, j)$  is the product of the marginal female ( $m_{Fem}$ ) and male ( $m_{Male}$ ) propensities. Under this condition there should be no deviation from random mating when comparing the observed and expected frequencies within matings and the assortative mating pattern should not be observed (Carvajal-Rodríguez, 2018b). I distinguished models that generate a sexual selection pattern in just one sex or in both.

#### 2.4.1. Intra-female competition

Relaxing condition (5)-i implies that at least one female marginal propensity, say female of type  $A$ , is different from the rest of female types i.e.  $m_{Fem_A} \neq m_{Fem_B}$  with  $A \neq B$ . On the other side, the marginal propensity of males should be the same which means that there is no intra-male competition, all male types mate at an equal rate.

Herein I use lowercase  $a$  or  $b$  for noting competition parameters and  $c$  for choice parameters. Therefore, a model with intra-female competition is obtained by defining every mutual-propensity involving a female of type  $i$ , by an absolute (unnormalized) mating parameter  $a_i$  as follows

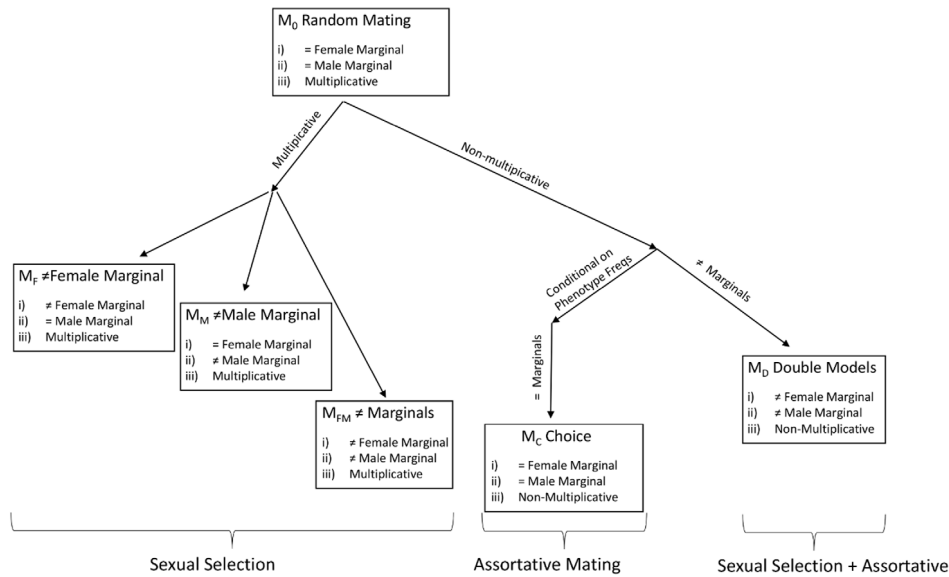
$$\begin{aligned} m'_{11} = m'_{12} = \dots = m'_{1k_2} &= a_1 \\ m'_{21} = m'_{22} = \dots = m'_{2k_2} &= a_2 \\ &\vdots \\ m'(k_1 - 1)_1 = m'_{k_12} = \dots = m'_{k_1k_2} &= a_{k_1-1} \\ m'_{k_11} = m'_{k_12} = \dots = m'_{k_1k_2} &= 1 \end{aligned} \quad (6)$$

with  $a_i > 0 \forall i$ .

Note that the relationships among the parameters will not be altered when dividing them by  $a_{k_1}$  so that  $a_{k_1} = 1$ . Under this model, there can be as much as  $k_1-1$  free mating parameters.

When computing the female and male marginal propensities (4) it is seen that

$$m_{Fem_1} = a_1/M; m_{Fem_2} = a_2/M \dots; m_{Fem_{k_1}} = 1/M$$



**Fig. 1.** Mating models defined by mate competition or mate choice, and their effect after relaxing some of the conditions imposed to the random mating model  $M_0$ .

$$m_{\text{Male}_1} = m_{\text{Male}_2} = m_{\text{Male}_3} = \dots = m_{\text{Male}_{k2}} = M/M = 1$$

where  $M$  is the mean mutual-propensity as defined above.

Model (6) has equal male marginal propensity and it is multiplicative. The MLE of the parameters is

$$\hat{a}_i = \frac{\lambda(a_i)}{\lambda(1)} \quad (7)$$

where  $\lambda(\theta)$  is defined as in (2). Thus,  $\lambda(a_i)$  expresses the sum of the observed matings having mutual-propensity  $a_i$ , divided by the sum of the product of the population frequencies from each partner type. Similarly,  $\lambda(1)$  corresponds to the sum of the observed matings having unity mating parameter divided by the sum of the corresponding products of population frequencies (details in Appendix A).

#### 2.4.2. Intra-male competition

Relaxing condition (5)-ii implies that at least one male marginal propensity, say male of type  $A$ , is different from the rest of male types i.e.  $m_{\text{Male}_A} \neq m_{\text{Male}_B}$  with  $A \neq B$ . On the other side, the marginal propensity of females should be the same which means that there is no intra-female competition, all female types mate at an equal rate. The corresponding model can be obtained just by interchanging rows with columns in (6). Noting the parameters as  $b_j$  instead of  $a_i$ , the maximum likelihood estimate is

$$\hat{b}_j = \frac{\lambda(b_j)}{\lambda(1)} \quad (8)$$

#### 2.4.3. Intra-female and male competition

By relaxing conditions (5)-(i) and (ii) the marginal propensities will be different within females and males. The corresponding model combines models (6) and (8) and has as much as  $(k_1 - 1) \times (k_2 - 1)$  parameters in the most parameterized case, and a minimum of two (female and male) for the less parameterized model, in order to maintain the multiplicativity condition (5)-(iii). This type of model may produce a pattern of sexual selection in both sexes without assortative mating. By notational convenience, I fix the category  $k_1$  in females and  $k_2$  in males as having unitary parameters. Therefore

$$m'_{ij} = a_i b_j, \quad i < k_1, j < k_2; \quad m'_{ik2} = a_i, \quad i < k_1; \\ m'_{k1j} = b_j; \quad j < k_2, \quad m'_{k1k2} = 1; \quad \text{with } a_i > 0, b_j > 0 \quad \forall i, j.$$

This model is multiplicative (see Appendix A) and the parameters MLE are

$$\hat{a}_i = \left( \frac{p_{1k1}}{p_{1i}} \right) \frac{\sum_{j=1}^{k2} n'_{ij}}{\sum_{j=1}^{k2} n'_{k1j}} = \frac{\lambda(a_i + \sum_j a_i b_j)}{\lambda_{\text{fem}}(1)} \quad (9)$$

$$\hat{b}_j = \left( \frac{p_{2k2}}{p_{2j}} \right) \frac{\sum_{i=1}^{k1} n'_{ij}}{\sum_{i=1}^{k1} n'_{ik2}} = \frac{\lambda(b_j + \sum_i a_i b_j)}{\lambda_{\text{male}}(1)}$$

where the lambda function  $\lambda(a_i + a_i b_1 + \dots + a_i b_j + \dots)$  is applied to the mutual-propensities that depend on the parameter  $a_i$ . Thus,  $\lambda(a_i + \sum_j a_i b_j)$  is the quotient between the number of observed mating phenotypes that depend on the parameter  $a_i$  (i.e.  $\sum_{1 \leq j \leq k2} n'_{ij}$ ) and the sum of their expected random mating frequencies (which is simply  $p_{1i}$ ). Correspondingly,  $\lambda_{\text{sex}}(1)$  is the quotient between the sum of cases that contribute with 1 to the mutual-propensity by the given sex (i.e.  $\sum_j n'_{k1j}$  for females) and the sum of the expected frequencies (which is  $p_{1k1}$  for females). Formulae (9) are similar to (7) and (8). Note that model in (9) becomes (7) by fixing every  $b_j$  as 1 while it becomes (8) by fixing every  $a_i$  as 1.

#### 2.5. Mate choice models

Mate choice models correspond to the class of non-multiplicative models, i.e. they can be obtained by relaxing the condition (5)-iii and may produce assortative mating patterns (positive or negative). If the female marginal propensities are equal and the same is true for the males (conditions (5)-i and ii hold) there would not be sexual selection neither in females nor males, and the model may produce only assortative mating patterns. However, this cannot be guaranteed in general because the occurrence of the sexual selection pattern is frequency dependent under non-multiplicative models (see below).

Consider a model where the unnormalized mutual-propensities are

$$m'_{ii} = c_i > 0 \quad \forall i \in \min\{k_1, k_2\} \quad \text{and} \quad m'_{ij} = 1 \quad \text{for } i \neq j.$$

Thus, the homotype ( $i \times i$ ) mutual-propensities are parameterized while the heterotype are not. This model is non-multiplicative in general, because the contribution of the type  $i$  to the mutual-propensity is distinct in  $m_{ii}$  that in  $m_{ij}$  or in  $m_{ji}$  (although with an



even number of types a multiplicative model can be obtained by setting  $m'_{ii} = 1/m'_{ij}$ .

By recalling the definition of marginal propensities in (4), the condition for equal female marginal  $m_{Fem_i} = m_{Fem_j}$  is

$$p_{2i}(c_i - 1) = p_{2j}(c_j - 1) \tag{10}$$

and in males

$$p_{1i}(c_i - 1) = p_{1j}(c_j - 1)$$

In general, depending on the conditions in (10), the mate choice models have double effect i.e. they produce assortative pattern jointly with sexual selection in at least one sex.

The maximum likelihood estimate for the model parameters is

$$\hat{c}_i = \frac{\lambda(c_i)}{\lambda(1)} \tag{11}$$

Note that the homotype mating parameter may imply higher mutual-propensity than the heterotype ( $c_i > 1$ , positive assortative mating) or vice versa, the homotype has lower mutual-propensity ( $c_i < 1$ , negative assortative). The number of different parameters ranges from 1 ( $c_1 = c_2 = \dots = c_i$ ) to  $H$ ; where  $H = \min\{k_1, k_2\}$  corresponds to the maximum possible number of different homotype matings.

It is also possible to define mate choice models with the heterotype mutual-propensities parameterized instead of the homotype ones (see Appendix A for details).

