

Dear Sara Magalhaes, I have resubmitted a revised version of the preprint

<https://doi.org/10.1101/305730>

"Multi-model inference of non-random mating from an information theoretic approach". I also attached a pdf with the changes in red.

I fully acknowledge the positive feedback from you and the reviewers. All of the comments has been addressed. Please, find below the detailed answer to all questions. The questions appear in black bold and the answer in normal font.

### **Comment from the editor**

All reviewers found merit in the approach you're proposing, but they also raised several issues. I concur with their appreciation and comments. I think this model could be useful to people working on sexual selection. However, I think that the clarity of the manuscript could be improved. In addition to the referees comments, I have a few of my own. I hope that addressing all of them will significantly improve the clearness of your manuscript.

- 1. As an empiricist, I would like to have some information on the type of experimental set-up that should be used in order to apply the model to the data. It is valuable to include an application of the model to empirical data, but this does not solve the problem, because the experimental set-up used is not specified in this example.**

### RESPONSE

The type of experimental set up is any that permits to obtain a mating table jointly with population phenotypic frequencies. However, the proposed framework assumes random encounters, i.e. the occurrence of an encounter between two phenotypes depends on the population phenotypic distribution. Then the mating pattern is the product of the population phenotypic distribution and the individual preferences. As a consequence, 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. 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 mutual-propensities might not define the same sexual selection pattern over the season.

The power of the information indices in such situations have been studied in a previous paper (Carvajal-Rodríguez, 2019).

Also, to study the impact of monogamy on the multimodel inference I have divided the simulation section in two subsections namely 4.1 polygamous species and 4.2 monogamous species (lines 621-637) and added a new appendix C for the estimates for monogamous species with large and small population size.

The above is discussed in lines 722-739 (discussion simulation section).

Concerning the example application I have now added a couple of lines indicating how the analysed data were obtained by the authors (see lines 656-662 in section 5)

- 2. In line with this, both the Introduction and the Discussion would gain in generality if these sections would try to reach out to empiricists. For example, the Discussion could evaluate whether incomplete set-ups (e.g., with only one type of female choosing) could still provide valuable information. Also, the Discussion should integrate the empirical example with the model, and not address them in two separate parts.**

#### RESPONSE

Yes, this is a very good idea. Concerning incomplete set-ups I added a new appendix-D to show how the analysis can be performed with only one phenotype from one sex (e.g. females) and two or more from the other. This is now briefly commented in the discussion (lines 758-763). Concerning the empirical example, it is now discussed in the general section.

- 3. I agree with one of the reviewers that the definitions provided in the Introduction are slightly cumbersome. They are not necessarily incorrect, but they are not the most widely used in the sexual selection field. At least, there should be a bridge built between the definitions provided in the text and the most widely used in the field. I was particularly puzzled by presenting mate choice as a feature that is dissociated from sexual selection, whereas I see it as part of the sexual selection process (e.g., line 62). I realize that this may be because I see sexual selection precisely as a process, whereas it is presented in the introduction as a pattern. All in all, I find this presentation slightly confusing, but again, not necessarily wrong. Also, and related to my previous point, the scope of the introduction should be widened beyond providing definitions if the aim is to attract a wider range of readers.**

#### RESPONSE

Yes I agree with your points. Besides, this is a recurrent problem for us with the different definitions of sexual selection. I have completely redone the Introduction section (new lines 30-100) while trying to build a bridge between the classical concepts and the population genetic definitions I will use.

First I begin with the Darwin definition of sexual selection and the distinction, already made by Darwin, of the two biological mechanisms mate competition and choice. Then I briefly mention that sexual selection has been controversial from its very beginning to nowadays. I argue that the controversy may be explained in part by the distinct emphases that different scientific fields put on the various aspects of sexual selection theory. To make things worse sexual selection is sometimes described as a process and sometimes as a pattern.

At this point (lines 49-55), the concepts of pattern and process are defined and the distinction between them is noted.

I also indicate (lines 56-65), that sometimes the distinction between pattern and process may be obscured because a biological concept can be meaningfully defined as both a process and a pattern. I show this is the case with sexual selection which when viewed as an evolutionary agent of change is a process, but it is not when viewed as a pattern of change in frequencies.

Now (lines 66-70) I adhere to the definition of sexual selection in population genetics where the pattern of sexual selection is caused by the process of mate competition (that produce intrasexual selection) and the process of mate choice (that produce intersexual selection).

