# Non-random mating and information theory

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## Abstract

1   In this work, mate choice is modeled by means of the abstract concept of mutual mating

2   propensity. This only assumes that different type of couples can have different mating

3   success. The model is adequate for any population where mating occurs among distinct

4   types. There is no extra assumption about particular mating scheme or preference

5   model. The concept of mutual mating propensity permits to express the observed

6   change in the mating phenotypes as the gain in information with respect to random

7   mating. The obtained expression is a form of the Price equation in which the mapping

8   between ancestral and descendant population is substituted by a mapping between

9   random mating and non random mating population.

10  At the same time, this framework provides the connection between mate choice and the

11  exact mathematical partition of the choice effects, namely sexual isolation, sexual

12  selection and a mixed effect. The sexual selection component is the sum of the intra-

13  sexual male and female selection.

14  The proposed framework helps to unveil previously hidden invariants. For example, if

15  the mutual preference between partner types is multiplicative there is no sexual isolation

16  (inter-sexual selection) effect on the frequencies, i.e. the only possible effect of mate

17  choice is intra-sexual selection. On the contrary, whatever the contribution of each

18  partner to the mutual preference, if it comes as a non-multiplicative factor, there is at

19  least an inter-sexual selection detectable effect.

20  This new view over the mate choice problem, permits to develop general mating

21  propensity models and to make predictions of the mate choice effects that may emerge

22  from such models. This possibility opens up the way for setting a general theory of

23  model fitting and multimodel inference for mate choice.

24    Thus, it is suggested that the proposed framework, by describing mate choice as the

25    flow of information due to non-random mating, provides a new important setting for

26    exploring different mating models and their consequences.

27

28   **1. Introduction**

29   Mate choice is arguably one of the most active areas of evolutionary research. There has

30   been a lot controversy regarding the concept of mate choice. The debate around mate

31   choice was due in part to its importance for fields so diverse as population genetics,

32   evolutionary-ecology, animal behavior, sociology, or psychology. In addition, there has

33   been an excess of verbal models and imprecise terminology regarding different aspects

34   of mate choice (Edward, 2015). Mate choice can be broadly described as the effect of

35   some expressed traits leading to non-random mating. Under this broad definition there

36   are various aspects that can be considered. Yet Darwin (1871) distinguishes between

37   intrasexual selection and intersexual selection. The first arises directly from competition

38   among individuals of the same sex while the second arises from choice of mates by the

39   other sex (Kuijper et al., 2012). Alternatively, from a population genetics point of view,

40   mate choice is defined as the observed mating frequency deviation with respect to

41   random mating, considering population gene or phenotype frequencies. So defined,

42   mate choice can be partitioned into (intra)sexual selection, defined as the observed

43   change in gene or phenotype frequencies in mated individuals with respect to

44   population frequencies, and sexual isolation (behavioral isolation or intersexual

45   selection), defined as the deviation from random mating in mated individuals (Rolán-

46   Alvarez and Caballero, 2000). In this work I followed these definitions of mate choice,

47   intrasexual and intersexual selection.

48   For an alternative description of these concepts and a discussion about some of the most

49   widely used descriptions of evolutionary change within the context of sexual selection, I

50   refer the reader to (Kuijper et al., 2012; Rosenthal, 2017).

51    The many aspects and complexity of mate choice justifies the extensive research that

52    has been made in the last decades producing several theoretical models and empirical

53    tests. Related to modeling and detection of mate choice, there is the question about the

54    correct null hypothesis for testing the evolution of mate choice. The Lande-Kirpatrick

55    (L-K) model has been proposed as a null model (Kirkpatrick, 1982; Lande, 1981; Prum,

56    2010; Roff and Fairbairn, 2014). This model assumes neutral genetic variation for the

57    mating preference trait while the target trait can be under natural selection. However,

58    the L-K role as a null model is not clear when the preference is set by similarity

59    (preference and target trait coincide) and the trait is under divergent selection (Servedio

60    et al., 2011), i.e. the trait is "magic" sensu Gavrilets (2004), because in this case the

61    preference trait is already under selection (Hughes, 2015).

62    Therefore, there is still a need for both, null models and a general framework, where the

63    key essential facts of the mate choice can be adequately described. Here, I argue that the

64    formalism provided by the information theory in the form of the Jeffreys' divergence is

65    the right tool to do so.

66    The information theory has already been elegantly applied for describing evolutionary

67    change (Frank, 2009; Frank, 2012b; Frank, 2013). The present work takes advantage of

68    that mathematical structure and applies it for modeling the change in mating frequencies

69    due to mate choice. As far as I know there is no previous attempt of describing mate

70    choice from the viewpoint of the information theory. Nevertheless, the potential of the

71    informational view for evolutionary ecology has been already suggested (Dall et al.,

72    2005).