2.6. Models with mate competition and mate choice parameters

I have shown that mate choice models may generate both kinds of patterns, assortative mating and sexual selection, depending on the within sex population frequencies. While it is not possible to assure that the mate choice model produces no sexual selection, it is possible to combine the previous models to ensure that there are parameters directly linked to mate competition and parameters directly linked to mate choice. These combined models have the property that when the mate choice parameter is set to 1, there is only a known sexual selection effect caused by the competition parameter (female, male, or both). When the mate choice parameter is added, the assortative mating pattern appears and also, an extra effect of frequency-dependent sexual selection may be added to that of the original competition parameter.

2.6.1. Models with male competition and mate choice: independent parameters

Consider the model  $m'_{i1} = \alpha$ ;  $m'_{ii} = c$  for  $i \neq 1$  and  $m'_{ij} = 1$  otherwise; with  $i \leq k_1, j \leq k_2$ . An example of this kind of model can be seen in Fig. 2.

For the particular case of  $\alpha \neq 1, c = 1$ ; the model has within male competition that corresponds to the marginal propensity  $\alpha$  of the A-type male compared with the other males, so, a male sexual selection pattern may be generated. On the contrary, the female marginal propensities are equal so there is no female competition. Considering mate choice and the assortative mating pattern, when  $c = 1$  the model is multiplicative so assortative mating should not occur. In fact, in this case the pair sexual isolation statistics (PSI) are equal (see Appendix A for details) and the assortative mating is 0, i.e., the overall index of sexual isolation  $I_{PSI} = 0$  (by recalling the definition  $I_{PSI} = (4 \sum \text{PSI}_{ii} - \sum \text{PSI}_{ij}) / (4 \sum \text{PSI}_{ii} + \sum \text{PSI}_{ij})$  which is 0 if the PSI are equal) (Carvajal-Rodríguez, 2018b).

However, by taking  $c \neq 1$  a new component is added to the sexual selection pattern. The parameter  $c$  corresponds to mate choice and produces positive ( $c > 1$ ) or negative ( $c < 1$ ) assortative mating. The value of  $I_{PSI}$  is a function of the parameter

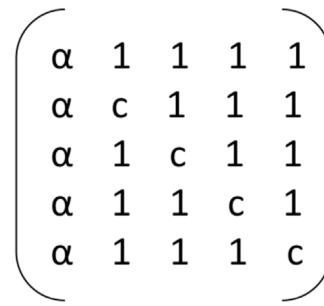


Fig. 2. An example of male competition and mate choice independent parameters model with 5 × 5 mating phenotypes.  $\alpha$  is the male competition parameter and  $c$  is the choice parameter. Rows are females, columns are males.

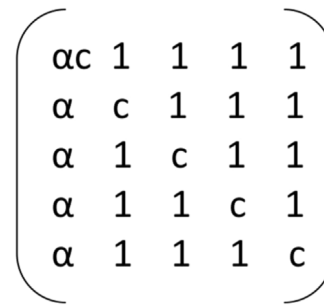


Fig. 3. An example of male competition and mate choice compound parameters model with 5 × 5 mating phenotypes.  $\alpha$  is the male competition parameter and  $c$  is the choice parameter. Rows are females, columns are males.

$c$  and the population frequencies. Female sexual selection may also emerge depending on the value of  $c$  and the population frequencies.

The MLEs of both parameters are

$$\hat{\alpha} = \frac{\lambda(\alpha)}{\lambda(1)}$$

$$\hat{c} = \frac{\lambda(c)}{\lambda(1)}$$

A variant of the above model can be generated by changing the  $c$  parameter from the main diagonal to the anti-diagonal. Similarly female sexual competition linked to the  $\alpha$ -parameter is obtained by transposing the matrix of the model.

2.6.2. Models with male competition and mate choice: compound parameters

Consider the model  $m'_{11} = c\alpha$ ;  $m'_{i1} = \alpha$  and  $m'_{ii} = c$  for  $i > 1$ ; and  $m'_{ij} = 1$  otherwise; with  $i \leq k_1, j \leq k_2$ . An example of this model can be seen in Fig. 3.

When  $c = 1$  the model is the same as the previous one. When  $c \neq 1$ , the mate choice parameter provokes an extra effect of sexual selection in males and females, plus assortative mating. The MLE of  $\alpha$  and  $c$  are

$$\hat{\alpha} = \frac{\sum_{i=1}^{k_1} n'_{i1} / (cq_{11} + \sum_{i>1} q_{ii})}{\lambda(1)} = \frac{\lambda_{c,11-}(\alpha)}{\lambda(1)}$$

where  $\lambda_{c,11-}(\alpha)$  indicates that for matings with parameter  $\alpha$ , the expected frequency indexed as 11 (i.e.  $q_{11}$ ) is weighted by  $c$ . Similarly,

$$\hat{c} = \frac{\sum_{i=1}^{k_1} n'_{ii} / (\alpha q_{11} + \sum_{i>1} q_{ii})}{\lambda(1)} = \frac{\lambda_{\alpha,11-(c)}}{\lambda(1)}$$

$$\begin{pmatrix} \alpha c_1 & 1 & 1 & 1 & 1 \\ \alpha & c_1 & 1 & 1 & 1 \\ \alpha & 1 & c_3 & 1 & 1 \\ \alpha & 1 & 1 & c_4 & 1 \\ \alpha & 1 & 1 & 1 & c_5 \end{pmatrix}$$

**Fig. 4.** Male sexual selection and mate choice compound model with  $5 \times 5$  mating phenotypes.  $\alpha$  is the male sexual selection parameter and  $c_k$ 's are the choice parameters with  $c_2 = c_1$ . Rows are females, columns are males.

where  $k = \min\{k_1, k_2\}$  and  $\lambda_{\alpha,11-(c)}$  indicates that for matings with mating parameter  $c$ , the expected frequency indexed as 11 is weighted by  $\alpha$ .

The above estimates are dependent one on each other, so, for obtaining the estimates of this compound parameter model I have used a numerical bounded Nelder–Mead simplex algorithm, with restriction  $\alpha > 0, c > 0$  (Gao and Han, 2012; Press, 2002; Singer and Singer, 2004).

**2.6.3. General model with male competition and mate choice parameters**

The general model with male competition and mate choice parameters is  $m'_{11} = c_1\alpha; m'_{ii} = \alpha$  and  $m'_{ij} = c_k$  for  $i > 1$ ; and  $m'_{ij} = 1$  otherwise; with  $i \leq k_1, j \leq k_2$ . A particular case of this model can be seen in Fig. 4.

Note that to distinguish the competition and mate choice parameters, it is necessary that at least one  $c_k$  parameter is equal to  $c_1$  (as in Figs. 3 and 4) or that  $c_1 = 1$  as in Fig. 2, otherwise the parameter for  $m_{11}$  does not distinguish competition and choice. Therefore, the model in Fig. 4 has  $H$  parameters with  $H = \min\{k_1, k_2\}$  from which,  $H - 1$  are choice parameters ( $c$ ) plus one male competition parameter  $\alpha$ . The MLE are

$$\hat{\alpha} = \frac{\sum_{i=1}^{k_1} n'_{i1}/(c_1q_{11} + \sum_{i>1} q_{i1})}{\lambda(1)} = \frac{\lambda_{c1,11-(\alpha)}}{\lambda(1)}$$

$$\hat{c}_1 = \frac{n'_{11}/(\alpha q_{11})}{\lambda(1)} = \frac{\lambda_{\alpha,11-(c_1)}}{\lambda(1)}$$

$$\hat{c}_{k>1} = \frac{n'_{kk}/(q_{kk})}{\lambda(1)} = \frac{\lambda(c_k)}{\lambda(1)}$$

The model parameters  $c_{k>1}$  can be estimated directly from the sample; on the contrary, the  $\alpha$  and  $c_1$  estimates are dependent on each other, so, for obtaining these estimates, I used a numerical bounded Nelder–Mead simplex algorithm with restriction  $\alpha > 0, c_1 > 0$  (Gao and Han, 2012; Press, 2002; Singer and Singer, 2004).

Previous models were simplified versions of the general model. For example, the model in Fig. 2 is the general model with restrictions  $c_1 = 1; c_2 = c_3 = \dots = c_k = c$ . Also, the model in Fig. 3 corresponds to  $c_1 = c_2 = c_3 = \dots = c_k = c$ . Another particular case that could be defined is  $c_1 = c; c_2 = c_3 = \dots = c_k = 1$ . In the latter, the MLE of the parameters can again be expressed as a quotient of lambdas similar to the compound parameter case

$$\hat{\alpha} = \frac{\lambda_{c1,11-(\alpha)}}{\lambda(1)}$$

$$\hat{c} = \frac{\lambda_{\alpha,11-(c)}}{\lambda(1)}$$

It is also possible to define another general model with the mate choice parameters in the anti-diagonal. Using the  $\lambda$  notation,

the estimates follow the same formulae as defined for the general model with the choice parameters in the main diagonal. Concerning models with female competition and mate choice, they are obtained just by transposing the matrices of the mating parameters.

**2.7. General double effect models**

The mating parameters  $m_{ij} = \theta_{ij}$  with the restriction that at least some are equal to one, permit to generate any particular model. In general, these models produce patterns of sexual selection and assortative mating with each parameter possibly linked to the occurrence of both (see Appendix A). The MLE is

$$\hat{\theta}_{ij} = \frac{\lambda(\theta_{ij})}{\lambda(1)} \tag{12}$$

The most parameterized model of this kind is the saturated, with  $K - 1$  parameters. In such case, as already mentioned, the estimates in (12) are the corresponding pair total indices (PTI).

All the above derived MLE formulae have been verified by numerical approximation using the bounded Nelder–Mead simplex algorithm (Gao and Han, 2012; Press, 2002; Singer and Singer, 2004). The set of described models jointly with their expected effects are summarized in Table 1.

**3. Model selection and multi-model inference**

Relying on the previous section, it would be possible to generate mate competition and mate choice models and, given a mating table, to apply some information criteria to select the best-fit candidates and estimating the mating parameter values based on the most supported models. Next, I briefly review the information criteria and model selection concepts and show how to apply them to perform model selection and multi-model inference among mate competition and mate choice models.

Information-based model selection and multi-model inference can be applied to describe uncertainty in a set of models to perform inference on the parameters of interest (Barker and Link, 2015; Burnham et al., 2011; Claeskens, 2016; Grueber et al., 2011). There are several information criteria at hand, although trusting on a single form of information criterion is unlikely to be universally successful (Aho et al., 2014; Brewer et al., 2016; Dziak et al., 2019; Liu and Yang, 2011; Vrieze, 2012). In the present work, two Kullback–Leibler divergence-based measures plus the so-called Bayesian information criterion are considered.

