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Multi-model inference of mate choice effects from an information theoretic approach

A. Carvajal-Rodríguez

Departamento de Bioquímica, Genética e Inmunología. Universidad de Vigo, 36310 Vigo, Spain.

*: A. Carvajal-Rodríguez. Departamento de Bioquímica, Genética e Inmunología. Universidad de Vigo, 36310 Vigo, Spain. Phone/Fax: +34 986130052/986813828

email: *acraaj@uvigo.es*

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Abstract

Mate choice is an important biological phenomenon with a significant impact on the evolution of organisms. Here, we relied in previous results on the description of mate choice effects as a flow of information, for developing different classes of models distinguished by their evolutionary effects: sexual selection and/or isolation.

We obtained formulas for the maximum likelihood estimates of each model and compared three different information criteria (AICc, KICc, and BIC) for performing multimodel inference. Simulation results showed a good performance of both model selection and parameter estimation. We applied the modelling framework to real data, and estimated the mating preference parameters in the Galician *Littorina saxatilis* ecotypes, confirming the pattern of positive assortative mating in this species.

As far as we know, this is the first standardized methodology for model selection and multimodel inference of mate choice effects. The full methodology was implemented in a software called InfoMating (available at http://acraaj.webs.uvigo.es/InfoMating/Infomating.htm).

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Introduction

Mate choice is an active area of evolutionary research. It can be broadly described as the effect of the expression of some traits leading to non-random mating. The biological complexity lying behind mate choice has generated an extensive research producing different theoretical descriptions and empirical tests (Edward 2015a, b; Hoquet 2015; Hughes 2015; Roff 2015; Ah-King and Gowaty 2016).

There are several types of models than could be linked to the causes of mate choice. Mate choice has been approached from the phenotypic, population genetics, and quantitative genetics sides, being developed under either a probabilistic or a deterministic framework. More realism can be still added by including ecological and behavioural aspects (Kokko et al. 2006; Roff 2015).

However, from an evolutionary perspective, non-random mating has importance by its consequences, as long as it implies a systematic change in phenotype and genotype frequencies. Therefore, when studying mate choice, we can also focus on its evolutionary consequences.

From an evolutionary point of view, mate choice is defined as the difference between the observed and expected (by random) mating frequencies. So defined, the consequences of mate choice can be partitioned into sexual selection (intrasexual selection) and sexual isolation (behavioural isolation or intersexual selection).

The decomposition of mating behaviour into sexual selection and sexual isolation effects has been made from multiple-choice experiments in *Drosophila* (Merrell 1950; Spieth and

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Ringo 1983; Knoppien 1985); see also (Rolán-Alvarez and Caballero 2000) and references therein.

Sexual selection refers to the observed change in gene or phenotype frequencies in mated individuals with respect to population frequencies (Anderson et al. 1994; Hartl and Clark 1997). Because population frequencies are involved, the comparison includes non-mated individuals.

Sexual isolation (intersexual selection) considers the deviation from random mating within mated individuals. Because only frequencies within the sample of mating are considered, the comparison does not involve non-mated individuals. Note that for simplicity, by sexual isolation we are referring to intersexual selection that can be consequence of any of both, positive or negative assortative mating (Merrell 1950; Lewontin et al. 1968; Spieth and Ringo 1983).

The immediate causes of sexual selection and/or isolation can be a different preference or discrimination between different mating types (e.g. A females prefer A males) and/or different mating energy or vigour of a type from one sex for mating whatever couple (e.g. B males systematically invest more energy on mating).

In a previous work (Carvajal-Rodríguez 2018), we showed that both types of cause can be modelled jointly, 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 females prefer A males then this is modelled as a higher mutual mating propensity between these types as compared with the mating propensity of the A females

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with B males ($m_{AA} > m_{AB}$). On the other hand, if B males are more vigorous or prone for mating whatever the female is, this is modelled by a higher average male propensity of such males (marginal propensity, see below).

By modelling the mating as a differential mutual mating propensity among different types of couples, it is possible to express the mean change in mating phenotypes as the information gained due to mate choice (Carvajal-Rodríguez 2018). The expression of the effects of mate choice in terms of information also permitted to identify the necessary and sufficient conditions of random mating (see below).

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

We proceed as follows:

1.- First, we set the conditions for random mating obtained from the mutual mating propensity formalism. Afterwards, we develop different classes of effects models and their maximum likelihood estimates, namely: sexual selection, sexual isolation or double (sexual selection and isolation) models with different number of independent mating propensity parameters.