73    First, I defined a general model that only requires an abstract functional relationship

74    connecting the observed mating frequencies with the expected by random mating from

75    the population gene or phenotype frequencies. This suffices for developing a general

76    information equation for mate choice that can be adequately partitioned into intrasexual

77    and intersexual information components, plus a mixed term provoked by the

78    confounding effect of the marginal frequencies when the mating propensity effects are

79    asymmetric. Interestingly, the three terms can be separately estimated from the observed

80    frequencies and so, the researcher can study how different models and parameters

81    translate into the different mate choice components. Also, it is proposed that this setting

82    provides the baseline for solving the mate choice null hypothesis problem, since the null

83    model emerges naturally from the idea of zero information. Thus, the correct null

84    should not rely on neutral preference or trait genes but on zero information.

85    The utility of this framework is shown by analyzing a real data example. I will show

86    how the view obtained from the unveiled relationships can be utilized to classify

87    different general models from its consequences which facilitates the multimodel

88    inference of the mate choice. However, a deeper study on the outcomes of different

89    forms of the mating preference functions is out of the scope of the present article and is

90    part of a different paper.

91

92    **2. Model of Mate Choice**

93    As mentioned above, the following model is as a particular specification of the

94    information theory interpretation for evolutionary models, proposed in (Frank, 2012b;

95    Frank, 2013). The general framework developed by this author fits perfectly for the

96    purpose of describing the occurrence of non-random mating and the flow of information

97    that it provokes. Remarkably, once the basic equation for the gain in information due to

98    non-random mating is formalized, the relationship between mate choice and its different

99    evolutionary outcomes emerges naturally, providing a clear and useful picture of the

100   intrasexual and intersexual selection effects.

101

102   *2.1 General model*

103   Let consider a population with a number of $n_1$ females and $n_2$ males. For a given female

104   phenotype $X$ (e.g. shell color) with $K$ different classes having values $X_1, X_2 \ldots X_k$, the

105   frequency of the phenotype $X_i$ in the female population is $p_{1i} = n_{1Xi} / n_1$, i.e. the number

106   of females with that phenotypic value divided by the total number of females. Similarly,

107   for the male phenotype $Y$ (could be the same as $X$) with $K'$ classes, the frequency of $Y_j$ in

108   the male population is $p_{2j} = n_{2Yj} / n_2$.

109   In this way, by using the frequency of the phenotype for each sex, the expected mating

110   frequencies if mating is at random is

111        $q_{ij} = p_{1i} \times p_{2j}$.

112   Now, given a female phenotype $X_i$ and a male phenotype $Y_j$, let's define the mutual

113   mating propensity $m_{ij}(x, y, e)$ as the number of matings of $X_i$ with $Y_j$ after their

114   encounter in the environment $e$. The normalized mating propensity is

115        $m_{ij}(x,y,e)/M$

116   where $M = \sum_{i,j} q_{ij} m_{ij}(x, y, e)$.

117   Then, the observed mating frequencies in a given environment $e$ can be expressed as

118        $q'_{ij} = q_{ij} \dfrac{m_{ij}(x,y,e)}{M}$      (1)

119    Therefore, the observed mating frequencies are the result of the functions $m_{ij}(x,y,e)$

120    (hereafter noted as $m_{ij}$), that can be any kind of composition of the preference of female

121    $X_i$ for male $Y_j$, and vice versa, in the environment $e$.

122    Note that random mating is a particular case of the model in (1) when the propensities

123    are equal for every mating pair. The mutual mating propensity functions can represent

124    empirical or analytical functions, as for example the Gaussian-like preference functions

125    (reviewed in Carvajal-Rodriguez and Rolán-Alvarez, 2014). Moreover, each $m_{ij}$ can be

126    composed of female and male preferences, so mutual mate choice models (Bergstrom

127    and Real, 2000) are also available under this setting. The standardized $m_{ij}$ values could

128    also be estimated a posteriori from the data. In this case they coincide with the pair total

129    index i.e. the ratio of the frequency of the observed types divided by the expected pair

130    types calculated from the total frequencies ($PTI_{ij} = q'_{ij}/q_{ij}$, Rolán-Alvarez and Caballero,

131    2000) which becomes an observation of the mutual mating propensity from the mating

132    phenotypes (see below).