**3.1. Information criteria**

The Akaike information criterion (AIC) provides the link between the asymmetric Kullback–Leibler divergence, that measures the matching between two distributions (Kullback, 1997), and the maximized log-likelihood of a given model (Akaike, 1973). Here I use the sample-corrected version AICc, because it is asymptotically equivalent and may work better for small sample size

$$AIC_c = -2\ln(L) + 2P_m + (2P_m(P_m))/(n' - P_m - 1)$$

where  $L$  is the maximum likelihood of the model,  $P_m$  the total number of estimated mating parameters and  $n'$  is the number of matings in the sample.

Similarly, the KICc information criterion (Cavanaugh, 2004; Keeratibool, 2014) relies on the symmetric Kullback–Leibler divergence (Kullback, 1997). It seems adequate to consider the KICc criterion because the mating pattern obtained from the mutual-propensity models can be described by the informational

**Table 1**

Mutual mating propensity models as defined by different parameters in a case with two different phenotypic classes in each sex ( $k_1 = k_2 = 2$ ). The unnormalized  $m'_{ij}$  values not explicitly given are assumed to be 1.

Name (abbreviation)	Model	MLE	Effect
Random ( $M_0$ )	$m'_{ij} = 1 \forall i, j$		Random mating
Competition multiplicative models			
Female competition ( $S_{Fem-1P}$ )	$m'_{11} = m'_{12} = a$	$\hat{a} = \lambda(a)/\lambda(1)$	Fem sexual selection
Male competition ( $S_{Male-1P}$ )	$m'_{11} = m'_{21} = b$	$\hat{b} = \lambda(b)/\lambda(1)$	Male sexual selection
Female and male competition ( $S2-2P$ )	$m'_{11} = ab$ $m'_{12} = a$ $m'_{21} = b$	$\hat{a} = \lambda_{fem}(a)/\lambda_{fem}(1)$ $\hat{b} = \lambda_{male}(b)/\lambda_{male}(1)$	2-sex sexual selection
Mate choice models			
One-parameter (C-1P)	$m'_{11} = m'_{22} = c$	$\hat{c} = \lambda(c)/\lambda(1)$	Assortative mating + sex sel (freqdep)
General mate choice (C-HP)	$m'_{11} = c_1, m'_{22} = c_2$	$\hat{c}_i = \lambda(c_i)/\lambda(1)$	Assortative mating + sex sel (freqdep)
Competition and mate choice			
2 independent parameters ( $S_{FemC-2P}$ )	$m'_{ij} = \alpha \forall j$ ; $m'_{ij} = c; j > 1$	$\hat{\alpha} = \lambda(\alpha)/\lambda(1)$ $\hat{c} = \lambda(c)/\lambda(1)$	$\alpha$ -sexual selection in one sex + mate choice effect c-assortative mating
2 parameters (1 compound: $S_{FemC-2Pc}$ )	$m'_{11} = c\alpha; j > 1$ ; $m'_{ij} = \alpha; m'_{ij} = c$ ;	$\hat{\alpha} = \lambda_{c.11}(\alpha)/\lambda(1)$ $\hat{c} = \lambda_{\alpha.11}(c)/\lambda(1)$	$\alpha$ -sexual selection in one sex + mate choice effect c-assortative mating
H parameters (1 compound: $S_{FemC-HPc}$ )	$m'_{11} = c1\alpha; j > 1$ ; $m'_{ij} = \alpha; m'_{ij} = c_k$ ;	$\hat{\alpha} = \lambda_{c.1.11}(\alpha)/\lambda(1)$ $\hat{c}_1 = \lambda_{\alpha.11}(c_1)/\lambda(1)$ $\hat{c}_{k \neq 1} = \lambda(c_k)/\lambda(1)$	$\alpha$ -sexual selection in one sex + mate choice effect $c_k$ -assortative mating
General double models (D-xP)			
Saturated ( $M_{sat}$ )	$m'_{ij} = c_{ij}; m'_{k_1k_2} = 1$	$\hat{c}_i = \lambda(c_i)/\lambda(1)$	Assortative mating + sex sel (freq dep)

$k_1$ : number of female categories;  $k_2$ : number of male categories;  $H = \min\{k_1, k_2\}$ ; sexsel (freqdep): frequency dependent sexual selection.

flow from the mating frequencies, in the form of the symmetric Kullback–Leibler divergence (Carvajal-Rodríguez, 2018b) so,

$$KIC_c = -2\ln(L) + n'\ln(n'/(n' - P_m)) + P_2$$

with  $P_2 = n'[(n' - P_m)(2P_m + 3) - 2]/[(n' - P_m - 2)(n' - P_m)]$  Finally, the Bayesian information criterion (BIC Schwarz, 1978) permits an approximation to the Bayes factor applied for model comparison (Wagenmakers, 2007)

$$BIC = -2\ln(L) + P_m \ln(n')$$

### 3.2. Overdispersion

In the context of model selection, data overdispersion, i.e. greater observed variance than expected, could generate the selection of overly complex models. The simplest approach to estimate overdispersion is by computing a single variance inflation factor ( $v$ ). This inflation factor is the observed variation in the data divided by that expected under the model with the highest likelihood ( $M_c$ ), other than the saturated, among the proposed ones (Richards, 2008; Symonds and Moussalli, 2011). It can be asymptotically approximated by the deviance i.e. twice the difference between the log-likelihood of the saturated ( $M_{sat}$ ) and the  $M_c$  model, divided by the difference in the number of parameters ( $P_{Msat} - P_{Mc}$ ) between both models

$$v = 2[\ln(L_{Msat}) - \ln(L_{Mc})]/df$$

where  $df = P_{Msat} - P_{Mc}$ .

We rely on the deviance  $v$  as an approximation of the inflation factor. If  $1 \leq v \leq 4$  this indicates overdispersion, while if higher than 4–6 this may indicate poor model structure and the construction of the set of models should be reconsidered (Burnham and Anderson, 2002). For  $v$  values around 1 to 4, quasi-likelihood theory provides a way to analyse over dispersed data (Anderson et al., 1994; Richards, 2008). The quasi-likelihood is the likelihood

divided by an estimate of  $v$ . The quasi-likelihood version of the various information criteria, namely QAICc, QKIC<sub>c</sub> (Kim et al., 2014) and QBIC, is obtained simply by replacing the likelihood with the quasi-likelihood in the corresponding formula. In such cases, the number of parameters is increased by one and the model variance is multiplied by  $v$  (see below). When the quasi-likelihood version is used, it must be done for all models and criteria.

### 3.3. Model weights

Let IC be any information criterion. For a particular criterion and for any set of  $R$  models there is a minimum criterion value e.g. AIC<sub>min</sub>, BIC<sub>min</sub>, etc. Thus, the models can be ranked regarding the difference with that minimum

$$\Delta_i = IC_i - IC_{min}, \text{ for } i = 1, 2, \dots, R$$

where  $IC_i$  refers to any specific information criterion for the model  $i$ .

Models can also be ranked by their weights from higher to lower. The weight  $w_i$  refers to the strength of evidence for that model (Burnham et al., 2011; Claeskens, 2016)

$$w_i = l_i / \sum l_j \text{ for } j = 1, 2, \dots, R$$

where  $l_i = \exp(-0.5\Delta_i)$  is the relative likelihood of each model given the data.

### 3.4. Multi-model inference

Multi-model-based inference estimates the parameters of interest based on a group of models instead of on a best-fit single model (Burnham and Anderson, 2002; Burnham et al., 2011; Symonds and Moussalli, 2011). The multi-model inference is performed as a model averaged prediction for the parameters that are variables in the best model.

In our modelling framework and before performing the average of the estimated parameter values, the different models should be translated to the same scale of mutual-propensity. For example, a model like  $m'_{11} = 2, m'_{12} = m'_{21} = m'_{22} = 1$ , is not in the same scale that  $m'_{11} = 2, m'_{12} = m'_{21} = m'_{22} = 0.5$ . Without loss of generality, the latter can be transformed into an equivalent model  $m'_{11} = 4, m'_{12} = m'_{21} = m'_{22} = 1$ , which is now in the same scale as the first model.

The averaged parameter estimates were computed as a weighted mean where the weights are the strength of evidence for each model as obtained under a given information criterion. The parameters were averaged only over the models for which they appear as a variable. Because the weights need to sum up to 1, it was necessary renormalize them by dividing by the accumulated weight in the confidence subset.

Therefore, for each parameter  $m$  included in the confidence subset  $R_s$ , the average was computed as

$$\hat{m} = \frac{\sum_i^{R_s} w_i \hat{m}_i}{\sum_i^{R_s} w_i}$$

This way of performing the model averaged prediction is called natural averaging (Symonds and Moussalli, 2011).

Finally, the reliability of each parameter estimate was measured as the unconditional standard error

$$Se(\hat{m}) = \sum_i^{R_s} w_i \sqrt{vV(\hat{m}_i) + (\hat{m}_i - \hat{m})^2}$$

where  $V(\hat{m}_i) = V(m_i | \text{model } i) = V(q') = q'(1-q')/n'$  is the model standard error squared and  $v$  is the variance inflation factor.

The use of the sum of weights to estimate variable importance in regression models has been criticized because of multicollinearity among the predictor variables and the imprecision of the weight measures (Cade, 2015; Galipaud et al., 2014, 2017). However, the mutual-propensity parameters do not belong to a regression model and their average is performed in the same scale and with comparable units. Therefore, under the mutual mating propensity setting, the multi-model inference would work well as it was confirmed by Monte Carlo simulation (next section).

## 4. Simulations

### 4.1. Polygamous species (sampling with replacement)

To test how well the above methodology is able to distinguish among the different classes of models and estimate the mating parameters, I used the sampling with replacement algorithm in the program MateSim (Carvajal-Rodríguez, 2018a) to generate mating tables by Monte Carlo simulation (see Appendix B for detailed explanation).

The simulated cases correspond to one-sex competition and mate choice models. The resulting mating tables were consequence of the mating system and the sampling process, and consisted in two types of information (Fig. B.1 in Appendix B). First, the population frequencies (pre-mating individuals) which were generated randomly for each simulation run. Second, the sample of 500 mating pairs ( $n' = 500$ ) for a hypothetical trait with two classes at each sex. Because the simulated species had large population size ( $n = 10\,000$ ) the mating process was represented as a sampling with replacement, and the population frequencies were constant over the mating season. The minimum phenotype frequency (MPF) allowed was 0.1.