2.- We apply distinct information criteria for selecting the best candidate models and estimating the values of the mutual mating propensity parameters based on the most supported models.

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

Mutual Mating Propensity Models

Consider a sample of n' matings. The total number of possible mating types is $K = k_1 \times k_2$ where k_1 is the number of female types and k_2 the number of male types. Let have n'_{ij} matings of i-type females with j-type males from the sample. If the probability of the mating $i \times j$ is q'_{ij}, then the logarithm of the likelihood function lnL of the sample is

$$lnL = C + \sum_{ij}^{K} n'_{ij} \ln (q'_{ij})$$

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

SATURATED NON-RANDOM MATING MODEL M_{SAT}

Consider a population with 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 in the population. 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 $p_{2j} = n_{2j} / n_2$.

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The mating probability between types *i* and *j* can be expressed as $q'_{ij} = m_{ij}q_{ij}$ (Carvajal-Rodríguez 2018) where q_{ij} is the product of the population female and male frequencies of each type ($q_{ij} = p_{1i} \times p_{2j}$) and m_{ij} is the normalized mutual mating propensity that refers to the number of matings after an encounter between females of type *i* and males of type *j*. The values m_{ij} are normalized so that $\Sigma q'_{ij} = 1$.

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

$$lnL_{sat} = C + \sum_{ij}^{K} n'_{ij} \ln(m_{ij}q_{ij}) \qquad (1)$$

We note this model as saturated (M_{sat}) because there are as many parameters as independent mating propensities, $P_{sat} = K - 1$. *T*he last propensity is not independent and can be calculated from the others as

$$m_{k1k2} = (1 - \sum m_{ij}q_{ij}) / q_{k1k2}$$

where the summation is over the K -1 remaining categories.

The female and male population frequencies, p_1 and p_2, are considered to be known or, alternatively, they need to be estimated in all the models. Therefore, in terms of model comparison we can ignore the population frequencies 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 frequency of the observed pair types divided by the expected frequency under random mating (Rolán-Alvarez and Caballero 2000).

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The model M_{sat} is the most complex model that can be fitted to the available data. The principle of parsimony suggests that we may consider reduced special cases of this saturated model.

Following, we computed the ML estimates of different classes of reduced general models that require less fixed parameters. All of them can be expressed as particular cases of the saturated model.

RANDOM MATING MODEL M_0

The random model M_0 corresponds to the simplest, most reduced model, and it is nested with all the other (is a particular case of any other model) while we cannot derive any simplified version from it. This model assumes that the within-population mating probability is at random.

When mating is at random, the mating probability between types i and j is $q'_{ij} = q_{ij} = p_{1i} \times p_{2j}$. This model is a particular case of the saturated one when the mating propensity is equal for every mating type. The number of mating parameters is $P_0 = 0$.

The log-likelihood of the sample of mating is

$$lnL_0 = C + \sum_{ij}^{K} n'_{ij} \ln(q_{ij}) \qquad (2)$$

Now, let's define the marginal propensitiy m_{Fem_i} for a female of type i as

$$m_{Fem_i} = \sum_{j}^{males} p_{2j} \frac{m\prime_{ij}}{M} \qquad = \sum_{j}^{males} p_{2j} m_{ij} \qquad (3)$$

Similarly for a male of type j

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

Where we have noted the absolute (unnormalized) propensity as m'_{ij} and the mean propensity M

$$M = \sum_{i,j} q_{ij} m'_{ij}$$

Interestingly, the M_0 model corresponds to M_{sat} subjected to the following restrictions:

i) $m_{ij} = m_{Fem_i} \times m_{Male_j} \; \forall \; i, j$ (4)

ii) $m_{Fem_i} = m_{Fem_j} \; \forall \; i, j$

iii) $m_{Male_i} = m_{Male_j} \; \forall \; i, j$

Thus, given the model M_{sat}, we may define M_0 as a particular case that has three additional restrictions. These restrictions provoke that all the propensities are the same, so mating just depends on the frequencies of each type. It is useful to express M_0 in terms of the three restrictions because by relaxing some of them, we can generate different classes of models.

Therefore, we produced three general classes of models defined by their consequences after relaxing some of the conditions in (4), namely, sexual selection, sexual isolation, and double effect models (Fig. 1).

