QInfoMating: Sexual selection and assortative mating estimation

A. Carvajal-Rodríguez*

Centro de Investigación Mariña (CIM), Departamento de Bioquímica, Genética e Inmunología. Universidade de Vigo, 36310 Vigo, Spain.

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

email: acraaj@uvigo.es

Keywords: quantitative traits, sexual selection, assortative mating, Jeffreys divergence, infomating.

Abstract

Motivation: Sexual selection theory is a multifaceted area of evolutionary research that has profound implications across various disciplines, including population genetics, evolutionary ecology, animal behavior, sociology, and psychology. It explores the mechanisms by which certain traits and behaviors evolve due to mate choice and competition within a species. In the context of this theory, the Jeffreys divergence measure plays a key role in quantifying the information obtained when a deviation from random mating occurs for both discrete and continuous data.

Despite the critical importance of understanding mating patterns in the context of sexual selection, there is currently no software available that can perform model selection and multimodel inference with mating data. Recognizing this gap, we have developed QInfoMating, a dedicated software program designed to address this specific need. QInfoMating is poised to significantly advance research in the field by providing a comprehensive solution for analyzing and interpreting mating data within the framework of sexual selection theory.

Results: The program QInfoMating incorporates a user-friendly interface for performing statistical tests, best-fit model selection, and parameter estimation using multimodel inference for both discrete and continuous data.

Availability and implementation: QInfoMating, its source code and documentation are available at https://acraaj.webs.uvigo.es/InfoMating/QInfomating.htm.

Contact: acraaj@uvigo.es

Introduction

By this point, there is no doubt about the importance of sexual selection theory and its impact in areas such as population genetics, evolutionary ecology, animal behavior, and even sociology and psychology. There are several strategies for measuring the impact of

sexual selection, depending on the field of study and whether the available data pertain to discrete or continuous traits. In previous works (Carvajal-Rodríguez 2018, 2020, 2023), it has been demonstrated that the symmetric Kullback-Leibler divergence (Jeffreys divergence, noted as J_{PTI} in Carvajal-Rodríguez 2018) corresponds to the increase in information when mating is not random. This divergence can be broken down additively into one component that measures sexual selection and another that measures assortative mating and these statistics can be applied both to discrete and continuous data. Therefore, J_{PTI} unifies the measure of sexual selection for both discrete and continuous traits (Carvajal-Rodríguez 2023).

The program QInfoMating is a major update of the previous Infomating program (Carvajal-Rodríguez 2018, 2020) that incorporates the new quantitative methods developed in (Carvajal-Rodríguez 2023). The previous version (Infomating version ≤0.4) have already been utilized in empirical studies (Estévez et al. 2020; Lau et al. 2021). While there are other software options available for computing sexual selection and assortative mating from mating tables, such as JMating (Carvajal-Rodríguez and Rolan-Alvarez 2006), to the best of our knowledge, QInfoMating is the only software for applying model selection theory to mating data, enabling the estimation of sexual selection and assortative mating for both discrete and quantitative data.

Methods

The program can be used via the user interface (Figure 1-A) or directly from the console. Detailed usage instructions, specifying input formats, parameter meanings, models, and an explanation of result files, are provided in the program's manual. In summary, QInfoMating offers the capability to analyze both continuous and discrete data for sexual selection and assortative mating. It begins by conducting relevant tests

and subsequently identifies the best-fit model. The program employs multi-model inference techniques to estimate parameter values.

Difference of QInfoMating with the previous version (Infomating)

Unlike the previous version (Infomating), which lacked a user-friendly interface and only analyzed discrete data, QInfomating now accepts continuous data as input (see the format specification in the program manual). When continuous data is provided, the new statistical tests for sexual selection and assortative mating detection, as developed in (Carvajal-Rodríguez 2023), are performed.

In the case of continuous data, model selection is only executed if any of the statistical tests yield a significant result. Following this, the program automatically calculates the frequency distribution (classes) for the continuous data and proceeds with multi-model estimation. The algorithm for obtaining the frequency distribution is detailed in the program manual.

In the new version, there are also differences in the set of models considered for discrete and continuous cases. In the discrete case, there is a default set of models that can be modified by the user. Conversely, for the continuous case, the program, rather than the user, selects models based on the statistical significance of various tests.

Specifically, if there is a statistically significant pattern of assortative mating but no sexual selection, the program uses a set of models that incorporate mate choice and bias in conjunction with random mating and the saturated model, but it does not include competition models. On the other hand, if there is a statistically significant pattern of both assortative mating and sexual selection in both sexes, QInfoMating includes double-effect models among the models to be tested. These models are not included by default when the data is discrete.