133    Once we have the mating frequencies as defined in (1), the change with respect to

134    random mating is

135    $$\Delta q_{ij} = q'_{ij} - q_{ij} = q_{ij}(\frac{m_{ij}}{M} - 1)$$

136    The mean population change for a combined phenotype Z= X ∗Y is

$$\Delta Z = \sum_{i,j} \Delta q_{ij}\, Z_{ij}$$

137    Because the relationship in (1) is defined by ratios is more natural to express the

138    quantities in the logarithmic scale and so we can express $m_{ij}$ as

139 $$m_{ij} = M \frac{q'_{ij}}{q_{ij}}$$

140 which in the logarithmic scale becomes

141 $$l_{ij} = log(m_{ij}) = log(M) + log\left(\frac{q'_{ij}}{q_{ij}}\right)$$

142 Thus, if we take the logarithm of the propensity as the combined phenotype $Z$ and by

143 noting that $\Sigma\Delta q_{ij} = 0$ and that $log(M)$ is constant through the summation, then we can

144 measure the mean population change $\Delta L$ in relative propensity as

145 $$\Delta L = \sum_{i,j} \Delta q_{ij} l_{ij} = \sum_{i,j} \Delta q_{ij} log\left(\frac{q'_{ij}}{q_{ij}}\right) = J(q', q) \equiv J_{PTI} \quad (2)$$

146 which is the Kullback-Leibler symmetrized divergence (noted as Jeffreys in Frank,

147 2012b), that measures the gain in information when the differential mating propensity

148 moves the population from mating frequencies $q$ to $q'$ or vice versa. Note that if the

149 propensity is equal for every pair i.e. $M = m_{ij} \ \forall \ i,j$ then $q' = q$ so that $J = 0$ which is the

150 minimum information value since $J$ cannot be negative.

151 Recall from equation (1), that each $m_{ij}/M$ is the ratio of the frequency of the observed

152 types divided by the expected pair types from the total frequencies. This is, by

153 definition, the pair total index $PTI$ (Rolán-Alvarez and Caballero, 2000) and so, the

154 logarithmic term in $\Delta L$ is the logarithm of the $PTI$ values. Therefore, $J(q', q)$ measures

155 the gain in information as captured by the $PTI$ coefficients, confronting the hypothesis

156 of mate choice against random mating. Hereafter, we note this $J$ as $J_{PTI}$.

157 Interestingly enough, the Jeffreys' divergence computed as $J_{PTI}$ (by taking the natural

158 logarithm and multiplying (2) by the total number of matings) is well approximated by a

159     chi-square for the null hypothesis of random mating with $KK'-1$ degrees of freedom

160     (Evren and Tuna, 2012).

161     The information obtained from $J_{PTI}$ has been computed using the different propensities

162     as classes for classifying the couples i.e. we considered $log(m)$ as the phenotype $Z$.

163     When the classes are based upon other phenotypes rather than propensities, we are

164     conveying a specific meaning for the change in frequencies, say, the change in mating

165     frequencies due to differential mutual propensities is observed in terms of change in

166     shell color mating frequencies. Therefore, the phenotype can be viewed as other scale

167     on which we can measure this information (Frank, 2013). Of course, different kinds of

168     phenotypes can be more or less involved in mate choice and so, different scales are

169     more or less useful for measuring the mate choice information.

170

171     *2.2 Relative propensity and phenotypes*

172     When we observe any mating pair $(i,j)$, we need to identify the mating by a given

173     characteristic (e.g. shell color) since we cannot directly classify it by the value of the

174     propensity function $m_{ij}$. In general, we ignore the specific form of the mutual mating

175     propensity function $m$ and so, we may assume that some phenotype matches it perfectly,

176     as we did above (each phenotypic pair was perfectly differentiated by specific $m_{ij}$

177     mating propensity).

178     Thus, if $T$ is the trait that is the target of the choice, we call $J_{PTI}$ to the change in the

179     numbers of matings when these matings were classified by $T$.

180

181 Therefore, we may think on different traits $Z$ that classify the mating pairs; $Z$ can be a

182 composition of female trait $X$, e.g. preference, and male target $Y$, or can be any kind of

183 different traits or alternatively the same trait in both sexes as size, age or color. In any

184 case, we measure the mean change in $Z$ caused by differences in $m$, as

185   $$\Delta_m Z = \sum_{\alpha,\beta} \Delta q_{\alpha\beta} Z_{\alpha\beta} = \sum_{\alpha,\beta} q_{\alpha\beta}\left(m_{\alpha\beta} - M_z\right)\frac{Z_{\alpha\beta}}{M_z} = \frac{cov(Z,m_z)}{M_z} \qquad (3)$$

186 Where $cov$ is the population covariance in the sense of Price (1972) as highlighted in

187 Frank (2012a). The subscripts $\alpha$, $\beta$ emphasize that we are looking at pairs with observed

188 phenotypes that not necessarily are the phenotypes exactly connected with the choice.

189 Therefore, the propensities for the matings classified under these phenotypes can be

190 different to the propensities for the trait $T$, then we note $m_z$ and $M_z$ to distinguish from

191 the propensities ($m$) and mean propensity ($M$) measured directly from the real choice

192 trait.