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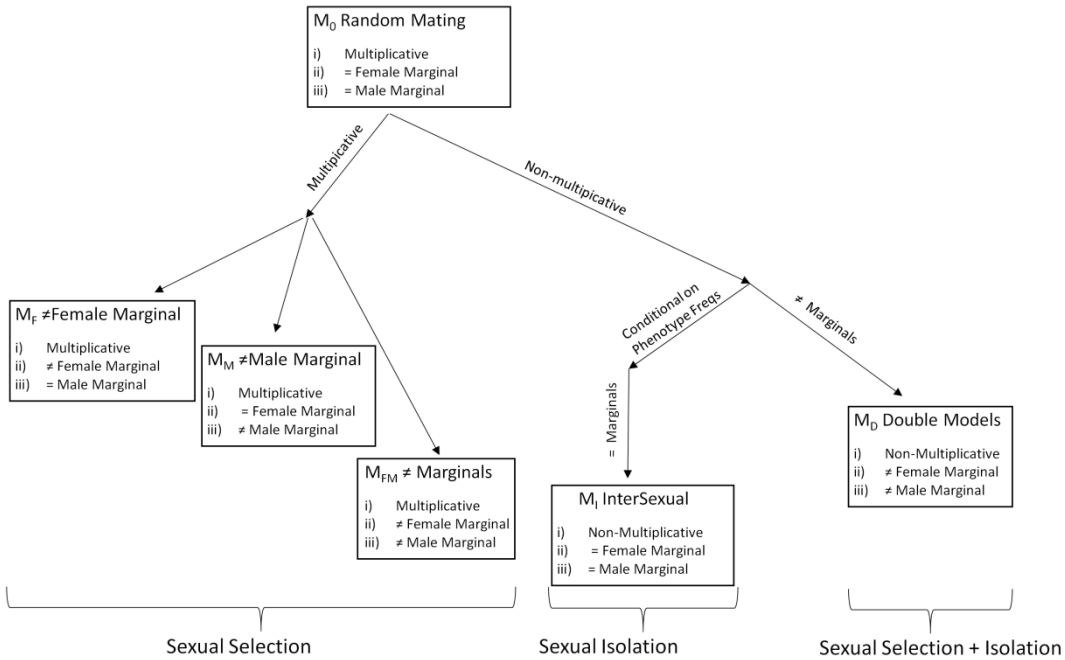

Fig 1. Mating models as defined by their effect after relaxing some of the conditions imposed to the random mating model M_0.

SEXUAL SELECTION EFFECTS MODELS

This class of model corresponds to relaxing the second and/or third conditions in M_0 while maintaining the condition of multiplicativity (4-i). The maintenance of the first condition implies that the propensity of a mating pair (i,j) is the product of the marginal female (m_{Fem}) and male (m_{Male}) propensities. And because 4-i) is maintained, sexual isolation effects cannot occur (Carvajal-Rodríguez 2018). We distinguished models with sexual selection in just one sex or in both sexes.

Female Sexual Selection

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For generating models having sexual selection only in females, we relaxed condition (4-*ii*). This implies that at least one female marginal propensity, say female of type *A*, is different from the rest of female types i.e. $m_{Fem_A} \neq m_{Fem_j}$ with *j* being any other type than *A*.

Therefore, we set a different absolute (unnormalized) propensity a_h for each female type *h* as follows

$$m'_{11} = m'_{12} = \ldots = m'_{1k2} = a_1$$

$$m'_{21} = m'_{22} = \ldots = m'_{2k2} = a_2$$

.

.

.

$$m'_{(k1-1)1} = m'_{k12} = \ldots = m'_{k1k2} = a_{k1-1}$$

$$m'_{k11} = m'_{k12} = \ldots = m'_{k1k2} = 1 \qquad (5)$$

with $a_h > 0 \; \forall \; h$.

Note that the relationships among the propensities will not be altered if we divide by a_{k1} so that we have fixed $a_{k1} = 1$. Thus, under female sexual selection models we can consider $H_1 \in [1, k_1 - 1]$ different parameters.