Then I clarify (lines 79-83) the meaning of mate competition in its broad sense and the pattern it generates (intrasexual selection) and I also clarify the meaning of mate choice and the pattern it generates (intersexual selection and assortative mating, lines 84-89)

Afterwards I give several references for extended details and alternative definitions.

To end the bridge connecting sexual selection classics with the definitions that will be used, I summarize that “the evolutionary consequences of mate competition and mate choice are sexual selection and assortative mating” and give the definitions of the corresponding patterns for discrete traits in terms of change in the phenotype frequencies with respect to the population, i.e. sexual selection; or with respect to the mating sample, i.e. assortative mating (lines 96-103).

Now I return to the original introduction (line 104-) to indicate that the observed deviation from random mating can occur in the form of sexual selection or assortative mating patterns and then introduce my previous work...

- 4. In general, there are several spelling and grammatical mistakes throughout the manuscript. I provide a few examples below but urge you to carefully double check the article throughout before resubmitting it.**

RESPONSE

Done

## 5. Minor comments:

- Line 11: “to perform”; Done
- Line 13: please state “in the marine gastropod” before the species name. Done
- Line 22: explain what you mean by “both kind of patterns”. Done
- Line 22: remove “models”. Done
- Line 51: “a posteriori” from what? Done
- Lines 102-103: replace by “Let a sample have n’ matings”. Done
- Line 123: replace by “are either known or they need to be estimated”. Done
- Line 131: “it is convenient”. Done
- Line 135: remove “Let”. Done
- Lines 157-158: either you explain which conditions you are referring to or remove this and state it later. Done (removed).
- Line 160: Replace “Following” by “Next”. Done
- Line 165: “within all others (it is...”. Done
- Line 177: remove the first “model”. Done
- Line 186: “if some males have a different value than the other matings”. Done
- Line 191: “relaxing the first”. Done
- Line 193: “produce an assortative mating pattern”. Done
- Line 194: “involves mate choice, which”. Done
- Line 202: “models”. Done
- Line 205: “there should be no”. Done
- Line 215: “all mate types mate at an equal rate”. Done
- Line 228: “there can be as much”. Done
- Line 246: “all femate types mate at an equal rate”. Done
- Line 267-270: I found this section pretty unclear, can you reformulate?  
Done (lines 304-310)
- Line 286: remove “Let”. Done
- Line 312: “produces”. Done
- Line 377: “to distinguish”. Done
- Line 423-424: It would be nice to add a few sentences to explain what you’ll be doing in this section.  
Done (lines 464-469)
  
- Line 424: “applied to describe”. Done
- Line 425: “to perform”. Done
- Line 461: “this indicates”. Done
- Line 489: the average of what? Done  
of the estimated parameter values (line 534)
- Line 510: “because of”. Done
- Line 566: please explain “likewise size-assortative mating...”.  
within morph size-assortative mating (line 650)
- Line 581: “possibly”. Done
- Line 619: “from these models”. Done
- Line 623: “SU males do not discriminate between female ecotypes”. Done
- Line 783: “consists in building”. Done

RESPONSE

Done

## Comments from the reviewers:

### -Reviewer 1

#### General comment

I have reviewed the preprint entitled “Multi-model inference of non-random mating from an information theoretic approach” by Antonio Carvajal-Rodríguez (doi: <https://doi.org/10.1101/305730>). Based on previous work (Carvajal-Rodríguez 2018. Non-random mating and information theory. *Theor. Pop. Biol.* 120:103-113) the author derived procedures for performing multimodel inference behind from a mating table. My first comment is that the manuscript is not easy reading and the notation is not always introduced in the right place. For instance, on page 7  $m_{ij}$  refers to the normalized mating propensity, but its meaning is not clear until next page. I know this was defined in the previous paper, but it would be helpful to have this clear from the beginning. Starting from the most reduced random mating model, a subset of models are obtained by relaxing some conditions. Mate choice results when the assumption of multiplicability is relaxed. On the other hand, when multiplicability is assumed one obtains a pattern of sexual selection. The author then considers several models of increasing complexity and provides the MLE estimates of the different parameters.

#### RESPONSE

Regarding the  $m_{ij}$  definition I have followed the reviewer suggestion and have explicitly defined it the first time it appears (lines 162-).