Five different model cases were simulated, namely random mating with mutual-propensities  $m'_{11} = m'_{22} = m'_{12} = m'_{21} = 1$  ( $M_0$  in Table 2), female competition ( $\alpha = 2$ ) and mate choice ( $c = 3$ ) with independent parameters  $m'_{11} = m'_{12} = 2, m'_{22} = 3,$

$m'_{21} = 1$  (SfC Table 2), and with compound parameters  $m'_{11} = 6, m'_{12} = 2, m'_{22} = 3, m'_{21} = 1$  (SfCc Table 2), and male competition ( $\alpha = 2$ ) and mate choice ( $c = 3$ ) with independent parameters  $m'_{11} = m'_{21} = 2, m'_{22} = 3, m'_{12} = 1$  (SmC Table 2), and with compound parameters  $m'_{11} = 6, m'_{21} = 2, m'_{22} = 3, m'_{12} = 1$  (SmCc Table 2). Each case was simulated 1000 times.

For each simulation run, and given the normalized mutual-propensities  $m_{ij}$ , the number of occurrences for each mating class  $i \times j$  was obtained as

$$Q(i,j) = n' \times p_{1i} \times p_{2j} \times m_{ij}$$

where  $n'$  is the sample size,  $p_{1i}$  is the female population frequency for the phenotype  $i$ ,  $p_{2j}$  is the male population frequency for the phenotype  $j$ .

Once the mating tables were obtained I proceeded with the multi-model inference analysis using InfoMating. Note that there were 1000 different tables for each simulated case so, in the simulation study, it is better to consider the mean multi-model estimates instead of the full list of analysed models (which would imply 1000 lists for each simulated case). Also, it is worth noting that with real data, the exactly true model is not necessarily included in the set of assayed models and so, it is important to evaluate the accuracy of the multi-model parameter estimates because, if the parameter estimates are correct, the model that would arise from that estimates and the set of most supported candidate models must be a good guess of the true one.

The sequence of analyses was as follows. For each mating table, InfoMating generates a set of 17 models (see the simulation models in the link from the data accessibility section), from the simplest random model  $M_0$  to the saturated  $M_{\text{sat}}$ , including mate competition and choice models with one or two parameters (see all the types in Table 1). Then, the program computes the information criteria for each model and performs the multi-model inference as explained in the previous section. Thus, for each of the 5 simulated cases, 1000 parameter estimates were obtained, and their average and standard error computed (Table 2).

It can be appreciated that the random mating was perfectly estimated by the three IC methods. The competition plus mate choice parameter estimates were fairly good under the three criteria. The estimates were slightly better under AICc and slightly less accurate under BIC.

The whole simulation process was repeated using a small sample size ( $n' = 50$  matings) and the results were qualitatively similar. However, the parameter estimates tended to be low-biased possibly because the power to detect deviations from random mating was low (see Table C.1 in Appendix C).

### 4.2. Monogamous species (sampling without replacement)

For monogamous species, the mating process is without replacement (from the point of view of the available phenotypes) and can be represented via mass-encounters (Carvajal-Rodríguez, 2018a; Gimelfarb, 1988). The pattern obtained under the mass-encounter monogamous scenario (when the population size is large) was qualitatively similar to the polygamous species. However, there was less power to detect deviation from random mating and so the estimates were low-biased, especially in the case of the compound parameter. Regarding sample size, it seems that the estimation was not very much affected (see Tables C.2 and C.3 in Appendix C).

Not surprisingly, the case of monogamous species with small population size ( $N = 200$ ) was the worst scenario for multi-model estimation under the assumption of constant population phenotype frequencies (see Table C.4 in Appendix C). Under this case and when most of the adults were involved in the mating



**Table 2**

Average ( $\pm$  standard error) parameter estimates under sample size 500 for a polygamous species with large population size ( $N = 10\,000$ ).

Model		$m'_{11}$	$m'_{12}$	$m_{21}$	$m_{22}$
$M_0$	Expected	1	1	1	1
	AICc	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$
	KICc	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$
	BIC	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$
SfC	Expected	2	2	1	3
	AICc	$1.94 \pm 0.0017$	$1.99 \pm 0.0009$	$1.0 \pm 0.0000$	$2.95 \pm 0.0025$
	KICc	$1.94 \pm 0.0024$	$1.99 \pm 0.0020$	$1.0 \pm 0.0000$	$2.95 \pm 0.0029$
	BIC	$1.90 \pm 0.0060$	$1.94 \pm 0.006$	$1.0 \pm 0.0000$	$2.90 \pm 0.0074$
SfCc	Expected	6	2	1	3
	AICc	$5.93 \pm 0.0044$	$2.0 \pm 0.0001$	$1.0 \pm 0.0000$	$2.97 \pm 0.0027$
	KICc	$5.92 \pm 0.0051$	$2.0 \pm 0.0001$	$1.0 \pm 0.0000$	$2.97 \pm 0.0028$
	BIC	$5.87 \pm 0.0086$	$2.0 \pm 0.0017$	$1.0 \pm 0.0000$	$2.96 \pm 0.0044$
SmC	Expected	2	1	2	3
	AICc	$1.94 \pm 0.0020$	$1.0 \pm 0.0000$	$1.99 \pm 0.0013$	$2.94 \pm 0.0030$
	KICc	$1.93 \pm 0.0032$	$1.0 \pm 0.0000$	$1.98 \pm 0.0029$	$2.93 \pm 0.0037$
	BIC	$1.90 \pm 0.0062$	$1.00 \pm 0.0000$	$1.93 \pm 0.0065$	$2.88 \pm 0.0080$
SmCc	Expected	6	1	2	3
	AICc	$5.93 \pm 0.0046$	$1.0 \pm 0.0000$	$2.0 \pm 0.0001$	$2.97 \pm 0.0029$
	KICc	$5.92 \pm 0.0052$	$1.0 \pm 0.0000$	$2.0 \pm 0.0001$	$2.97 \pm 0.0029$
	BIC	$5.87 \pm 0.0085$	$1.0 \pm 0.0000$	$2.0 \pm 0.0010$	$2.97 \pm 0.0037$

$M_0$ : Random mating model. SfC: female competition and mate choice with independent parameters. SfCc: female competition and mate choice with compound parameters. SmC: male competition and mate choice with independent parameters. SmCc: male competition and mate choice with compound parameters.

process (mating sample size = 100), the change in the population phenotype frequencies during the breeding season significantly affected the observed non-random mating patterns. Only when the deviation from random mating is as large as with the compound effect of choice and competition, the estimated mutual-propensities provided some information (SfCc in Table C.4).

## 5. Example of application

*Littorina saxatilis* is a marine gastropod mollusc adapted to different shore habitats in Galician rocky shores. There are two different ecotypes, an exposed-to-wave (smooth un-banded, SU), and a non-exposed (rough banded, RB) ecotype. Several experimental studies have shown that these ecotypes have evolved local adaptation at small spatial scale. For example, stronger waves on the lower shore may provoke that the SU ecotype becomes sexually mature at smaller size than the upper-shore (RB) ecotype. In addition, in some areas of the mid-shore habitat, the two ecotypes occasionally mate, producing apparently fertile intermediate morphological forms that are called hybrids (HY) (Rolan-Alvarez et al., 2015a).

Sexual isolation (positive assortative mating) between RB and SU morphs was observed in wild mating pairs in the mid-shore zone, likewise within-morph size-assortative mating in all shore levels (Cruz et al., 2001). It is assumed that the size is the key trait causing the increase of sexual isolation in this model system, being the males the choosy sex in this species (Rolan-Alvarez, 2007).

Here, I reanalyzed a *L. saxatilis* data set (Cruz et al., 2001) to estimate the mutual-propensity parameters between the RB, SU and HY morphs in the mid-shore habitat. In the original study, the authors analysed a hybrid zone encompassing 30 km of coast in Galicia (NW Spain) with two sampling locations (Centinela and Senin) and seasons (autumn and summer). Mating pairs were collected jointly with the 15 nearest non-mating individuals. The classification of morphs was made by considering as pure morphs those snails that had their shell ridged and banded (RB morph) or smooth and unbanded (SU morph). The hybrids (HY) were

**Table 3**

The population frequencies by sex and the sample of matings from Cruz et al. (2001) data.

	Total	RB	HY	SU
Female freqs	1254	0.22	0.11	0.67
Male freqs	1080	0.26	0.12	0.62
Matings		Males		
		RB	HY	SU
Females	RB	19	9	13
	HY	6	4	10
	SU	6	7	80

those snails that had a complete set of bands but lacked ridges, or vice versa, or those that, having both ridges and bands, had at least two incomplete bands (see details in Cruz et al., 2001). In the present reanalysis, I considered the pooled data of the two sampling locations and seasons (Table 3).

First, I computed the information partition (Carvajal-Rodríguez, 2018b) and the Chi-square test was significant only for the assortative mating component ( $J_{PSI}$   $p$ -value  $< 0.0000001$ ).

Second, I proceeded with the model estimation and initially assayed only the subset of models with male and/or female mate competition plus the saturated ( $M_{sat}$ ) and random mating ( $M_0$ ) models (see the empirical models in the link from the data accessibility section). The estimate of overdispersion was high (7.20) which points to poor model structure rather than an excess of variation in the data. The three information criteria gave similar output with the  $M_0$  as the best fit model. The multi-model estimates of the mutual-propensities were just one in every case as expected from random mating. Because in the simulation study, the AICc criterion gave the best estimates I will rely on this criterion from now on.

The next step was to study only models with choice parameter plus the saturated ( $M_{sat}$ ) and random mating ( $M_0$ ) models. The overdispersion was 4.65 that still indicates somewhat poor model structure. The best fit model was a choice model with one parameter. The multi-model inference gave a clear pattern of positive assortative mating, that was higher for the RB  $\times$  RB

	RB	HY	SU
RB	2	2	1
HY	1	2	1
SU	0.2	1	1

**Fig. 5.** Model D-2P-Rep3: Double two parameter model with three repetitions of the  $c_2$  parameter ( $c_1 = 0.2$ ,  $c_2 = 2$ ) producing female and male sexual selection plus positive assortative mating.

mating ( $m'_{RBRB} = 3$ ), intermediate for  $HY \times HY$  ( $m'_{HYHY} = 2.3$ ) and slightly lower for  $SU \times SU$  ( $m'_{SUSU} = 2$ ).