The normalization factor is the mean propensity $M = \sum m'_{ij} q_{ij}$. Now, if we compute the marginal female and male propensities (3) we see that

$$m_{Fem_1} = a_1/M;\; m_{Fem_2} = a_2/M \ldots;\; m_{Fem_k1} = 1/M$$

$$m_{Male_1} = m_{Male_2} = m_{Male_3} = \ldots = m_{Male_k2} = M/M = 1$$

For any parameter a_h, $1 \leq h < k_1$, the MLE under the female sexual selection models was

$$\hat{a}_h = \frac{\lambda(a_h)}{\lambda(1)} \qquad (6)$$

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where λ(θ) was defined in general for any set *A* of mating pair types having the same value of propensity θ as

$$\lambda(\theta) = \frac{\sum_t^A x_t}{\sum_{t1t2}^A p_{1t1} p_{2t2}} \qquad (7)$$

So, $\lambda(a_h)$ expresses the sum of the observed matings with propensity a_h divided by the sum of the product of the population frequencies from each partner type (see section S1 in Supporting Information for detailed explanation). Similarly, λ(1) corresponds to the sum of the observed matings having expected propensity 1 divided by the sum of the corresponding products of population frequencies.

Male Sexual Selection

Sexual selection in only males is generated in a similar way, by relaxing (4-iii), interchanging rows with columns in (5). If we note the parameters as b_h instead of a_h, the maximum likelihood estimate was

$$\hat{b}_h = \frac{\lambda(b_h)}{\lambda(1)} \qquad (8)$$

with $1 \leq h < k_2$.

Sexual Selection In Both Sexes

For generating models with sexual selection in both sexes, we only needed to maintain the condition (4-i). Therefore, for $K = k_1 \times k_2$ mating types we may introduce as much as (k_1-

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1)×(k_2-1) parameters for the most parameterized model, and a minimum of two (female and male effects) for the less parameterized model, in order to get a multiplicative model (no sexual isolation) with sexual selection in both sexes. By notational convenience, we fix the category k_1 in females and k_2 in males as having unitary propensity. Therefore

$$m'_{ij} = a_i b_j,\ i < k_1,\ j < k_2$$

$$m'_{ik2} = a_i,\ i < k_1$$

$$m'_{k1j} = b_j,\ j < k_2,$$

$$m'_{k1k2} = 1.$$

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

The maximum likelihood estimates were

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

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

Where $\lambda(a+b)$ stands for the sum of observed mating types having propensity a or b divided by the sum of their expected random mating frequencies (e.g. the sum of the expected frequencies of matings with propensity a_1 or $a_1 b_j$ for every male type, is p_{1i}), and $\lambda_{sex}(1)$ refers to the sum of cases that contribute with 1 to the propensity by the side of such sex divided by the corresponding sum of expected frequencies (e.g. in a multiplicative model as the above, every mating $k_1 \times j$ has contribution 1 by the female side and the sum of frequencies is p_{1k1}).

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The formulae in (9) is similar to (7) and (8). Note that (9) becomes (7) by considering every *b* as 1 while becomes (8) by considering every *a* as 1.

The percentage of sexual selection information corresponding to each sex, J_{S1} and J_{S2} in (Carvajal-Rodríguez 2018), would depend on the within sex population frequencies and on the propensity estimates.

SEXUAL ISOLATION EFFECT MODELS

Isolation (intersexual selection) corresponds to the class of non-multiplicative models, i.e. they can be obtained by relaxing the condition (4-i). Recall that we refer as sexual isolation to the effect of either positive or negative assortative mating.

If there is no sexual selection neither in females nor males, we may have only sexual isolation. However, this cannot be guaranteed in general as sexual selection is frequency dependent under non-multiplicative models (see below).

Let consider a model where unnormalized propensities are

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

Thus, homotype mating ($i \times i$) propensities are parameterized while heterotype are not. This model is non-multiplicative in general, because the contribution of the type *i* to the propensity is distinct in m_{ii} that in m_{ij} or in m_{ji} (although with an even number of types we could define a multiplicative model by setting $m_{ii} = 1 / m_{jj}$).

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By recalling the definition of marginal propensities in (3) we see that the condition for equal female marginal $m_{\text{Fem_i}} = m_{\text{Fem_j}}$ is

$$p_{2i}(a_i - 1) = p_{2j}(a_j - 1) \qquad (10)$$

and in males

$$p_{1i}(a_i - 1) = p_{1j}(a_j - 1)$$

If there is only one parameter, the different homotypes have the same propensity, thus $m'_{ii} = a$, whatever the type i. Then the condition (10) becomes $p_{2i} = p_{2j}$ and $p_{1i} = p_{1j}$ which for k_1 female and k_2 male types imply $p_{2i} = p_{2j} = 1 / k_2$ and $p_{1i} = p_{1j} = 1 / k_1$. Which means that under this symmetric model the occurrence of sexual isolation without sexual selection requires uniform frequencies.