Model selection is based on information theory, which was previously shown by the author to provide a valuable framework to make inferences. Simulations suggest that the framework is adequate to estimate the best model, and the procedures were applied to a real case with the gastropod *Littorina saxatilis*. Overall, I think the author has done a nice job and his framework can help to understand the role played by the different parameters in a particular case. My main complaint is that the paper is not easy to follow and could be regrettably ignored by some experimentalists. For example, the software MateSim is not user-friendly and it would be very helpful to implement an easier (e.g. windows-based) version. One thing is to perform numerical simulations to explore the parameter space or to test the validity of a given framework, and quite another is to offer a software to be of general use. I suggest the author to put some effort on this last point.

#### RESPONSE

Thank you for the positive feedback. I have tried my best following yours and the other reviewer suggestions to improve the manuscript legibility. Concerning the program MateSim, please note that it is independent of the methodology presented here. I agree however that a window interface is always helpful and I intend to produce a Python-based user-friendly interface in the near future.

#### Specific comments

**1. Line 37, page 3: “Mate choice (or intersexual choice) is a process driven by different preference between different mating types”. Not only because the pattern of mating which arises is in part due to mating preferences. Other processes (e.g. spatial distribution of types) can also affect the mate choice.**

#### RESPONSE

Yes, agree. I have extended the mate choice definition (lines 82-88): “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).”

**-Reviewer 2** Alexandre Courtiol

- 1. This preprint introduces a methodology aiming at studying matings between discrete types of individuals. Specifically, the methodology allows both for the estimation of mating propensities and for performing selection among different statistical models: it can compare models that differ in their assumptions about the mating propensities, which translates into investigating whether observed mating patterns are consistent with either sexual selection, assortative mating, or both. The author has implemented the new methodology in a free software called InfoMating. The author performs a rigorous methodological development which is conceptually interesting and which could benefit many empiricists. I want to highlight the conceptual interest (he is not just trying to sell a free software). The methodological development is directed connected to evolutionary biology and could interest people working on sexual selection, mate choice and/or speciation. I had provided extensive review comments on an earlier version of this manuscript for a journal. At the time, I was particularly criticising its presentation (and not the formal content, which was very good from the first version I got a chance to read). I am very pleased to say that the author has done a great job, substantially revising his paper in light of my (and others’) comments. Albeit remaining a paper rather slow to digest, the presentation is now much clearer and all my main criticisms have now been addressed. So I do recommend this paper for... publication(?)... or whatever PCI Evol Biol will do with it! If the author wants to submit this, I think it would now have good chances in many general journal in biology that is not reluctant to publish a few greek letters.**

## RESPONSE

Thank you for the positive feedback.

- 2. If it is possible, I think that minimal effort could further improve the paper. What is presented is mostly very good aside one part that I still find confusing: I do not quite understand how the analysis of the simulated data was done. I assume that this is the result of a model averaging, but I do not see where the models considered have been described. In each simulation assay, the author simulated the data according to one model (as described in Table 2), and I am tempted to assume that the estimation of mating propensities was based on all 5 models shown in the table, but as far as I can see, this is not mentioned. It is also unclear how often the best model turns out to be the one used to simulate the data. Doing so would be one way to actually fulfil**

**the expectation introduced at the beginning of this section (“To test how well the exposed methodology is able to distinguish the different classes of models”).**

## RESPONSE

As the reviewer correctly suggest in each case, the data is simulated accordingly to one model (Table 2). I agree that it was not clear how the estimates were obtained. I hope this is now explicit in the added paragraph before Table 2 in lines 590-605:

“Once the mating tables were obtained I proceeded with the multimodel inference analysis using InfoMating. Note that there were 1 000 different tables for each simulated case so, in the simulation study, it is better to consider the mean multimodel estimates instead of the full list of analysed models (which would imply 1 000 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 multimodel 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, 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 multimodel inference as explained in the previous section. Thus, for each of the 5 simulated cases, 1 000 parameter estimates were obtained, and their average and standard error computed (Table 2).”