Then, I considered jointly the previous competition and choice models and added new ones having separated competition and choice parameters. The overdispersion was 3.4 that is an acceptable value for multinomial models and can be corrected by using quasi-likelihoods (see the overdispersion section above). Now, the best fit was a compound parameter model with female competition and choice. The estimates from this model were a RB female competition of  $\alpha = 1.7$  and choice  $c = 2.4$ . The multi-model estimates gave positive assortative mating,  $m'_{RBRB} = 3$ ,  $m'_{HYHY} = 3$ ,  $m'_{SUSU} = 2$  and sexual selection favouring RB females.

Finally, I considered all the previous models plus models having parameters with double effect (i.e. one parameter may generate both sexual selection and assortative mating patterns). This implies a total of 35 models including  $M_0$  and  $M_{sat}$  (these models can be consulted from the empirical models link in the data accessibility section). The overdispersion was 2.5. The best model was the same for the three criteria and it was a double effect model with 2 parameters,  $c_1 = 0.2$  and  $c_2 = 2$ , distributed as indicated in Fig. 5. Approximately, the same model was obtained using the multi-model estimates.

It is also possible to focus only on the models with separated parameters for competition and choice. The best fit model from this subgroup involves female competition. Recall that in *Littorina saxatilis* the choosy sex are the males, so I considered that the competitive advantage from the side of the females is explained by the males preferring a given kind of females. The best fit model is  $S_{Fem}C-2Pc$  (see Table 1) with RB female competitive advantage of 1.7 more times matings than the other females and a choice parameter of 2.4. The qualitative pattern obtained from these models is similar to that in Fig. 5; the RB females (first row) are preferred and there is a choice for within ecotype mating. The combination of competition and choice explains that the mating  $RB \times RB$  is preferred by RB males (first column in Fig. 5), the matings  $RB \times HY$  and  $HY \times HY$  are preferred by HY males (second column in Fig. 5), and finally, it seems that the SU males (third column in Fig. 5) do not discriminate between female ecotypes.

## 6. Discussion

### 6.1. Simulations

have simulated mating tables corresponding to random mating, mate competition and mate choice models. The random mating pattern was accurately estimated in all runs. For the other models, the competition and choice parameters were estimated quite accurately when the mating system resembles a sampling with replacement. Not surprisingly, BIC was slightly more conservative, while AICc presented slightly more accurate estimates in most cases. The KICc criterion performed similar to the best AICc and BIC cases. In general, the estimation was accurate and

even in the cases with extreme phenotypic frequencies, the mean estimates were closer to the real value than to random mating.

The proposed multi-model approach is based on a previous formalization showing that the mating distribution caused by mate competition and/or choice can be expressed as a gain in information with respect to random mating (Carvajal-Rodríguez, 2018b). In that work, the population phenotype frequencies had been considered constant during the breeding season and only required mating tables for detecting the effects of non-random mating. Hence, to correctly identify the processes that produce the patterns of sexual selection and assortative mating, it is assumed that the encounters occur at random, i.e. the encounter between two phenotypes depends on the population phenotypic distribution, and that the mating pattern is the product of the phenotypic distribution of the population and the individual preferences (Carvajal-Rodríguez, 2018a). Therefore, the availability of phenotypes should not be affected by the matings that have already occurred, as expected for polygamous species, or even for monogamous species, when the number of available individuals is higher than the mating pairs within each type of females and males.

The above assumption is likely to be violated in the case of monogamous species with low population size, or even in large population sizes with local competition for mates (if the number of individuals in the patches is low) and/or spatial-temporal constraints. In such cases, the mating process resembles a sampling without replacement and the population phenotype frequencies may be altered during the reproductive season so that the sexual selection and assortative mating patterns would be more difficult to detect. The non-random mating information formalism was generalized and the constant frequencies restriction alleviated in a posterior work (Carvajal-Rodríguez, 2019). As before, the non-random mating information can be partitioned into sexual selection, assortative mating (sexual isolation) and their mixed effect. However, under this generalization the connection between the mating behaviour, as captured by the mutual propensities, and the data pattern in the mating table was not always maintained if the sampling had not been made at each mating round, and therefore the present multimodel inference formalization could be less accurate. Yet, it was shown that in the assortative mating scenario, the constant indices still perform well under variable population frequencies and so, the multimodel estimation based on that indices, should still work (Carvajal-Rodríguez, 2019). Actually, the simulations (see Appendix C) showed that the performance of the multi-model inference is affected by the sampling and the mating system (polygamous or monogamous) but it is still quite robust for detecting non-random mating in the parameter values except in the worst scenario of monogamous species with small population sizes.

### 6.2. General

The advantages of model selection and multi-model inference in evolutionary ecology has been widely discussed, jointly with the pros and cons of applying any information criteria (Aho et al., 2014, 2017; Barker and Link, 2015; Burnham et al., 2011; Dziak et al., 2019; Link and Barker, 2006) or the reliability of the obtained estimates (Cade, 2015; Galipaud et al., 2014, 2017; Giam and Olden, 2016).

Multi-model inference has been however, rarely utilized to study the mating patterns that may emerge from mate choice and mate competition. Here, by developing general models that incorporate competition and mate choice, and providing their maximum likelihood estimates, I am proposing a standardized methodology for model selection and multi-model inference of the mating parameters producing the sexual selection and assortative mating patterns.

The set of *a priori* models permits to perform an *a posteriori* quantification of the data-based evidence and provide confidence sets on plausible non-trivial models while allowing for multi-model inference of the parameter values. The approach was implemented by allowing three different information criteria. Under the scenarios assayed, they performed similarly for simulated and real data.

Regarding the methodology, it is worth noting that although the mating tables require at least two phenotypes by sex ( $2 \times 2$  dimensions or higher) for fitting mate competition and mate choice models, the proposed approach can still be applied if some sex, say females, have only one phenotypic class. In this case, we just need to duplicate the row (see Fig. D.1 in Appendix D). Obviously, there cannot be any assortative pattern and sexual selection can only be measured in the sex with more than one phenotypic class.

The statistical tools developed in this work have been also applied to empirical data. Previous studies in the Galician *L. saxatilis* hybrid zone showed that mate choice favours within-morph pairs (reviewed in Rolán-Alvarez, 2007). The estimates obtained by multi-model inference support the positive assortative mating for the ecotype. In addition, another result emerged from the analysis: The RB females are preferred in general i.e. RB male with SU female has less mutual-propensity than SU male with RB female ( $m_{\text{SURB}} < m_{\text{RBSU}}$ ). This pattern may be favoured by the physical difficulty for the mating involving bigger RB males with the smaller SU females, and could be related with the somehow more frequent occurrence of mating pairs having females bigger than males (a typical trend in gastropods, E. Rolán-Alvarez personal communication). Besides the mating pattern depicted by the multi-model approach, the estimates of the mutual-propensities were also obtained. Testing the reliability of these estimates is, however, out of the scope of the present manuscript, and it was left for future work.

To conclude, I present a methodology to distinguish among several models of mate competition and choice behind the observed pattern of mating and the phenotypic frequencies in the population. From an empirical point of view it is much easier to study patterns than processes and this is why the causal mechanisms of natural and sexual selection are not so well known as the patterns they provoke. I propose a new tool that will help to distinguish among different alternative processes behind the observed mating pattern.

**Software, code and data accessibility**

The developed methodology has been fully implemented in a program called InfoMating available at <http://acraaj.webs6.uvigo.es/InfoMating/Infomating.htm> or upon request to the author. The simulations and empirical model sets are available at [doi:10.5281/zenodo.3492107](https://doi.org/10.5281/zenodo.3492107)

The simulations data set is available at [doi:10.5281/zenodo.3497325](https://doi.org/10.5281/zenodo.3497325)

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**Appendix A. Mutual mating propensity models**

*Saturated non-random mating model: λ notation.*

Consider the total number of possible mating phenotypes  $K = k_1 \times k_2$  and the saturated multinomial model for the  $K - 1$  free mating parameters  $m'_{ij}$ .

The log-likelihood function is

$$\ln L_{\text{sat}} = C + \sum_{1 \leq i < k_1} \sum_{1 \leq j < k_2} n'_{ij} \ln(m'_{ij} q_{ij}) + n'_{k_1 k_2} \ln \left( a \left( 1 - \sum_{ij}^{K-1} q_{ij} \right) \right) - n' \ln(M)$$

where  $n'$  is the number of matings in the sample and  $n'_{ij}$  is the number of matings between  $i$ - type females and  $j$ -type males. I have fixed the parameter  $m'_{k_1 k_2}$  to  $a$ .

Compute the first derivative of the likelihood with respect to  $a$

$$\frac{d \ln L_{\text{sat}}}{da} = \frac{n'_{k_1 k_2}}{a} - \frac{n}{M} q_{k_1 k_2}$$

then by taking  $a = 1$  and equating to 0 we get

$$n/M = n'_{k_1 k_2} / q_{k_1 k_2} \equiv \lambda(1)$$

that corresponds to the number of observed matings having unity mating parameter divided by the corresponding product of population frequencies. Under the saturated model there is only one (for convenience  $m'_{k_1 k_2}$ ) mating parameter having unitary value and so the number of observed matings is  $n'_{k_1 k_2}$  and the product of the corresponding population frequencies is  $p_{1k_1} \times p_{2k_2} = q_{k_1 k_2}$ .

Now, let find the  $m'_{ij}$  parameter value that maximizes the likelihood

$$\frac{d \ln L_{\text{sat}}}{dm'_{ij}} = \frac{n'_{ij}}{m'_{ij}} - \frac{n}{M} q_{ij} = 0$$

$$\widehat{m'_{ij}} = \frac{n'_{ij} / q_{ij}}{n/M} \equiv \frac{\lambda(m'_{ij})}{\lambda(1)}$$

The  $\lambda$  notation can be generalized for any set  $A$  of mating pairs having the same value of propensity  $\theta$  as follows

$$\lambda(\theta) = \frac{\sum_{ij \in A} n'_{ij}}{\sum_{ij \in A} q_{ij}}$$

where  $n'_{ij}$  represents the number of mating pairs having absolute (non-normalized) mating parameter  $\theta$  and  $q_{ij}$  is the product of the population frequencies  $p_{i1}$  and  $p_{2j}$  i.e. the expected frequency of the  $\theta$ -mating phenotypes under random mating.