In general, depending on the conditions in (10), the sexual isolation models are double effect models i.e. with sexual selection in at least one sex.

The maximum likelihood estimate was

$$\hat{a}_h = \frac{\lambda(a_h)}{\lambda(1)} \qquad (11)$$

with $1 \leq h \leq min\{k_1, k_2\}$.

Therefore, (11) provides the maximum likelihood estimate for the parameters of any sexual isolation effects model in which the mating considered as heterotype has an absolute propensity of 1 while the homotype mating has a different value. Note that this may involve models in which the homotype mating has higher propensity (positive assortative mating,

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$a_h > 1$) or vice versa, the homotype mating has lower propensity than the heterotype one (negative assortative, $a_h < 1$).

The number of parameters ranges from 1 to the maximum possible number of mating types considered as distinct homotypes, which is the minimum of $\{k_1, k_2\}$.

We could further define other sexual isolation models in which the homotype mating has absolute propensity of 1 while the different heterotypes have absolute value of a_{ij} (see S1 section in Supporting Information).

DOUBLE EFFECT MODELS

We have seen that the sexual isolation models may have double effect (sexual isolation + sexual selection) depending on the within sex frequencies. While it is not possible to assure that the isolation model have not sexual selection, we can however, develop models that are double in their effects still under frequencies satisfying (10).

Double Models Under Uniform Frequencies

The details of these models are given in the Supporting Information S1 section. Some of them include an additive parameter of the type $m'_{jj} = 1 + c$ restricted to $|c| < 1$ instead of $m'_{jj} = a$ restricted to $a > 0$. These additive parameters are required for the model to produce double effects under uniform frequencies.

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The ML estimates for some of these double effect models were obtained using the Nelder-Mead simplex numerical algorithm (see below).

General Double Effect Models

We also generated any particular model with propensities $m_{ij} = \theta_{ij}$ with the restriction that at least one propensity had value of 1. The MLE of the parameters was

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

where $\lambda(\theta_{ij})$ is defined as in (7).

The most parameterized model has K-1 parameters and coincides with the saturated model so that, only in this case, the estimates in (12) are the corresponding pair total indices (PTI).

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

Table 1. Mutual mating propensity models as defined by different parameters and their effects in a case with two different types at each sex ($k_1 = k_2 = 2$). When the value of m'_{ij} is not explicitly given is assumed to be 1.

Name (abbreviation)	Model	MLE	Effect

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Random (M_0)	$m'_{ij} = 1\ \forall i,j$		Random mating
Multiplicative Sexual Selection Models			
Female sexual selection (S_{Fem}-1P)	$m'_{11} = m'_{12} = a$	$a = \lambda(a)/\lambda(1)$	Fem sexual selection
Male sexual selection (S_{Male}-1P)	$m'_{11} = m'_{21} = b$	$b = \lambda(b)/\lambda(1)$	Male sexual selection
Two sex sexual selection (S2-2P)	$m'_{11} = ab$ else		2-sex sexual selection
	$m'_{12} = a$ else	$a = \lambda_{fem}(a)/\lambda_{fem}(1)$	
	$m'_{21} = b$	$b = \lambda_{male}(b)/\lambda_{male}(1)$	
Sexual Isolation Models	non-multiplicative		Isolation freq-dep
Symmetric sexual isolation (I-1p)	$m'_{11} = m'_{22} = a$	$a = \lambda(a)/\lambda(1)$	Isolation UF
Full sexual isolation (I-$2p$)	$m'_{11} = a_1$, $m'_{22} = a_2$	$a_i = \lambda(a_i)/\lambda(1)$	Isolation freq-dep
General Double Models (D-gp)			Isolation+Sex Sel
Saturated (M_{sat})	$m'_{ij} = a_{ij;}$, $m'_{k1k2} = 1$	$a_i = \lambda(a_i)/\lambda(1)$	

k_1: number of female categories; k_2: number of male categories; UF: uniform frequencies; $K = k_1 \times k_2$.

Model Selection And Multimodel Inference

Information-based model selection and multi-model inference can be applied for describing uncertainty in a set of models and performing inference on the parameters of interest (Burnham et al. 2011; Grueber et al. 2011; Barker and Link 2015; Claeskens 2016).