193 Equation (3) is in fact, a form of the Price equation with a different mapping for the

194 populations involved. While the Price equation (Frank, 2012a; Price, 1972) describes

195 the change in phenotype between two connected ancestor and descendant populations;

196 in our equation (3), the mapping is between the random mating population and the one

197 obtained under a given mutual mating propensity scheme.

198 The variable $Z$ can be any desired trait including, as we assumed above, the logarithm of

199 the propensities. So, if we take $Z$ equal to the logarithm of $m$, then by substituting in (3)

200 we obtain the mean population change $\Delta L_z$ as

201   $\Delta L_z = cov(m_z, l_z) / M_z$

202 where the subscript $z$ indicates that the propensities are now indexed by the trait $Z$.

203    Recalling the relationship in (2), we now define

204    $$JZ_{PTI} \equiv \Delta L_z = cov\,(m_z, l_z)\,/\,M_z = \alpha_z J_{PTI}$$

205    where if $J_{PTI} > 0$

206    $$\alpha_z = (\beta(m_z, l_z) \times D_z)\,/\,(\beta(m, l) \times D)$$

207    with $l_z = log(m_z)$, $D_z = V(m_z)/M_z$, $l = log(m)$ and $D = V(m)\,/\,M$

208    or $\alpha_z = 1$ if $J_{PTI} = 0$.

209    Note that $D$ and $D_z$ are the indexes of dispersion over the choice and $Z$ traits

210    respectively, so $\alpha_z$ is the quotient of the regressions multiplied by the index of

211    dispersion at each phenotypic scale.

212    From the point of view of the estimation with real data, if we cannot measure directly

213    the values of $m$ then we simply compute $J$ based on trait $Z$ and therefore we are really

214    computing $JZ_{PTI}$.

215    In this case, note that the *PTI* coefficients are no longer the exact estimate of the mutual

216    mating propensities because the ratio of frequencies $q'_{\alpha\beta}/q_{\alpha\beta}$ does not correspond to

217    $m_{ij}/M$  but to $m_{\alpha\beta}/M_z$ which is a proxy that would be more or less precise depending on

218    the importance of the measured phenotype over the mating choice. For example, if shell

219    size is driving mate choice, the measure of $JZ_{PTI}$ ($Z =$ shell size) would correspond well

220    with $J_{PTI}$ ($J_{PTI} > 0$; $\alpha_z \approx 1$). However, if other phenotype as shell color has nothing to do

221    with mate choice (and is not correlated with shell size) then the measure of $JZ_{PTI}$ ($Z =$

222    shell color) would be zero ($J_{PTI} > 0$; $\alpha_z = 0$). Further details about the distinction

223    between $JZ_{PTI}$ and $J_{PTI}$ are given in appendix A.

224    The mate choice mediated by the differences in mutual mating propensity would

225    produce a deviation from random mating. At the same time, this may cause two

226    different effects, namely, intrasexual selection and intersexual selection, hereafter noted

227    as sexual selection and sexual isolation, respectively.

228

229    *2.3. Sexual selection*

230    Sexual selection is defined as the observed change in gene or phenotype frequencies in

231    mated individuals with respect to total population frequencies (Rolán-Alvarez and

232    Caballero, 2000). This change can be studied using the frequencies within each sex, or

233    considering jointly both sexes, by using the pair sexual selection coefficient (*PSS*,

234    Rolán-Alvarez and Caballero, 2000). I will show that, when the *PSS* coefficients are

235    considered a priori as the marginal propensities for the mating types, the information

236    gained due to sexual selection is the sum of the information from each sex. When the

237    focus is on the phenotypes instead on the propensities, the partition continue to be true,

238    provided that the same phenotypic scale is applied when computing the *PSS* coefficients

239    and the intrasexual components.

240    From the general model, the population frequency of the female phenotype $X_i$ is $p_{1i}$. The

241    observed frequency of $X_i$ in mated individuals, $p'_{1i}$, is computed as the sum of the

242    mating frequencies involving a female $X_i$

243    $$p'_{1i} = \sum_j^{males} q'_{ij} = p_{1i} \sum_j p_{2j} \frac{m_{ij}}{M} = p_{1i} \frac{m'_{fi}}{M}$$

244    where $m'_{fi}$ is the marginal mating propensity for the female type $i$.

245    Similarly for males, the frequency of phenotype $Y_j$ is $p_{2j}$ and the frequency for the male

246    type $j$ in mated individuals is

247    $$p'_{2j} = p_{2j} \frac{m'_{mj}}{M}$$

248    where $m'_{mj}$ is the marginal mating propensity for the male type $j$.