- 3. Also, with respect of the simulation, I would have like to see just a little bit more. In particular, since the author concludes “[t]he proposed framework should ideally work under scenarios where the availability of individuals is not affected by the matings that have already occurred”, a question is naturally popping up in my mind: What happens when this assumption is violated? In some taxonomic groups, such as mammals, this assumption is actually very doubtful. Perhaps not in the sea snails that the author studies, but even in largely abundant species the assumption is likely to be violated if there is local competition for mates, or if the number of potential mate encountered is low (due to spatio-temporal constraint on mate sampling). For these reasons, I would have like to see results of an additional simulation analysis based on more limited number of individuals. This would have shown how robust the inference method is in the case of the departure of the assumption of constant frequency of types. This would have thus helped empiricists to anticipate with respect of their favourite species if InfoMating is a tool that may be suitable for them or not. Perhaps InfoMating allows for one to run such tests easily, I do not know. Also, it would be fair to mention local competition and spatio-temporal constraints in the conclusion, as just having more individuals than mating pair really does not cut it. For these reasons, I would have like to see results of an additional simulation analysis based on more limited number of individuals. This would have shown how robust the inference method is in the case of the departure of the assumption of constant frequency of types. This would have thus helped empiricists to anticipate with respect of their favourite species if InfoMating is a tool that may be suitable for**

**them or not. Perhaps InfoMating allows for one to run such tests easily, I do not know. Also, it would be fair to mention local competition and spatio-temporal constraints in the conclusion, as just having more individuals than mating pair really does not cut it**

## RESPONSE

I agree that the assumption of the modelling framework is violated for example when the species is monogamic and the population size is small. In this case, the population frequencies may be altered during the reproductive season and so, the mating process might not define the same non-random mating pattern over the season. I have extended the simulations (see section 4 lines 616-637) to study the effect of low sample size in large population polygamous and monogamous species (supplementary tables C1-C3). I have also added a worst scenario of a monogamous species with small population size (supplementary Table C4).

It can be seen that the performance of the multimodel inference is affected by the sampling and the mating system (polygamous or monogamous) but it is still quite robust for detecting non-random mating deviation in the parameter values except in the worst scenario. Under this case and when most of the adults were involved in the mating 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 C4).

The performance of the information statistics for monogamous species (sampling without replacement from the view of the available phenotypes have been studied in a previous paper (Carvajal-Rodríguez, 2019).

By other side, it is true that local competition for mates and/or space-temporal constraints may affect the assumption of mating as a process with replacement provided that the number of individuals in the patches is low and there is monogamy (see discussion lines 731-740).

#### **4. Another small caveat is that Aside these minor criticisms, I have a small list of trivial comments:**

**-L61: I would drop the “However” as there is not explicit contradiction. Done**

**-L86: I would put caps on “pair total indices”. I left without caps because the original work (Rolán-Alvarez and Caballero 2000) did not use caps.**

**- Eq2: the A and t(s) do not quite match the convention used in other equations and do not seem defined. Done**

**-L165: “withIN all the other”. Done**

- L166: perhaps “When random mating occurs”, instead of “When mating is at random”. Done
- L246: “they mate equal in average” is not quite idiomatic. Changed by “all female types mate at an equal rate”
- Fig2: Say that rows are males and column females. Done, but rows are females and columns males.
- L334: What is a “joint isolation index”? This falls from the sky and should be introduced (not simply referred to another paper). Done
- L356: “When  $c = 1$ ”, not “With  $c = 1$ ”. Done
- L382-383 and elsewhere: two different signs are used to represent alpha and it makes things a little confusing since they do not look alike at all (at least in my pdf viewer). Done
- L403: “at least some is” seems grammatically incorrect. Changed by “at least some are”
- L430: dash missing between “so” and “called”. Done
- L551-553: Some extra dots are present in the text of the table legend. Done
- Fig3: Why “Rep3” in the model name? In Fig 5: Because of the three repetitions of the b parameter. Now stated in the foot.
- L617: Is SfemC-2Pc actually better than D-2P-Rep3? In fact it is not because it was not the best when the whole set of models was included.
- L639-641: I would drop this confusing sentence because sexual selection is retained in the final best model. Done
- L656: space missing before “or”. Done

RESPONSE

Done

-Reviewer 3

1. This manuscript provides a statistical method for estimating which processes (mate choice vs intrasexual competition) underlie patterns of non-random mating, in the case where there is a finite number of discrete phenotypes in each sex. It applies maximum likelihood and model selection methods to the mating table (i.e. the table showing which male-female pairs mated). The statistical framework is sound as far as I could tell, although I would recommend an expert in model selection be invited as reviewer if this has not been done already. However, I think the interpretation of the statistics diverges from mainstream sexual selection theory (in particular in the use of words like ‘mate choice’, ‘intrasexual competition’ and ‘sexual selection’) and is likely to confuse readers who do not understand the formalism. The manuscript uses the following definitions: sexual selection: ‘the a posteriori observed change in gene or phenotype frequencies in mated individuals with respect to population frequencies’ intrasexual selection (paraphrased): some individuals (or classes thereof) have uniformly higher mating success than others, independent of the phenotypes of potential partners mate choice: ‘a process driven by different preference between different mating types’ assortative mating: ‘the a posteriori deviation from random mating within mated individuals’ The most problematic are the definitions of mate choice and intrasexual selection. Most authors (e.g. the classic monograph on sexual selection: Andersson 1994) use ‘intrasexual selection’ in relation to processes like contest and scramble competition, which