There are several information criteria at hand, although trusting on a single form of information criterion is unlikely to be universally successful (Brewer et al. 2016; Aho et al. 2017). In consequence, we considered two Kullback-Leiberg divergence-based measures plus the well-known Bayesian information criterion.

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INFORMATION CRITERIA

The Akaike information criterion (AIC) provides the link between the Kullback-Leiberg divergence and the maximized log-likelihood of a given model (Akaike 1973). The sample-corrected version AICc is asymptotically equivalent and may work better for small sample size so from herein we use the AICc version computed as

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

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

There is also a version for the symmetric K-L divergence (Jeffrey's) called the KICc criterion (Cavanaugh 2004; Keerativibool 2014). Because mate choice models can be described by the informational flow in the mating phenotypes, in the form of the Jeffrey's divergence (Carvajal-Rodríguez 2018), it seems adequate considering KICc criterion besides the AICc one.

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

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 (via the difference between BIC values) an asymptotic approximation to the Bayes factor applied for model comparison (Wagenmakers 2007)

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

Overdispersion

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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 divided by the expected under the most complex model (M_c) 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 $df = P_{Msat} - P_{Mc}$.

If $1 \leq v \leq 4$ this indicate 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 overdispersed data (Anderson et al. 1994; Richards 2008). The quasi-likelihood is the likelihood divided by an estimate of v, and so we can consider a quasi-likelihood version of the various information criteria, namely QAICc, QKICc (Kim et al. 2014) and QBIC 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.

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Model Weights

Hereafter, we denote by IC when referring generically to any information criteria. For a particular criterion and for any set of *R* models there is a minimum criterion value e.g. AIC_{cmin}, BIC_{min}, etc. Thus, the models can be ranked regarding the difference with that minimum

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

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)

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

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

MULTI MODEL INFERENCE

If we are interested in estimating a mating parameter, we can obtain the value from the best-fit model. Alternatively, we can make the inference based on a group of the most credible models. The latter strategy is called multi-model-based inference (Burnham and Anderson 2002; Burnham et al. 2011; Symonds and Moussalli 2011).

Therefore, we can perform a model averaged prediction for the parameters that are variables in the best model.

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Before performing the average, we should translate the different models to the same scale of 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 a equivalent model $m'_{11} = 4$, $m'_{12} = m'_{21} = m'_{22} = 1$, which is now in the same scale that 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 a parameter included in the confidence subset R_s we have

$$\widehat{m} = \frac{\sum_i^{Rs} w_i \widehat{m}_i}{\sum_i^{Rs} w_i}$$

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

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

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

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The use of the sum of weights to estimate variable importance in regression models has been criticized because multicollinearity among the predictor variables and the imprecision of the weight measures (Galipaud et al. 2014; Cade 2015; Galipaud et al. 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 multimodel inference would work well as we confirmed by simulation (next section).

Simulations

To test how well the exposed methodology is able to distinguish the different classes of effects models and estimate the mating parameters, we used the sampling with replacement algorithm in the program MateSim (Carvajal-Rodriguez 2018b) for generating mating tables by Monte Carlo simulation (see section S2 in Supporting Information for detailed explanation).

We have simulated mating tables corresponding to sexual isolation and sexual selection mate choice effects. These effects correspond to an a priori mating pattern defined by the mating propensity distribution (Table S1 and Fig. S1). The resulting mating tables were consequence of the mating pattern and the sampling process.

The mating tables consisted in two types of information (Fig. S2). First, the population frequencies (premating individuals) which were generated randomly for each simulation

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run. Note that the minimum phenotype frequency (MPF) allowed was 0.05. Second, we counted 500 mating pairs (n' = 500) for a hypothetical trait with two classes at each sex.

Because we simulated a species with high 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.

Concerning the mating pairs, the number of occurrences for each mating type $i \times j$ was obtained as

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

where n' is the sample size and m_{ij} is the normalized propensity of the mating pair.

The propensities assayed corresponded to random mating, $m'_{11}=m'_{22} = m'_{12} =m'_{21} =1$ (M_0 in Table 2); positive assortative mating, $m'_{11}=m'_{22} = 2$, $m'_{12}=m'_{21}=1$ (Isol in Table 2); and female sexual selection, $m'_{11}=m'_{12} = 2$, $m'_{21}=m'_{22}=1$ (SS_{Fem} in Table 2). The parameter estimates were averaged over 1000 runs for each case.