249    The mean change in information due to sexual selection within each sex is, in terms of

250    the female marginal propensity (female intrasexual selection)

251    $$\Delta_m L_x = \sum_i^{females} \Delta p_{1i} X_i = \sum_{ij} p_i (m'_{fi} - M) \frac{X_i}{M} = J(p'_1, p_1) \equiv J_{S1}$$

252    and, in terms of male marginal propensity (male intrasexual selection)

253    $$\Delta_m L_y = \sum_j^{males} \Delta p_{2j} Y_j = J(p'_2, p_2) \equiv J_{S2}$$

254    The term $J_S$ has been obtained in a similar way as for the general case, i.e. by expressing

255    each marginal $m'_{fi}$ and $m'_{mj}$ in function of their respective ratio of frequencies multiplied

256    by the mean propensity $M$ and substituting the phenotype $X$ or $Y$, by the logarithm of the

257    corresponding (female or male) marginal $m'$.

258    The change to the scale of phenotypes produces

259    $$\Delta_m \bar{X} = \alpha_x J_{S1} \equiv J X_{S1}$$

260    with

261    $$\alpha_x = [\beta(m'_{xf}, l_{xf}) \times D_{xf}] / [\beta(m'_f, l_f) \times D_f] \text{ or 1 if } J_{PS1} = 0$$

262    where $l_{xf} = log(m'_{xf})$, $D_{xf} = V(m'_{xf})/M_z$, $l_f = log(m'_f)$, $D_f = V(m'_f)/M$.

263    And

264    $$\Delta_m \bar{Y} = \alpha_y J_{S2} \equiv J Y_{S2}$$

265 $\qquad \alpha_y = [\beta(m'_{ym}, l_{ym}) \times D_{ym}] / [\beta(m'_m, l_m) \times D_m]$ or 1 if $J_{PS2} = 0$

266 where $l_{ym} = log(m'_{ym})$, $D_{ym} = V(m'_{ym})/M_z$ .

267 Note that the subscripts $x$ (females) or $y$ (males) refer to the matings classified by

268 phenotype instead of the true choice trait, also note that the mean of both female and

269 male marginals is the same and equal to the mean propensity ($M_z$ or $M$ depending on the

270 scale).

271 $JX_{S1}$ and $JY_{S2}$ are the Jeffrey's divergence that expresses the gain of information due to

272 intrasexual selection measured on the combined phenotypic scale $Z$.

273 *2.4. Pair sexual selection*

274 In addition to the computation within each sex, we can compare the expected pair types

275 under random mating calculated in mated individuals, with the expected pair types from

276 total numbers (*PSS*, see above). Thus, $PSS_{ij} = (p'_{1i}p'_{2j}) / (p_{1i}p_{2j}) = m'_{fi}m'_{mj} / M^2$. The latter

277 term can be viewed as an a priori expression of the *PSS* coefficients. Again, the

278 difference between the observed and the expected distribution can be expressed as

279 $\qquad \Delta_{PSS}L = \sum_{i,j} \Delta(p_{1i}p_{2j}) log\left(\frac{p'_{1i}p'_{2j}}{p_{1i}p_{2j}}\right) = J(p'_1 p'_2, p_1 p_2) \equiv J_{PSS},$

280 where $\Delta(p_{1i}p_{2j}) = p'_{1i}p'_{2j} - p_{1i}p_{2j}$.

281 In the scale of phenotypes

282 $\qquad \Delta_{PSS}L_z = \alpha_{pss}J_{PSS} \equiv JZ_{PSS}$

283 with

284 $\qquad \alpha_{pss} = (\beta(m'_z, l'_z) \times D'_z) / (\beta(m', l') \times D')$ or 1 if $J_{PSS} = 0$

285   where $m'_z = m'_{xf} \times m'_{ym}$, $m' = m'_f \times m'_m$, $D'_z = V(m'_z)/M^2_z$, $l'_z = log(m'_z)$, $l' = log(m')$, $D'$

286   $= V(m')/M^2_z$.

287   The change in the phenotype due to sexual selection is driven by the aprioristic version

288   of *PSS,* and is expressed in term of the information accumulated and rescaled from the

289   marginal propensities to *Z.*

290   The relationship between sexual selection measured within sex and the pair sexual

291   selection measured by *PSS* is (details in Appendix B)

292       $J_{PSS} = J_{S1} + J_{S2}$

293   And in the scale of phenotypes

294       $JZ_{PSS} = JX_{S1} + JY_{S2}$    (4)

295   provided that the same phenotypic scale applies in the pair sexual selection statistic and

296   in the intrasexual components (i.e. the criteria utilized for classifying the different

297   couples is the same).

298   The information captured in the *PSS* coefficients is the sum of the sexual selection

299   within each sex.