**involve competition among members of one sex without the active involvement of the other sex. In contrast, ‘intersexual selection’ or ‘mate choice’ are generally used where the other sex actively influences the outcome of competition. Doubtless this distinction is hard to make cleanly in all cases, but the current manuscript uses a fundamentally different conceptual taxonomy. E.g. imagine a scenario where males are widely dispersed and never interact with one another. Females travel from male to male and evaluate their phenotypes, mating with preferred males. If some males are preferred by all types of females, the authors would classify this as ‘intrasexual selection’ rather than ‘mate choice’. In their usage, mate choice only occurs if there is variation in preferences among choosers.**

## RESPONSE

I have completely redone the Introduction section (lines 30-100) giving some context and making connections between the different definitions. I also make the distinction between process and pattern. The latter was previously expressed as “a posteriori observed” which was obscure.

I explicitly adhere to the definition of sexual selection as used in population genetics, i.e. sexual selection is caused by the processes of mate competition, that may produce intrasexual selection patterns, and/or processes of mate choice, that may produce intersexual selection and/or assortative mating patterns.

The definitions of mate choice and mate competition are extended: the process of mate competition is referred in the broad sense, including the access to matings by courtship, intrasexual aggression and/or competition for limited breeding resources. 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... The pattern obtained by mate choice may be reflected into a change in trait frequency in the other sex (intersexual selection) and/or into a pattern of correlation for the trait within the mating pairs (assortative mating).

Summarizing, the evolutionary consequences of mate competition and mate choice are sexual selection and assortative mating. When the traits under study are discrete, the sexual selection pattern corresponds to the observed change in gene or phenotype frequencies in mated individuals with respect to population frequencies (Hartl and Clark, 1997). Similarly, assortative mating corresponds to the deviation from random mating frequencies measured within matings.

**2. The mating table does not contain the relevant information to distinguish between inter- and intra-sexual selection in their traditional senses, whereas it can distinguish between these processes using the authors’ definitions. I’m agnostic about whether the authors’ distinction is biologically useful. Perhaps some people will find it informative for their system. I would consequently recommend that the manuscript be re-written to make clear exactly what is being estimated and making the deviation from common usage clear (or, even better, coming up with some new terms that better capture the meaning of the**

authors' definitions).

## RESPONSE

Yes. 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. The goal of the present work was to propose a new tool that help to distinguish among different alternative processes behind the observed mating pattern.

Of course, the relevant information for distinguishing among the mating behaviours requires knowledge about the species under study. However, the mating table may contain relevant information to distinguish between processes of mate competition (intrasexual i.e. without the active involvement of the other sex) vs mate choice (where the other sex actively influences the outcome of competition). Consider for example the following model of mutual mating propensities and assume this model is clearly the best fit to some data in a mating table

$$\begin{matrix} a & 1 \\ a & 1 \end{matrix}$$

where  $a = 2$

Let the males be the choosier sex, then this model indicates that there is a pattern of (intra)sexual selection explained by the parameter  $a$ , which may imply that the males in the first column are  $a$  times more 'competitive' (in whatever sense) than the males in the second column.

Alternatively, consider the same model but for a species in which females instead males are the choosers, then the observed (inter)sexual selection pattern indicates that there is female choice favouring first column males. Of course, if both sexes are choosers we cannot distinguish between both situations but we have discarded other models and obtained an estimate of the parameter  $a$ , then we will need additional information other than a mating table, to distinguish between intra and intersexual causes.

Furthermore, the best fit model could be more complex e.g.

$$\begin{matrix} a & 1 \\ a & c \end{matrix}$$

where  $a = 2, c=3$

Now, if both sexes are choosers we face the same problem as before but in this case we know, yes or yes, that there is at least a mate choice component with parameter  $c$ . So, even in this case the study of the pattern in the mating table is giving some clues about the processes that may cause it.