In Table 2, we present the results of the multimodel inference from the simulated tables. We may appreciate that random mating was perfectly estimated by the three IC methods. The mate choice effects models were also similarly estimated by the three criteria. The sexual selection model estimates were slightly less accurate which is caused by the variation in the population frequencies that may generate scenarios with double effect models (sexual selection + sexual isolation) and/or sexual selection in both sexes.

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Table 2. Average (standard error) parameter estimates for different models under sample size 500.

Model		m'_{11}	m'_{12}	m_{21}	m_{22}
M_0	Expected	1	1	1	1
	AICc	1.0±0.0000	1.0±0.0000	1.0±0.0000	1.0±0.0000
	KICc	1.0±0.0000	1.0±0.0000	1.0±0.0000	1.0±0.0000
	BIC	1.0±0.0000	1.0±0.0000	1.0±0.0000	1.0±0.0000
Isol	Expected	2	1	1	2
	AICc	2.0±0.004	1.0±0.013	1.0±0.001	2.0±0.004
	KICc	2.0±0.005	1.0±0.009	1.0±0.001	2.0±0.005
	BIC	2.0±0.006	1.0±0.003	1.0±0.001	2.1±0.006
SS_{Fem}	Expected	2	2	1	1
	AICc	2.1±0.183	1.9±0.013	1.0±0.007	1.0±0.006
	KICc	2.1±0.163	1.9±0.010	1.0±0.007	1.0±0.006
	BIC	1.8±0.010	1.8±0.013	1.0±0.009	1.0±0.006

M_0: Random mating model. Isol: isolation model; SS_{Fem}: Female sexual selection model.

The results were similar with lower sample size (n'=100, Table S2) but female sexual selection were less accurately estimated specially under the BIC criteria. The loss of accuracy is caused by some few cases having frequency values close to the minimum in

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which, after sampling, there were no power to distinguish from the random mating pattern. However, if the frequencies were uniformly distributed, i.e. p_{1i}=1/2 and p_{2j} = 1/2, then even under sample size of 100, the estimation of female sexual selection was accurate resulting in the correct parameter estimates (m'_{11}=2, m'_{12}=2, m'_{21}=1, m'_{22}=1) for the three information criteria (see $SS_{FEM}U$ case in Table S2).

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. 2015).

Sexual isolation between RB and SU morphs was observed in wild mating pairs in the mid-shore zone, likewise size-assortative mating in all shore levels (Rolán-Alvarez et al. 1999; 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 male the choosy sex in this species (Rolan-Alvarez 2007).

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Here, we analysed two *L. saxatilis* data sets (Table 3) corresponding to two sampling years (Rolán-Alvarez et al. 1999; Cruz et al. 2001) for estimating the mutual mating propensity parameters between the RB, SU and HY morphs.

Table 3. The population frequencies by year and sex, from Rolán-Alvarez et al. (1999) and Cruz et al. (2001) autumn data.

	Year	**Sample size**	**RB**	**HY**	**SU**
Female	1999	1222	0.36	0.12	0.52
	2001	598	0.29	0.13	0.58
Male	1999	1140	0.35	0.12	0.53
	2001	476	0.36	0.15	0.49

We first computed the information partition (Carvajal-Rodríguez 2018) and saw that there was significant sexual isolation in both data sets (J_{PSI} p value < 0.0001) while no significant sexual selection was detected.

Then, we considered 27 models from the different classes (Fig. 1 and Table S1), including M_0 (random mating, 0 mating parameters), various isolation, sexual selection and double effect models with up to 7 parameters and the M_{sat} (8 independent mating parameters) model. Each data set was analysed separately, computing the maximum likelihood estimates and the corresponding information criteria.

The data from 1999 were more dispersed and the uncertainty in the models higher than in the data from 2001. However, in both years and for the three information criteria, the

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models with at least 5% of weight were always double effect models (sexual isolation + sexual selection) with only 1 or 2 parameters. These models implied a pattern of positive assortative mating.

To better compare the mating pattern for the different data we evaluated the mating parameter values obtained by multimodel inference. The major difference among the different criteria and years corresponded to the mating involving hybrids. However, in every case, the most favourable matings were RB×RB and SU×SU and the less favourable mating was SU female by RB male (SU×RB). The three criteria produced similar relative estimates. Therefore, we present only the AICc multimodel estimates averaged over the two years (Table 4). For clarity, the estimates within each year were divided by the estimate of the HY×SU mating so that the value of m_{HYSU} is always 1.