In any case, QInfoMating allows us to generate a mating table from the quantitative data, enabling us to create an input file for analysis in discrete mode, employing the default set of models or the ones selected by the user.

Real data use case

Echinolittorina malaccana, a marine intertidal snail commonly found on rocky shores in the Indo-West Pacific region (Reid 2007), exhibits mate selection behaviors. Males have shown a clear preference for females slightly larger than themselves (Ng et al. 2019). In a subsequent study conducted by Lau et al. (2021) the continuous trait of size (specifically, shell length) was transformed into categorical variables by creating four distinct size classes. This transformation allowed for the creation of a mating table, (see Supplementary Table S1), which enabled the utilization of the advanced multimodel inference techniques available in the previous version of the program (Infomating). This approach provided a more profound insight into the intricate dynamics of mate choice. The analysis ultimately confirmed that the most suitable model for mate choice in Echinolittorina malaccana involves a size bias, resulting in both assortative mating and the presence of sexual selection favoring larger individuals.

In a recent study (Carvajal-Rodríguez 2023), the same onshore data, originally presented in Lau et al. 2021, and accessible via (Rolán-Alvarez et al. 2021), was directly used without converting the continuous shell length trait into discrete classes. This approach aimed to demonstrate the computation of Jeffreys divergence indices (Carvajal-Rodríguez 2018) for quantitative traits. The research revealed that the statistical tests for the quantitative data yielded similar conclusions as the previous analysis using the statistical tests for discrete data. However, the quantitative data lacked the necessary structure for applying the model selection methodology.

In this current study, we will leverage QInfoMating to conduct a quantitative analysis of the same dataset. The program will apply the quantitative statistical tests and automatically transform data into classes to facilitate model selection and multi-model inference. This analysis aims to compare the results with those obtained in Lau et al. (2021). For consistency, we will employ the Akaike Information Criterion (AIC), the same criterion used in Lau et al., and additionally, the more conservative Bayesian Information Criterion (BIC) to showcase the software's versatility and utility.

Results

A CSV file containing shell length data for individual snails and their mate pairs served as the input for QInfoMating (referred to as QIM). Although the original study by Lau et al., used four classes, QIM segmented the data into three classes (Supplementary Table S2), before proceeding with the model selection process.

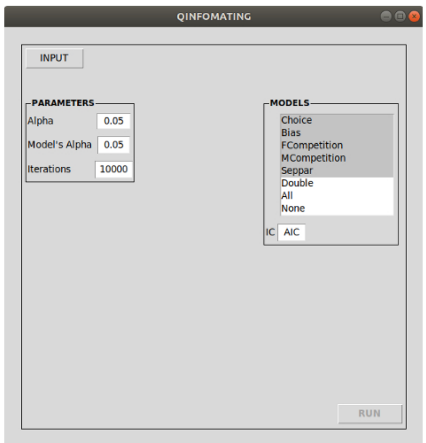
If Figure 1-B the best-fit models from Lau et al 2021 (B-7P model) and the two best obtained by QIM (D-3P and B-5P) are presented. The D-3P model is a model with double effect i.e., generates sexual selection and assortative mating patterns. From Figure 1-B we appreciate that the choice parameters (main diagonal) are c_1 and c_3. The parameter c_1 can also be considered a male sexual selection parameter jointly with c_2 since they change the marginal propensity for the second class males (second column). However, from the point of view of biased choice, the parameter c_2 can be seen as a bias (subdiagonal) in a model in which individuals in the shorter class have more difficulty mating. In fact, the second best model was B-5P, which is the equivalent model to B-7P when there are three classes instead of four.

The best model by Lau et al. had a weight of 99%, so it is almost exact to the multi-model inference parameter matrix. In the case of QIM, the best model had only 28% of

the weight and other models such as B-5P (21%), D-5P (21%), D-4P (18%) and D-6P (8%), are necessary to capture more than 95% of the weight. The pattern obtained using the Bayesian Information Criterion (BIC) was similar to that obtained using the AIC criterion (Supplementary Table S3).

However, the structure of all these models is very similar: large males choose females larger than themselves, especially for the largest classes.

A



B

B-7P model

C_1	1	1	1
B_1	C_2	1	1
1	B_2	C_3	1
1	1	B_3	C_4

Best model in Lau et al.