*Intrafemale competition models*

The model is

$$m'_{ij} = a_i \text{ with } a_i > 0 \forall i < k_1 \text{ and } m'_{k_1 j} = a = 1 \forall j.$$

There are  $k_1 - 1$  independent parameters. Note that the parameters  $m'_{k_1 j}$  have been fixed to  $a = 1$ . The log-likelihood function is

$$\ln L = C + \sum_{i=1}^{k_1-1} \sum_{j=1}^{k_2} n'_{ij} \ln(a_i q_{ij}) + \sum_{j=1}^{k_2} n'_{k_1 j} \ln(a q_{k_1 j}) - n \ln(M)$$

Now, assume that the parameter  $a$  is not fixed and compute the first derivative of the likelihood with respect to  $a$

$$\frac{d \ln L}{da} = \frac{\sum_j^{k_2} n'_{k_1 j}}{a} - \frac{n}{M} \sum_j^{k_2} q_{k_1 j} = 0$$

then by taking  $a = 1$  and equating to 0 we get

$$n/M = \sum_j n'_{k1j} / \sum_j q_{k1j} \equiv \lambda(1)$$

Now find the  $a_i$  parameter value that maximizes the likelihood

$$\frac{d \ln L}{da_i} = \frac{\sum_j^{k2} n'_{ij}}{a_i} - \frac{n}{M} \sum_j^{k2} q_{ij} = 0$$

Solving for  $a_i$

$$\hat{a}_i = \frac{\sum_j^{k2} n'_{ij} / \sum_j^{k2} q_{ij}}{\frac{n}{M}} \equiv \frac{\lambda(a_i)}{\lambda(1)}$$

The formula expressed as the quotient of lambdas is valid for any number  $h$  of different parameters,  $1 \leq h < k_1$ . In the particular case of having only one parameter the sum of observed matings having propensity  $a_1$ , implies  $\sum \sum n'_{ij}$  where the first summation is for all the female types except females of type  $k_1$ , and the second is over all male types. The sum of the product of frequencies is  $1 - p_{1k1}$ .

As before,  $\lambda(1)$  also corresponds to the sum of the observed matings having expected propensity 1 divided by the sum of the corresponding products of population frequencies. The model for male sexual selection is solved in a similar way.

*Intrasexual competition in both sexes*

The model is

$$m'_{ij} = a_i b_j, i < k_1, j < k_2; m'_{ik2} = a_i, i < k_1; m'_{k1j} = b_j, j < k_2; m'_{k1k2} = 1$$

with  $a_i > 0, b_j > 0 \forall i, j$ .

It is easy to see that is multiplicative. Let  $A = \sum_i^{k1-1} a_i p_{1i} + a p_{1k1}$  and  $B = \sum_j^{k2-1} b_j p_{2j} + b p_{2k2}$ .

The mean mutual mating propensity is

$$M = \sum_{ij} q_{ij} m'_{ij} = \sum_{i=1}^{k1} \sum_{j=1}^{k2} a_i b_j p_{1i} p_{2j} = AB$$

with  $a_{k1} = a$  and  $b_{k2} = b$ .

The marginal propensity for  $i$ -type females is

$$m_{Fem,i} = a_i \sum_j^{males} p_{2j} \frac{b_j}{M} = a_i \frac{B}{M}$$

Similarly, the marginal for  $j$ -type males

$$m_{Male,j} = b_j \frac{A}{M}$$

with  $a_{k1} = a$  and  $b_{k2} = b$ .

The condition (5)-(iii) for a multiplicative model implies that  $m_{ij} = m_{Fem,i} \times m_{Male,j}$ . In addition,  $m_{ij} = a_i b_j / M$  that jointly with the multiplicative condition requires  $a_i b_j / M = m_{Fem,i} \times m_{Male,j} = a_i b_j A / M^2$  solving for  $M$  we get  $M = AB$  which we have already seen it is true.

The log-likelihood function

$$\ln L = C + \sum_{i=1}^{k1} \sum_{j=1}^{k2} n'_{ij} \ln(a_i b_j q_{ij}) - n \ln(M)$$

with  $a_{k1} = a = 1$  and  $b_{k2} = b = 1$ .

Consider the derivatives

$$\frac{dA}{da_i} = p_{1i}; \frac{dB}{db_j} = p_{2j}; \frac{dM}{da_i} = p_{1i}B; \frac{dM}{db_j} = p_{2j}A$$

Now by taking the derivative of the log-likelihood with respect to  $a_i$  or  $b_j$  and equating to 0 we get the estimates

$$\hat{a}_i = \frac{\sum_j^{k2} n'_{ij} / \sum_j^{k2} q_{ij}}{\frac{n}{M} B} = \frac{\lambda(a_i + \sum_j a_j b_j)}{\lambda_{fem}(1)}$$

$$\hat{b}_j = \frac{\sum_i^{k1} n'_{ij} / \sum_i^{k1} q_{ij}}{\frac{n}{M} A} = \frac{\lambda(b_j + \sum_i a_i b_j)}{\lambda_{male}(1)}$$

where

$$\frac{n}{M} B = \frac{\sum_j^{k2} n'_{k1j}}{p_{1k1}} \equiv \lambda_{fem}(1)$$

$$\frac{n}{M} A = \frac{\sum_i^{k1} n'_{ik2}}{p_{2k2}} \equiv \lambda_{male}(1)$$

*Mate choice models with parameterized heterotypes*

Consider models in which the homotype mating has absolute propensity of 1 while the different heterotypes have absolute value of  $c_{ij}$ . The maximum likelihood estimate is

$$\hat{c}_{h1h2} = \frac{\lambda(c_{h1h2})}{\lambda(1)}$$

The number of parameters in this type of model is  $K - \min\{k_1, k_2\} - \sum_s (C_s - 1)$  where the sum is over the set of different heterotype matings and  $C_s$  is the cardinality of each set.

*Double effect models*

The following models generate a double pattern of sexual selection and assortative mating even when the population frequencies are uniform.

*Double effect models producing sexual selection in one sex under uniform frequencies*

A simple approach consists in building a new model by setting  $m'_{ii} = 1$  and  $m'_{ij} = 1 + c$ . Then, if we desire assortative mating jointly with sexual selection only in females we additionally set  $m'_{ij} = 1 - c$ ; on the contrary, if we desire selection only in males we set  $m'_{ji} = 1 - c$  with  $-1 < c < 1$ . If the frequencies are not uniform the model generates assortative mating jointly with sexual selection in both sexes.

In the case of the model with  $m'_{ij} = 1 - c$  (female sexual selection if frequencies are uniform) the maximum likelihood estimate of  $c$  is one of the roots of the quadratic

$$(x_{jj} - x_{ij} + n'D) - c[x_{ij} + x_{jj} + D(x_{jj} - x_{ij})] - c^2 D[n' - (x_{ij} + x_{jj})] = 0$$

where  $D = q_{ij} - q_{jj}$  and  $n' = \sum x_{ij}$  is the number of matings (sample size).

If the frequencies are uniform and  $k_1 = k_2$ , i.e.  $p_{1i} = p_{1j} = p_{2i} = p_{2j} \forall i, j$  then

$$\hat{c} = \frac{x_{jj} - x_{ij}}{x_{jj} + x_{ij}}$$

The case for male sexual selection is obtained simply by interchanging  $x_{ij}$  by  $x_{ji}$  and  $q_{ij}$  by  $q_{ji}$  in the formulae.

The above model has only one parameter  $c$ ; we can introduce a more complex two parameter model,  $M_{(a,c)}$  by setting  $m'_{ii} = a$ ,  $m'_{ij} = 1 + c$  and  $m'_{ji} = 1 - c$ , for female sexual selection (or  $m'_{ji} = 1 - c$  for male sexual selection). For obtaining the MLE of this two parameter double model, with restrictions  $a > 0, c < |1|$ , I have used a numerical bounded Nelder-Mead simplex algorithm (Gao and Han, 2012; Press, 2002; Singer and Singer, 2004).

*Double effect models with sexual selection in both sexes under uniform frequencies*

To get assortative mating jointly with sexual selection in both sexes under uniform frequencies, we just need to combine the



above uniform one parameter models of each sex, so that  $m'_{ii} = 1$ ,  $m'_{jj} = 1 + c$  and  $m'_{ij} = m'_{ji} = 1 - c$ .

The maximum likelihood estimate of  $c$  involves the solution of the quadratic

$$[x_{ij} - x_s + n'D_2] - c[x_{ij} + x_s + D_2(x_{ij} - x_s)] + c^2 D_2[x_{ij} + x_s - n'] = 0$$

where  $x_s = x_{ij} + x_{ji}$  and  $D_2 = q_{ij} + q_{ji} - q_{jj}$ .

#### General double effect models

We can also define a set of general models where any propensity  $m'_{ij}$  has parameter  $\theta_{ij}$  with at least one propensity having value of 1. The MLE of the parameters of this kind of model is

$$\hat{\theta}_{ij} = \frac{\lambda(\theta_{ij})}{\lambda(1)}$$

where  $\lambda(\theta_{ij})$  is defined as in (A2).

The simplest model defined in this way is

$$m'_{ii} = c \text{ and } m'_{ij} = m'_{ji} = m'_{jj} = 1,$$

which produces assortative mating and sexual selection in both sexes.

Consider as an example of this model, the case with  $k_1 = k_2 = 2$  so that  $0 < p_{11} < 1$ ;  $0 < p_{21} < 1$ ;  $m'_{11} = c$  and  $m'_{12} = m'_{21} = m'_{22} = 1$ . The mean mating propensity is  $M = q_{11}(c - 1) + 1$ . The absolute marginal propensity for the first female type  $m'_{Fem\_1} = cp_{21} + 1 - p_{21} = p_{21}(c - 1) + 1$ , and for the second female type  $m'_{Fem\_2} = 1$ . Similarly the male marginals are  $m'_{Male\_1} = p_{11}(c - 1) + 1$  and  $m'_{Male\_2} = 1$ .