300

301   *2.5. Sexual isolation*

302   Sexual isolation is defined as the deviation from random mating in mated individuals

303   (Rolán-Alvarez and Caballero, 2000). The pair sexual isolation statistic (*PSI*) is the

304   number of observed pair types divided by the expected pair types from mates. In terms

305   of our model this is the ratio of frequencies

306 $$PSI_{ij} = q'_{ij}/(p'_{1i}p'_{2j}) = (m_{ij}/M) / (m'_{fi}m'_{mj} / M^2) \equiv \delta_{ij} \qquad (5)$$

307 The term $\delta$ refers to an aprioristic (depends on the $m$'s from the model) definition of the

308 $PSI$s. The joint isolation index for $PSI$ can be expressed as

309 $$I_{PSI} = \frac{(k-1)\sum_i \delta_{ii} - \sum_{ij} \delta_{ij}}{(k-1)\sum_i \delta_{ii} + \sum_{ij} \delta_{ij}}$$

310 where $k$ is the number of phenotypic classes involved in the classification of the matings

311 (Carvajal-Rodriguez and Rolan-Alvarez, 2006).

312 As with the previous pairwise statistics, we may obtain the equations of change between

313 observed and expected pair types in terms of $J$.

314 $$\Delta_{PSI}L = \sum_{i,j} \Delta(p'_{1i}p'_{2j})log\left(\frac{q'_{ij}}{p'_{1i}p'_{2j}}\right) = J(q', p'_1 p'_2) \equiv J_{PSI},$$

315 where $\Delta(p'_{1i}p'_{2j}) = q'_{ij} - p'_{1i}p'_{2j}$.

316 In the scale of phenotypes

317 $$\Delta_{PSI}L_z = \alpha_\delta J_{PSI} \equiv JZ_{PSI}.$$

318 The scaling factor $\alpha_\delta$ is not always easy to compute. Provided that there is no sexual

319 selection ($J_{PSS} = 0$) then $\alpha_\delta = \alpha_z$ and so $JZ_{PTI} = JZ_{PSI} = \alpha_z J_{PSI}$. Otherwise we need to

320 rescale the factor $E_0$ (see below) to finally get the transformation between $JZ_{PSI}$ and $J_{PSI}$

321 (see Appendix $C$).

322 The $JZ_{PSI}$ index provides the correct metric to express the part of change in mating

323 information that translates into sexual isolation. Presenting the $PSI$'s under this

324 formalism allow us to appreciate some facts that are not obvious from the a posteriori

325 definition of coefficients estimated from data. We must realize (see equation 5) that if

326 the normalized propensity of each pair ($m_{ij} / M$) is the product of the normalized

327     marginal types of each partner then $\delta = 1$ and so, both, the values of $I_{PSI}$ and $J_{PSI}$ are

328     zero indicating no sexual isolation at all. Thus, in any model in which the mutual mating

329     propensity is multiplicative, the only possible outcome from mate choice is intrasexual

330     selection.

331     We can illustrate the multiplicative effect by means of a simple model based on a real

332     species scenario. The bird sage grouse (*Centrocercus urophasianus*) has elaborate

333     courtship rituals. In the spring season, males congregate in leks that are visited by the

334     females that actively choose one of the males for mating. The number of females

335     visiting a male seems to be  related with the male long-range acoustic broadcasts

336     whereas the probability of mating once visited is related to the visual display (Gibson,

337     1996).

338     It has been suggested that both traits, acoustic broadcast and display rate, yield a

339     multiplicative preference for males with specific acoustic conditions and high display

340     rates (Gibson, 1996; Rosenthal, 2017).

341     Thus, we can define a model of the multiplicative effect of the aforementioned traits

342     (see details in Appendix D). Obviously, the real mating scenario is by far more

343     complex, but the example suffices to illustrate the point.

344      The females are the choosers and so our model assumes a single female phenotypic

345     class (*X*) and two male traits with two phenotypic classes each, *B*/*b* for acoustic

346     broadcast, and *D*/*d* for display rate, where in both cases the upper case refers to the

347     higher value of the trait. We define a multiplicative preference effect for acoustic

348     broadcast and display rate, so that the female propensity for males *BD* can be expressed

349     as the product of the female propensities for *Bd* and *dB*, i.e. $m_{XBD} = m_{XBd} \times m_{XbD}$

350     (supplementary Table S1).

351    Under this model, the mean propensity $M$ coincides with the female marginal, $m'_{fX} = M$.

352    The four male marginal propensities ($m'_{mBd}$, $m'_{mBD}$, $m'_{mbD}$, $m'_{mbd}$) have the same values

353    as their corresponding mutual propensities ($m_{XBd} = \alpha$, $m_{XBD} = \alpha\beta$, $m_{XbD} = \beta$, $m_{Xbd} = 1$; see

354    Appendix D).

355    The model is multiplicative since each normalized mutual propensity is equal to the

356    product of the normalized marginals, e.g. $m_{XBd} /M = (m'_{fX} /M) \times (m'_{mBd} /M)$.