**3. The definition of sexual selection is less fundamental to understanding this manuscript. However, I should note that most authors define sexual selection as a type of natural selection that arises via competition for mates or fertilisation opportunities (e.g. Andersson 1994; Shuker 2010). Thus, it is important to understand not only how individuals differ in mating success, but also how such differences translate into variation in individual fitness. Under the authors' definition, 'sexual selection' may not be selection at all.**

#### RESPONSE

As already commented, I have completely redone the Introduction section (new lines 30-100) while trying to build a bridge between the classical concepts and the population genetic definitions that will be used. If possible, please see also my response to the recommender.

From the classical definition (e.g. Andersson 1994; Shuker 2010) sexual selection may be viewed as a process i.e. an agent of evolutionary change but can also be viewed as a pattern of evolutionary change.

In this work, I adhere to the definition of sexual selection as 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).

Summarizing, 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 change 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 when measured within matings (Rolán-Alvarez and Caballero, 2000 and references therein).

Thus, the definition I give of sexual selection view it as a pattern. Of course, one can also say that the process of sexual selection shapes the pattern of phenotype frequencies within matings and may ask how this is linked with the individual fitness variation. This is not a trivial topic, as demonstrated by the current debate about sexual conflict and cooperation (see for example Parker and Pizzari, 2015).

Note that from an empirical point of view it is much easier to study patterns than processes and this is why the biological mechanism of natural and sexual selection are not so well known as the patterns they provoke. The goal of the present work is to propose a new tool that may help to distinguish among different alternative processes behind the observed patterns.

**4. Lastly, the authors' verbal definition of assortative mating does not quite**

**match up to their mathematical definition. E.g if some individuals have uniformly higher mating success than others, they may be overrepresented even among mated individuals, indicating a deviation from random mating even among this subpopulation. But the authors would not consider this assortative mating. The verbal definition can be fixed by referring to ‘matings’ rather than ‘mated individuals’.**

**If these definitional issues were explained clearly, I think this manuscript would make a useful contribution to the literature.**

## RESPONSE

Done

The current definitions are (lines 97-101): “sexual selection corresponds to the observed change 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 when measured within matings (Rolán-Alvarez and Caballero, 2000 and references therein).”

Just to clarify the point. It is true that A-type males having higher mating success would be overrepresented among mated individuals with respect to the expected by random from population frequencies and so the sexual selection pattern would be correctly detected. The assortative mating pattern is measured as the deviation of the observed frequencies of mating phenotypes with respect to the expected by random mating when calculated using the phenotype frequencies within mated individuals. Because the higher mating success of A-type males, they frequency would be overrepresented within mated individuals and we do not expect any deviation from random mating when computing assortative mating as indicated. We only see such deviation if there were mate choice.

Example:

Males A have more success. The population frequencies are uniform and equal to 0.5. Consider the mating table with 1,000 matings (rows are females, columns are males)

	A	B
A	450	50
B	450	50

A-type males are clearly overrepresented. The phenotype frequencies computed within the matings are A-males =  $900/1000 = 0.9$ , B-males =  $0.1$ , A-females = B-females =  $500/1000 = 0.5$ . The expected number of matings  $E(AA)$  under random mating computed using the frequencies within matings is  $0.5 * 0.9 * 1000 = 450$ ,  $E(AB) = 0.5 * 0.1 * 1000 = 50$ ,  $E(BA) = 450$  and  $E(BB) = 50$ . Clearly there is no deviation between observation and the random mating expectation within matings so there is no assortative mating pattern.

## 5 Minor comments:

**Line 32: I don't think 'variation in mating preferences' is necessary, just that there exist mating preferences at all (see above). Also intrasexual competition should be mentioned here already.** Agree. The section was redone completely.

**Line 37: Maybe something like 'driven by preferences for some traits over others'. The term 'mating type' has an existing meaning (molecular characteristics determining the compatibility of gametes) and in any case I don't think it's a good term here. Maybe just 'traits' or 'phenotypes'.** Done. Whenever necessary I changed it by "mating classes".

**Line 47: Is this really a 'decomposition'?** Changed. The whole section has been redone.

**There is an unusual number of typos and other small errors in this manuscript. I started off noting them as I read, but there were so many that I gave up. I would recommend that the authors get a colleague to read it before sending it out for review.** Done.

**I noticed two typos in the maths:**

**Line 144: Mismatch between 'theta' on left-hand side and 't' on right-hand side**  
Done

**Line 226: 'for all i'** Done

## RESPONSE

Done.

Sincerely,

Antonio

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Web: <http://acraaj.webs.uvigo.es>*

## References cited in this letter

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