0 ± 0	1 ± 0	1 ± 0	1 ± 0
2 ± 1	**2** ± 0.4	1 ± 0	1 ± 0
1 ± 0	**2** ± 0.3	**3** ± 0.4	1 ± 0
1 ± 0	1 ± 0	**5** ± 0.7	**12** ± 2

D-3P model

1	1	1
1	C_1	1
1	C_2	C_3

QIM best model (28%)

1 ± 0	1 ± 0	1 ± 0
1 ± 0	**3** ± 0.1	1 ± 0
1 ± 0	**6** ± 1	**23** ± 11

B-5P model

C_1	1	1
B_1	C_2	1
1	B_2	C_3

QIM model (21%)

3 ± 1	1 ± 0	1 ± 0
2 ± 0.4	**4** ± 0.1	1 ± 0
1 ± 0	**9** ± 2	**35** ± 17

Fig. 1. A. QInfoMating interface. **B.** Best fit models after re-analysis of Lau et al data. QIM: QInfoMating. The standard errors when minor than one were rounded to 1 decimal place.

The pattern behind the QIM models aligns with the findings reported by Lau et al. (2021) for the Multiple-design and Wild data, as depicted in their Figure 4. However,

there is a notable distinction: Lau et al. observed that the shorter class exhibited considerably lower mating ability. This difference may be attributed to the presence of their first class with a minimal number of individuals for both females and males, as documented in Supplementary Table S1.

However, one might wonder why QInfoMating did not clearly favor the B-5P model, which is most akin to the B-7P model chosen in the original analysis by Lau et al., when applied to the original four-class data. The explanation lies in how QInfoMating operates when handling quantitative data. As explained before, the program selects models based on the statistical significance of various tests and have included double-effect models (as D-3P, D-4P and D-6P) among the set of models to be tested. These particular models were not considered in the original Lau et al. study.

To further elucidate, we excluded the double-effect models and repeated the analysis using exactly the same set of models as in Lau et al (2021). Upon conducting this analysis, the best-fitting model becomes the B-5P, with a weight of 94%.

The program's preference for the D-3P model, when included, stems from its ability to explain the data with two fewer parameters, thus aligning with the principle of parsimony. In cases where both models are closely weighted, the choice between them is influenced by the researcher's experience and the biological plausibility of the results. Nonetheless, it's worth noting that the fundamental structure of these models remains quite similar: larger males tend to prefer females larger than themselves, whenever such a pairing is possible.

Consistent with the result of models, the statistical tests performed by QInfoMating detect assortative mating and sexual selection both in females and males (Table S4).

Discussion

Assortative mating based on size and other quantitative traits is common in many species, from gastropods (Ng et al. 2019) to humans (Robinson et al. 2017). The processes leading to assortative mating may not solely rely on similarity-based mechanisms and may not affect different phenotypic classes equally. This is where the power of model selection methodology becomes evident, as it doesn't require proposing a single ad hoc model. Instead, it allows best fit of data for a wide range of models, enabling researchers to study non-trivial mating patterns, some of which may not have been obvious before the experiment.

In conclusion, the application of information theory, model selection, and parameter estimation using multimodel inference are presented as powerful tools for the analysis of mating data, whether quantitative or categorical. The QInfoMating program is one of the few (if not the only) tools designed to perform this type of analysis.

Acknowledgements

Dedicated to my sister Paci. I thank E. Rolán-Alvarez for comments on the manuscript. This work was supported by Xunta de Galicia (Grupo de Referencia Competitiva, ED431C 2020/05), Ministerio de Economía y Competitividad (PID2022-137935NB-I00) and by Fondos FEDER (“Unha maneira de facer Europa”).

References

Carvajal-Rodríguez, A. 2020. Multi-model inference of non-random mating from an information theoretic approach. Theor. Popul. Biol. 131:38–53.

Carvajal-Rodríguez, A. 2018. Non-random mating and information theory. Theor. Popul. Biol. 120:103–113.

Carvajal-Rodríguez, A. 2023. The information theory formalism unifies the detection of the patterns of sexual selection and assortative mating for both discrete and quantitative traits. bioRxiv.

Carvajal-Rodríguez, A., and E. Rolan-Alvarez. 2006. JMATING: a software for the analysis of sexual selection and sexual isolation effects from mating frequency data. BMC Evol Biol 6:40.

Estévez, D., E. Kozminsky, A. Carvajal-Rodríguez, A. Caballero, R. Faria, J. Galindo, and E. Rolán-Alvarez. 2020. Mate Choice Contributes to the Maintenance of Shell Color Polymorphism in a Marine Snail via Frequency-Dependent Sexual Selection. Front. Mar. Sci. 7.