Recall that the condition for the sexual selection pattern within a given sex is that the marginal mating propensities are different which here is true for both sexes provided that  $c \neq 1$ . Regarding the assortative mating pattern it can be proved that the joint isolation index ( $I_{PSI}$ ) is 0 only if  $c = 1$ . However, it is sufficient to prove that the model is not multiplicative (Carvajal-Rodríguez, 2018b). Consider that the model is multiplicative, this implies,  $m'_{12}/M = (m'_{Fem\_1}/M) \times (m'_{Male\_2}/M)$  that given the model values becomes

$$M = (m'_{Fem\_1}) \times (m'_{Male\_2})$$

which can be true only when  $p_{11} = 1$  and so it is false by definition.

The estimate of  $c$  under this model is  $\lambda(c)/\lambda(1)$ .

The most parameterized model that can be defined in this way has  $K - 1$  free parameters and coincides with the saturated model so that the estimates are the corresponding pair total indices ( $PTI_{ij}$ ). Moreover, note that if no mutual propensity is fixed to 1 then  $\lambda(1) = (n - A)/(1 - P) = n$  where  $A =$  number of observations having value 1 = 0 and  $P =$  product of population frequencies of the involved types having mutual propensity 1 = 0. Therefore the estimate of  $\theta_{ij}$  can also expressed as  $\lambda(\theta_{ij})/n$  which is the observed frequency of mating pairs ( $i, j$ ) divided by the expected frequency by random mating which is the definition of the pair total index  $PTI_{ij}$  ( $K - 1$  are free and one  $PTI$  is dependent on the others).

All the above derived MLE formulae have been checked by a numerical bounded Nelder-Mead simplex algorithm (Gao and Han, 2012; Press, 2002; Singer and Singer, 2004).

#### Appendix B. Monte Carlo simulation of mating tables

The mating tables for the simulation experiments were generated by the program MateSim (Carvajal-Rodríguez, 2018a) available at <http://acraaj.webs.uvigo.es/MateSim/matesim.htm>.

```
# format number
0
# num of types
2
#premating male numbers
1626    3374
#premating female numbers
917    4083
# matings by rows (females)
30    62
133    275
```

**Fig. B.1.** Example of a table generated by the simulations. The format is the same as for the JMating software.

A		B	
# format number	0	# format number	0
# num of types	2	# num of types	2
#premating male numbers	277    133	#premating male numbers	277    133
#premating female numbers	269    269	#premating female numbers	269    269
# matings by rows (females)	70    39	# matings by rows (females)	100    9
	70    39		100    9

**Fig. D.1.** Examples of two toy models with only one type of female and two types of males. Note that the rows of the mating table are duplicated (same female type). A: Random mating B: Male sexual selection.

The number of replicates for each case was 1000. For each run the program first generated the number of premating males and females from a given population size. For example, if the population size consisted in  $n_1$  ( $= 5000$ ) females and  $n_2$  ( $= 5000$ ) males, the program got  $n_{1A} = n_1 \times U$  females of the A type and  $n_{1B} = n_1 - n_{1A}$  females of the B type, where  $U$  is a value sampled from the standard uniform distribution. The premating males were obtained similarly. Then, the female population frequencies were  $p_{1i} = n_{1i}/n_1$ , and  $p_{2i} = n_{2i}/n_2$  for the male ones. Finally, a sample of  $n'$  ( $= 500$ ) matings was obtained, where the number of counts for each mating phenotype  $i \times j$  was

$$Q(i,j) = n' \times p_{1i} \times p_{2j} \times m'_{ij}/M$$

where  $m'_{ij}$  are the mutual-propensity parameters as defined for each kind of model, and  $M = \sum p_{1i} \times p_{2j} \times m'_{ij}$ .

The format of the obtained tables was the same as the JMating (Carvajal-Rodríguez and Rolan-Alvarez, 2006) input files (Fig. B.1).

#### Appendix C. Polygamous species with low sample size and monogamous species

See Tables C.1–C.3.

#### Appendix D. Incomplete set-up: toy example

The proposed modelling framework requires at least two phenotypes by sex (mating tables of  $2 \times 2$  dimensions or higher) for measuring sexual competition and mate choice effects. However it still can be applied if some sex, say females, have only one phenotype. In this case we just need to duplicate the row (see Fig. D.1). Obviously, only male sexual selection can be measured.

The examples in Fig. D.1 correspond to a population with only one female but two male phenotypes (phenotype-1 and phenotype-2). There were sampled 269 females plus 277 males with phenotype-1 and 133 males with phenotype-2. In the first

**Table C.1**Average (standard error) parameter estimates under sample size 50 for a polygamous species with large population size ( $N = 10000$ ).

Model		$m'_{11}$	$m'_{12}$	$m_{21}$	$m_{22}$
$M_0$	Expected	1	1	1	1
	AICc	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$
	KICc	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$
	BIC	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$	$1.0 \pm 0.0000$
SfC	Expected	2	2	1	3
	AICc	$1.38 \pm 0.0106$	$1.45 \pm 0.0119$	$1.0 \pm 0.0003$	$2.03 \pm 0.0206$
	KICc	$1.32 \pm 0.0104$	$1.35 \pm 0.0110$	$1.0 \pm 0.0003$	$1.76 \pm 0.0226$
	BIC	$1.29 \pm 0.0106$	$1.29 \pm 0.0105$	$1.0 \pm 0.0003$	$1.64 \pm 0.0225$
SfCc	Expected	6	2	1	3
	AICc	$4.71 \pm 0.0204$	$1.86 \pm 0.0201$	$1.0 \pm 0.0000$	$2.36 \pm 0.0286$
	KICc	$4.45 \pm 0.0236$	$1.57 \pm 0.0216$	$1.0 \pm 0.0000$	$2.06 \pm 0.0316$
	BIC	$4.28 \pm 0.0283$	$1.42 \pm 0.0198$	$1.0 \pm 0.0000$	$1.99 \pm 0.0324$

$M_0$ : Random mating model. SfC: female competition and mate choice with independent parameters. SfCc: female competition and mate choice with compound parameters.

**Table C.2**Average (standard error) parameter estimates under sample size 500 for a monogamous species (mass-encounter mating process) with large population size ( $N = 10000$ ).

Model		$m'_{11}$	$m'_{12}$	$m_{21}$	$m_{22}$
$M_0$	Expected	1	1	1	1
	AICc	$1.07 \pm 0.0053$	$1.07 \pm 0.0053$	$1.07 \pm 0.0059$	$1.07 \pm 0.0056$
	KICc	$1.05 \pm 0.0044$	$1.04 \pm 0.0043$	$1.05 \pm 0.0052$	$1.04 \pm 0.0050$
	BIC	$1.01 \pm 0.0028$	$1.01 \pm 0.0020$	$1.01 \pm 0.0033$	$1.01 \pm 0.0026$
SfC	Expected	2	2	1	3
	AICc	$1.95 \pm 0.0158$	$1.95 \pm 0.0160$	$1.0 \pm 0.0001$	$2.04 \pm 0.0176$
	KICc	$1.93 \pm 0.0162$	$1.93 \pm 0.0166$	$1.0 \pm 0.0001$	$2.03 \pm 0.0180$
	BIC	$1.82 \pm 0.0183$	$1.82 \pm 0.0189$	$1.0 \pm 0.0000$	$1.93 \pm 0.0195$
SfCc	Expected	6	2	1	3
	AICc	$3.02 \pm 0.0341$	$2.07 \pm 0.0210$	$1.0 \pm 0.0001$	$2.84 \pm 0.0298$
	KICc	$3.0 \pm 0.0343$	$2.04 \pm 0.0216$	$1.0 \pm 0.0000$	$2.82 \pm 0.0302$
	BIC	$2.86 \pm 0.0353$	$1.92 \pm 0.0244$	$1.0 \pm 0.0000$	$2.73 \pm 0.0313$

$M_0$ : Random mating model. SfC: female competition and mate choice with independent parameters. SfCc: female competition and mate choice with compound parameters.

**Table C.3**Average (standard error) parameter estimates under sample size 50 for a monogamous species (mass-encounter mating process) with large population size ( $N = 10000$ ).

Model		$m'_{11}$	$m'_{12}$	$m_{21}$	$m_{22}$
$M_0$	Expected	1	1	1	1
	AICc	$1.0 \pm 0.0362$	$1.04 \pm 0.0414$	$1.0 \pm 0.0365$	$1.02 \pm 0.0406$
	KICc	$1.02 \pm 0.0339$	$1.03 \pm 0.0374$	$1.0 \pm 0.0324$	$1.02 \pm 0.0377$
	BIC	$1.03 \pm 0.0312$	$1.03 \pm 0.0340$	$1.0 \pm 0.0283$	$1.03 \pm 0.0361$
SfC	Expected	2	2	1	3
	AICc	$2.0 \pm 0.0568$	$2.05 \pm 0.0638$	$1.08 \pm 0.0155$	$2.23 \pm 0.0635$
	KICc	$1.76 \pm 0.0539$	$1.78 \pm 0.0605$	$1.06 \pm 0.0145$	$1.96 \pm 0.0597$
	BIC	$1.62 \pm 0.0515$	$1.66 \pm 0.0578$	$1.05 \pm 0.0143$	$1.79 \pm 0.0555$
SfCc	Expected	6	2	1	3
	AICc	$3.36 \pm 0.1004$	$2.19 \pm 0.0731$	$1.03 \pm 0.0073$	$3.11 \pm 0.0997$
	KICc	$3.06 \pm 0.0951$	$1.94 \pm 0.0715$	$1.03 \pm 0.0066$	$2.85 \pm 0.0964$
	BIC	$2.89 \pm 0.0919$	$1.79 \pm 0.0687$	$1.02 \pm 0.0048$	$2.68 \pm 0.0929$

$M_0$ : Random mating model. SfC: female competition and mate choice with independent parameters. SfCc: female competition and mate choice with compound parameters.

example (Fig. D.1-A) there were 70 matings involving the male phenotype-1 and 39 with male phenotype-2. In the second example (Fig. D.1-B) the matings were 100 with phenotype-1 and 9 with phenotype-2.

The analysis of the first case indicated that there was no significant deviation from random mating ( $J_{PTI} = 0.005$ ,  $P = 0.78$ ). The best model was the random mating model  $M_0$ . As expected,

the multi-model estimation of the mutual mating parameters was 1 for every parameter. The results were the same for the three information indices (AICc, KICc and BIC).

The analysis of the second case detected a deviation from random mating ( $J_{PTI} = 0.405$ ,  $P < 10^{-7}$ ) due to male sexual selection ( $J_{PS2} = 0.405$ ,  $P < 10^{-7}$ ) see Carvajal-Rodríguez (2018b) for details of the  $j$  indices. The best model was male sexual

**Table C.4**

Average (standard error) parameter estimates under sample size 100 for a monogamous species (mass-encounter mating process) with small population size ( $N = 200$ ).