The scenery depicted showed that the within-ecotype mating was preferred. RB males chose about twice as much the mating with RB females (m_{RBRB}) than with HY females (m_{HYRB}), while the mating with SU females (m_{SURB}) was ten times less frequent.

HY males had a quite variable mating pattern depending on the year, but it seems they preferred RB and HY females more than SU ones. The SU males showed the opposite pattern, they preferred SU over HY and RB females. Thus, as RB, the SU males also preferred the within ecotype mating although with not so strong effect.

Table 4. *Littorina saxatilis* data. Mutual-propensity estimates from multimodel inference under the AICc. Values are the average over the two year data plus/minus the standard error

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		Males		
		RB	**HY**	**SU**
	RB	1.9±0.09	1.5±0.38	1.0±0.0
Females	**HY**	1.0±0.0	1.5±0.34	1.0±0
	SU	0.16±0.01	1.0±0.0	1.7±0.23

Discussion

SIMULATIONS

We have simulated mating tables corresponding to random mating, sexual isolation and sexual selection mate choice effects. The random mating pattern was perfectly assessed independently of the sample size. Under the higher sample size (n' = 500), the multimodel inference accurately estimated the true effects both for sexual isolation and sexual selection. With low sample size (n' = 100) the accuracy was good for the isolation pattern but not so for the sexual selection pattern. This occurs because the sexual selection pattern underlying in the propensities matrix was not so well represented in the mating table in some runs, so the accuracy was lower in these cases because the pattern was not reflected in the sampling.

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Not surprisingly, BIC was slightly more conservative, while AICc presented slightly more accurate estimates in some cases. The KICc criterion performed similar to the best AICc and BIC cases.

In general, the estimation was accurate and even in the worst cases (lowest sample size and extreme phenotypic frequencies), the mean estimates were closer to the real value than to random mating.

EXAMPLE

Previous studies in the Galician *L. saxatilis* hybrid zone showed that mate choice favours within-morph pairs, whereas pairs including at least one hybrid morph seems to mate randomly. The latter is not so clear in our analysis, may be due to the low number of hybrid mating in the data (Fig. S3).

The estimates obtained by multimodel inference support the positive assortative mating for the ecotype. In addition, another result emerged from the analysis: The pair RB male with SU female, has less mutual preference than SU male with RB female ($m_{\mathrm{SURB}} < m_{\mathrm{RBSU}}$).

This pattern could be related with a physical difficulty for the mating involving bigger RB males with the smaller SU females, as mating pairs with female bigger than the male (a typical trend in gastropods) are somehow more frequent (E. Rolán-Alvarez personal communication).

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In addition to the mating pattern depicted by the multi-model approach, we also got the relative estimates of the mating parameters. Testing the reliability of these estimates is, however, out of the scope of the present manuscript, and it was left for future work.

GENERAL

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

Multimodel inference has been however, rarely utilized in the context of sexual selection and isolation effects of mate choice. Here, by proposing general models causing different type of effects, jointly with their maximum likelihood estimates, we are providing the first standardized methodology for model selection and multimodel inference of the mating parameters involved in sexual selection and isolation effects.

The set of *a priori* models (including user-defined ones) permits to perform an *a posteriori* quantification of the data-based evidence and provide confidence sets on plausible non-trivial models while letting at the same time, multi-model inference on the parameters.

The approach was implemented by allowing three different information criteria. Under the scenarios assayed, they performed similarly for simulated and real data.

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The proposed methodology should ideally work under scenarios for which the availability of individuals is not 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 that the mating pairs. In the case of monogamous species with low population size, the population frequencies may be altered during the reproductive season and so, the distribution of propensities could not define the same sexual selection pattern over the season. This could happen because the sexual selection effects are frequency dependent. On the contrary, the sexual isolation effects are not frequency dependent, and should not be affected by the variation of the population frequencies(Carvajal-Rodriguez 2018a).

The developed methodology has been fully implemented in a program called InfoMating available at http://acraaj.webs.uvigo.es/InfoMating/Infomating.htm or upon request to the author.

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SUPPORTING INFORMATION

The Supporting Information file includes:

S-1) Mutual Mating Propensity Models

S-2) Monte Carlo simulation of mating tables

S-3) Example data input file.

FIGURE LEGENDS

Fig 1. Mating models as defined by their effect after relaxing some of the conditions imposed to the random mating model M_0.