Lau, S. L. Y., G. A. Williams, A. Carvajal-Rodríguez, and E. Rolán-Alvarez. 2021. An integrated approach to infer the mechanisms of mate choice for size. Anim. Behav. 175:33–43.

Ng, T. P. T., E. Rolán-Alvarez, S. S. Dahlén, M. S. Davies, D. Estévez, R. Stafford, and G. A. Williams. 2019. The causal relationship between sexual selection and sexual size dimorphism in marine gastropods. Anim. Behav. 148:53–62.

Reid, D. G. 2007. The genus Echinolittorina Habe, 1956 (Gastropoda: Littorinidae) in the Indo-West Pacific Ocean. Zootaxa 1420:1–161.

Robinson, M. R., A. Kleinman, M. Graff, A. A. E. Vinkhuyzen, D. Couper, M. B. Miller, W. J. Peyrot, A. Abdellaoui, B. P. Zietsch, I. M. Nolte, J. V. van Vliet-Ostaptchouk, H. Snieder, S. E. Medland, N. G. Martin, P. K. E. Magnusson, W. G. Iacono, M. McGue, K. E. North, J. Yang, and P. M. Visscher. 2017. Genetic

evidence of assortative mating in humans. Nat. Hum. Behav. 1:1–13. Nature Publishing Group.

Rolán-Alvarez, E., G. Williams, T. Ng, D. Estévez-Barcia, M. Davies, S. Saltin, and R. Stafford. 2021. Data for: The causal relationship between sexual selection and sexual size dimorphism in marine gastropods. 1. Mendeley Data.

Supplementary material. QInfoMating: Sexual selection and assortative mating estimation

Table S1. Mating table for the Wild data used in Lau et al (2021). The data is classified in four classes.

Premating males numbers (421)			
23	181	167	50
Premating female numbers (455)			
23	146	190	96
Matings (228, rows are females)			
0	2	0	0
3	30	14	1
2	42	45	9
1	8	43	28

Table S2. Mating table generated by QInfoMating for the Wild data in Lau et al (2021). The data is classified in three classes.

Premating males numbers (421)		
76	333	12
Premating female numbers (455)		
57	370	28
Matings (228, rows are females)		
4	6	0
18	163	2
1	30	4

Table S3. Models that accumulate up to 95% of the weight. The parameter notation corresponds to the B-7P model where C_i represent the ith cell on main diagonal and B_i on the subdiagonal.

Analysis	**Models (>95%)**	**Weight**	**Parameter estimation**						
			C_1	**C_2**	**C_3**	**C_4**	**B_1**	**B_2**	**B_3**
Lau et al 2021	B-7P	99%	0	2	3	12	2	2	5
QInfoMating-AIC	D-3P	28%	1	3	22	-	1	6	-
QInfoMating-AIC	B-5P	21%	3	4	35	-	2	9	-
QInfoMating-AIC	D-5P	21%	3	4	35	-	2	9	-
QInfoMating-AIC	D-4P	18%	2	3	24	-	1	6	-
QInfoMating-AIC	D-6P	8%	3	4	36	-	2	10	-
QInfoMating-BIC	D-3P	85%	1	3	23	-	1	6	-
QInfoMating-BIC	D-4P	10%	2	3	24	-	1	6	-
QInfoMating-BIC	B-5P	2%	3	4	35	-	2	9	-
QInfoMating-BIC	D-5P	2%	3	4	35	-	2	9	-

Table S4. QInfoMating tests

Test type	Statistic	H_0	p-value
Quantitative	$QJ_{PSI} = 0.49$	no assortative mating	$<10^{-6}$
Quantitative	$QJ_{PS1} = 0.24$	no female sexual selection	$<10^{-6}$
Quantitative	$QJ_{PS2} = 0.07$	no male sexual selection	0.0004
Discrete	$J_{PSI} = 0.08$	no assortative mating	0.0009
Discrete	$J_{PS1} = 0.17$	no female sexual selection	$<10^{-6}$
Discrete	$J_{PS2} = 0.06$	no male sexual selection	0.002

Supplementary References

Lau, S. L. Y., G. A. Williams, A. Carvajal-Rodríguez, and E. Rolán-Alvarez. 2021. An integrated approach to infer the mechanisms of mate choice for size. Anim. Behav. 175:33–43.

Rolan-Alvarez, E., G. Williams, T. Ng, D. Estévez-Barcia, M. Davies, S. Saltin, and R. Stafford. 2021. Data for: The causal relationship between sexual selection and sexual size dimorphism in marine gastropods. 1. Mendeley Data.