Model		$m'_{11}$	$m'_{12}$	$m_{21}$	$m_{22}$
$M_0$	Expected	1	1	1	1
	AICc	1.07 ± 0.0083	1.10 ± 0.0141	1.09 ± 0.0141	1.07 ± 0.0090
	KICc	1.04 ± 0.0064	1.05 ± 0.0094	1.05 ± 0.010	1.04 ± 0.0070
	BIC	1.02 ± 0.0047	1.02 ± 0.0056	1.02 ± 0.0065	1.02 ± 0.0052
SfC	Expected	2	2	1	3
	AICc	1.15 ± 0.0173	1.11 ± 0.0157	1.07 ± 0.0118	1.11 ± 0.0145
	KICc	1.10 ± 0.0141	1.06 ± 0.0125	1.04 ± 0.0091	1.06 ± 0.0108
	BIC	1.03 ± 0.0072	1.03 ± 0.0079	1.02 ± 0.0059	1.03 ± 0.0060
SfCc	Expected	6	2	1	3
	AICc	1.85 ± 0.0555	1.30 ± 0.0317	1.07 ± 0.0124	2.12 ± 0.0757
	KICc	1.66 ± 0.0515	1.22 ± 0.0289	1.04 ± 0.010	1.94 ± 0.070
	BIC	1.49 ± 0.0476	1.13 ± 0.0248	1.02 ± 0.0039	1.71 ± 0.0637

$M_0$ : Random mating model. SfC: female competition and mate choice with independent parameters. SfCc: female competition and mate choice with compound parameters.

selection with one parameter (Smale-1P). The male sexual selection component indicated five times higher mating propensity of male phenotype-1 with respect to phenotype-2.

## References

- Aho, K., et al., 2014. Model selection for ecologists: the worldviews of AIC and BIC. *Ecology* 95, 631–636.
- Aho, K., et al., 2017. A graphical framework for model selection criteria and significance tests: refutation, confirmation and ecology. *Methods Ecol. Evol.* 8, 47–56.
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, pp. 267–281.
- Alonzo, S.H., Servodio, M.R., 2019. Grey zones of sexual selection: why is finding a modern definition so hard?. *Proc. R. Soc. B* 286, 20191325.
- Anderson, D.R., et al., 1994. AIC Model selection in overdispersed capture-recapture data. *Ecology* 75, 1780–1793.
- Andersson, M., 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Arnold, S.J., Wade, M.J., 1984. On the measurement of natural and sexual selection: applications. *Evolution* 72, 0–734.
- Barker, R.J., Link, W.A., 2015. Truth, models, model sets, aic, and multimodel inference: A Bayesian perspective. *J. Wildlife Manage.* 79, 730–738.
- Brewer, M.J., et al., 2016. The relative performance of aic, AICC and BIC in the presence of unobserved heterogeneity. *Methods Ecol. Evol.* 7, 679–692.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.
- Burnham, K.P., et al., 2011. AIC Model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35.
- Cade, B.S., 2015. Model averaging and muddled multimodel inferences. *Ecology* 96, 2370–2382.
- Carvajal-Rodríguez, A., 2018a. MateSim: Monte Carlo simulation for the generation of mating tables. *Biosystems* 171, 26–30.
- Carvajal-Rodríguez, A., 2018b. Non-random mating and information theory. *Theor. Popul. Biol.* 120, 103–113.
- Carvajal-Rodríguez, A., 2019. A generalization of the informational view of non-random mating: Models with variable population frequencies. *Theor. Popul. Biol.* 125, 67–74.
- Carvajal-Rodríguez, A., Rolan-Alvarez, E., 2006. JMATING: a software for the analysis of sexual selection and sexual isolation effects from mating frequency data. *BMC Evol. Biol.* 6, 40.
- Casares, P., et al., 1998. Disentangling the effects of mating propensity and mating choice in drosophila. *Evolution* 52, 126–133.
- Cavanaugh, J.E., 2004. Criteria for linear model selection based on Kullback's symmetric divergence. *Aust. N. Z. J. Stat.* 46, 257–274.
- Claeskens, G., 2016. Statistical model choice. *Annu. Rev. Stat. Appl.* 3, 233–256.
- Cruz, R., et al., 2001. Sexual selection on phenotypic traits in a hybrid zone of *Littorina saxatilis* (Olivi). *J. Evol. Biol.* 14, 773–785.
- Darwin, C., 1871. *The descent of man, and selection in relation to sex*. Murray.
- Dziak, J.J., et al., 2019. Sensitivity and specificity of information criteria. *bioRxiv*. 449751.
- Edward, D.A., 2015. The description of mate choice. *Behav. Ecol.* 26, 301–310.
- Endler, J.A., 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ.
- Estévez, D., et al., 2018. A novel method to estimate the spatial scale of mate choice in the wild. *Behav. Ecol. Sociobiol.* 72, 195.
- Fitze, P.S., Galiard, J.-F.L., 2011. Inconsistency between different measures of sexual selection. *Amer. Nat.* 178, 256–268.
- Futuyma, D.J., Kirkpatrick, M., 2017. *Evolution*. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts U.S.A.
- Galipaud, M., et al., 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. *Methods Ecol. Evol.* 5, 983–991.
- Galipaud, M., et al., 2017. A farewell to the sum of Akaike weights: The benefits of alternative metrics for variable importance estimations in model selection. *Methods Ecol. Evol.* 8, 1668–1678.
- Gao, F., Han, L., 2012. Implementing the Nelder–Mead simplex algorithm with adaptive parameters. *Comput. Optim. Appl.* 51, 259–277.
- Giam, X., Olden, J.D., 2016. Quantifying variable importance in a multimodel inference framework. *Methods Ecol. Evol.* 7, 388–397.
- Gimelfarb, A., 1988. Processes of pair formation leading to assortative mating in biological populations: Encounter-mating model. *Amer. Nat.* 131, 865–884.
- Grueber, C.E., et al., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.
- Hartl, D.L., Clark, A.G., 1997. *Principles of Population Genetics*. Sinauer Associates, Inc. Sunderland, MA.
- Jennions, M.D., Petrie, M., 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* 72, 283.
- Keeratibool, W., 2014. Unifying the derivations of kullback information criterion and corrected versions. *Thail. Stat.* 12, 37–53.
- Kim, H.-J., et al., 2014. Model selection criteria for overdispersed data and their application to the characterization of a host-parasite relationship. *Environ. Ecol. Stat.* 21, 329–350.
- Kokko, H., et al., 2012. Unifying cornerstones of sexual selection: operational sex ratio, bateman gradient and the scope for competitive investment. *Ecol. Lett.* 15, 1340–1351.
- Kullback, S., 1997. *Information Theory and Statistics*. Courier Corporation.
- Lewontin, R., et al., 1968. Selective mating, assortative mating, and inbreeding: definitions and implications. *Eugen Q* 15, 141–143.
- Link, W.A., Barker, R.J., 2006. Model weights and the foundations of multimodel inference. *Ecology* 87, 2626–2635.
- Liu, W., Yang, Y., 2011. Parametric or nonparametric? A parametricness index for model selection. *Ann. Statist.* 39, 2074–2102.
- Ng, T.P.T., et al., 2019. The causal relationship between sexual selection and sexual size dimorphism in marine gastropods. *Anim. Behav.* 148, 53–62.
- Parker, G.A., 2014. The sexual cascade and the rise of pre-ejaculatory (Darwinian) sexual selection, sex roles, and sexual conflict. *Cold Spring Harbor Perspect. Biol.* 6, a017509.
- Parker, G.A., Pizzari, T., 2015. Sexual selection: The logical imperative. In: Hoquet, T. (Ed.), *Current Perspectives on Sexual Selection: What's Left After Darwin?*. Springer Netherlands, Dordrecht, pp. 119–163.
- Press, W.H., 2002. *Numerical Recipes in C++ : The Art of Scientific Computing*. Cambridge University Press, Cambridge.
- Prum, R.O., 2012. Aesthetic evolution by mate choice: Darwin's really dangerous idea. *Philos. Trans. R. Soc. B* 367, 2253–2265.
- Richards, S.A., 2008. Dealing with overdispersed count data in applied ecology. *J. Appl. Ecol.* 45, 218–227.
- Rolan-Alvarez, E., 2007. Sympatric speciation as a by-product of ecological adaptation in the Galician *Littorina saxatilis* hybrid zone. *J. Molluscan Stud.* 73, 1–10.
- Rolán-Alvarez, E., Caballero, A., 2000. Estimating sexual selection and sexual isolation effects from mating frequencies. *Evolution* 54, 30–36.

- Rolan-Alvarez, E., et al., 2015a. The contribution of the genus *Littorina* to the field of evolutionary ecology. *Oceanogr. Mar. Biol.: Ann. Rev.* 53, 157–214.
- Rolan-Alvarez, E., et al., 2015b. The scale-of-choice effect and how estimates of assortative mating in the wild can be biased due to heterogeneous samples. *Evolution* 69, 1845–1857.
- Rosenthal, G.G., 2017. *Mate Choice: The Evolution of Sexual Decision Making from Microbes to Humans*. Princeton University Press.
- Roughgarden, J., et al., 2006. Reproductive social behavior: cooperative games to replace sexual selection. *Science* 311, 965–969.
- Schwarz, G., 1978. Estimating the dimension of a model. *Ann. Statist.* 6, 461–464.
- Shuker, D.M., 2010. Sexual selection: endless forms or tangled bank?. *Anim. Behav.* 79, e11–e17.
- Singer, S., Singer, S., 2004. Efficient implementation of the Nelder–Mead search algorithm. *Appl. Numer. Anal. Comput. Math.* 1, 524–534.
- Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multi-model inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21.
- Vrieze, S.I., 2012. Model selection and psychological theory: a discussion of the differences between the Akaike information criterion (AIC) and the Bayesian information criterion (BIC). *Psychol. Methods* 17, 228.
- Wacker, S., Amundsen, T., 2014. Mate competition and resource competition are inter-related in sexual selection. *J. Evol. Biol.* 27, 466–477.
- Wagenmakers, E.-J., 2007. A practical solution to the pervasive problems of p values. *Psychon. Bull. Rev.* 14, 779–804.