357    By computing the aprioristic expressions in (5), we see that $\delta_{Bd} = \delta_{BD} = \delta_{bD} = \delta_{bd} = 1$.

358    Thus, provided that the mating reflects the propensities, the result is that independently

359    of the phenotypes, the number of observed pair types would be equal to the expected

360    pair types from mates, which means that there is no sexual isolation.

361    On the other hand, the model predicts male sexual selection whenever $m_{XBd}$ and/or $m_{XbD}$

362    $\neq 1$.

363

364    **3. Relationship between Mate Choice, Sexual Selection and Sexual Isolation**

365    The information as captured by the $PTI$ coefficients can be partitioned in terms of $PSS$

366    and $PSI$. Recall the expression (2) for $J_{PTI}$

367    $$\Delta L = \sum_{i,j} \Delta q_{ij} log \left(\frac{q'_{ij}}{q_{ij}}\right) = J(q', q) \equiv J_{PTI}$$

368    The term $\Delta q_{ij}$ can be expressed as the sum of the frequency changes for sexual selection

369    and isolation

370    $$\Delta q_{ij} = \Delta(p_{1i}p_{2j}) + \Delta(p'_{1i}p'_{2j})$$

371   The logarithmic term $log(q'_{ij}/q_{ij})$ which we have also noted as $log(PTI)$ is also

372   partitioned in the sexual selection and isolation components

373         $$log(PTI) = log(PSS) + log(PSI).$$

374   Therefore

375         $$J_{PTI} = \Sigma_{ij} ([\Delta( p_{1i}p_{2j}) + \Delta( p'_{1i}p'_{2j})] \times [log(PSS_{ij}) + log(PSI_{ij})]) \text{ i.e.}$$

376         $$J_{PTI} = J_{PSS} + J_{PSI} + E_0$$

377   where $E_0 = \Sigma_{ij}(\Delta(p_{1i}p_{2j})log(PSI_{ij}) + \Delta( p'_{1i}p'_{2j})log(PSS_{ij}))$. However, note that

378   $\Delta(p'_{1i}p'_{2j})log(PSS_{ij})) = 0$ (see Appendix E) so finally

379         $$E_0 = \Sigma_{ij}(\Delta(p_{1i}p_{2j})log(PSI_{ij}) = cov(m'_f m'_m, log(PSI)) / M^2$$

380   thus $E_0$ is proportional to the covariance between the marginal propensities and the

381   logarithm of the $PSI$s.

382   The covariance expression is useful for defining a scaling factor (see Appendix C) i.e.

383         $$\alpha_E = \beta(m'_z, l_{zpsi}) \times D'_z / \beta(m', l_{psi}) \times D' \text{ or } 1 \text{ if } E_0 = 0$$

384   where $l_{zpsi} = log(PSI_z)$, $l_{psi} = log(PSI)$ and $m'_z$, $m'$, $D'_z$ and $D'$ are the same as defined for

385   $\alpha_{pss}$. The subscript in $PSI_z$ indicates that this is the value obtained under trait $Z$ contrary

386   to $PSI$ which is obtained directly under the choice trait.

387   Then, $\alpha_E$ permits to interchange between the scale of phenotypes and choice so, $ZE_0 =$

388   $\alpha_E E_0$.

389   Alternatively, we can also express $E_0$ (see Appendix E for details) as

390         $$E_0 = D'_{KL}(w, q'|| p')$$

391    which is a Kullback–Leibler-like divergence with weights $w_{ij} = (PSS_{ij} - 1)/ PTI_{ij}$ in the

392    observations $q'$. Note that contrary to the standard K-L divergence, $E_0$ can be negative

393    depending on the weights.

394    The total information is separated into the sexual selection ($J_{PSS}$) and isolation ($J_{PSI}$)

395    components plus the mixed term $E_0$. Note that $E_0$ appears only when both sexual

396    selection and sexual isolation effects occur so that the above given covariance is not

397    null.

398    If $E_0 = 0$ this means that $J_{PSS}$ and/or $J_{PSI}$ capture the complete information from mate

399    choice. When $E_0$ is positive it indicates that the information gathered from $J_{PSS}$ and $J_{PSI}$

400    separately is not the total information from mating choice. On the other side, when $E_0$ is

401    negative there is some inverse relationship between sexual selection and sexual isolation

402    information.

403    In the scale of phenotypes the partition still holds provided that the same phenotypic

404    classification is applied when computing the different measures

405        $$JZ_{PTI} = JZ_{PSS} + JZ_{PSI} + ZE_0 \quad (6)$$

406    where $ZE_0$ is the value of $E_0$ in the given phenotypic scale.

407    For any given logarithmic base, the amount of the total information, $JZ_{PTI}$, depends on

408    the magnitude of the differences among the mutual mating propensity values linked to

409    the population phenotypes under study.  The higher the differences encountered the

410    higher the value of $JZ_{PTI}$. Without loss of generality, from herein we consider the

411    natural logarithm because this facilitates testing against the null hypothesis of no

412    information by means of the chi-square distribution.

413    We have given formulae for the change in the phenotypic scale for every term in (6)

414    except $JZ_{PSI}$. In this case, we have to predict the change in the scale by computing the

415    remaining factors and solving for $JZ_{PSI}$ (Appendix C).

416    If, as expected, the observations used to compute the information statistics come from

417    the same sample, the sum in (6) is exact so it recovers the whole information gathered

418    from mate choice. On the contrary, if the computations has been performed using

419    different samples, it could be a remaining part of mate choice information that is non-

420    explained by the above statistics but that can be recovered by the error term

421    $$E_{PTI} = JZ_{PTI} - (JZ_{PSS} + JZ_{PSI} + ZE_0) \qquad (7)$$

422    that reflects how much information may be lost due to differences in the measurement

423    of the involved phenotypes when computing the different information components from

424    separate samples.

425

426    **4. Real Data Application**

427    The theoretical framework I have presented so far has been defined in a general way, for

428    any number of male and female phenotypic classes, and for any kind of mutual mating

429    propensities. The application of the $J$ statistics to a data sample of dimorphic traits (two

430    classes), is immediate. For clarity, I will use the same example that appears in the

431    pairwise statistics (*PTI*, *PSI* and *PSS*) original article (Rolán-Alvarez and Caballero,

432    2000). The correspondence between the pairwise statistics notation used by (Rolán-

433    Alvarez and Caballero, 2000) and ours is as follows. The two phenotypic types are

434    noted as *A* and *B*, the total number of observed matings is *t* and the number of *A* type

435    females (A' in Rolán-Alvarez and Caballero, 2000) becomes, under our notation, $p_{1A}n_1$,

436 and so $B'$ is $p_{1B}n_1$; the number of $A$ males becomes $p_{2A}n_2$ and $B$ males are $p_{2B}n_2$. The

437 observed absolute number for each pair $(i, j)$ would be $q'_{ij}t$ with $i, j \in \{A, B\}$ (see Table

438 1). The total number of expected mating pairs from population frequencies is $n_1 n_2$

439 corresponding to the quantity $S$ in (Rolán-Alvarez and Caballero, 2000).

440

441 **TABLE 1. The mating model for two phenotypic classes identified as types $A$ and**

442 **$B$. The number of observed mating pairs is $t$.**

| | Females | | | |
|---|---|---|---|---|
| | | $p_{1A}n_1$ | $p_{1B}n_1$ | |
| Males $p_{2A}n_2$ | $q'_{AA}\,t$ | $q'_{BA}\,t$ | $p'_{2A}\,t$ | |
| $p_{2B}n_2$ | $q'_{AB}\,t$ | $q'_{BB}\,t$ | $p'_{2B}\,t$ | |
| | $p'_{1A}\,t$ | $p'_{1B}\,t$ | | |

443 $p_{1i}$: observed relative frequency of type $i \in \{A, B\}$ in population females ; $n_1$: number of females in the

444 population; $p_{2i}$: observed relative frequency of type $i \in \{A, B\}$ in population males ; $n_2$: number of males in

445 the population; $p'_{1i}$: observed relative frequency of type $i$ in mating females; $p'_{2i}$: observed relative

446 frequency of type $i$ in mating males; $q'_{ij}$: observed relative frequency of mating pair $i, j$.

447

448 The data correspond to a multiple-choice experiment involving two different lines of

449 *Drosophila melanogaster* so called *M*-like and *Z*-like (Hollocher et al., 1997). Rolán-

450 Alvarez & Caballero applied the pairwise statistics to this data and confirmed the

451 previous results from Hollocher *et al* indicating stronger sexual isolation than sexual

452 selection. They also suggested a fitness advantage of females versus males but they

453 were not able of distinguishing between female sexual selection and male preference for

454 *M* females.

455    To perform the analysis, we expressed the observed data from that experiment in terms

456    of the information model as presented in Table 1. In doing so, and noting that the

457    observed number of mating pairs was $t = 1704$, we obtained the necessary quantities in

458    terms of our model (Table 2).

459    The total mate choice information obtained in $JZ_{PTI}$ is partitioned in 89% of sexual

460    isolation ($JZ_{PSI} / JZ_{PTI} = 0.468 / 0.526 = 0.89$; $I_{PSI} = 0.63$), 6% of sexual selection and

461    5% of mixed effects which explains the 100% of $JZ_{PTI}$. The information coming from

462    sexual isolation is 14 times that from sexual selection, result that matches pretty well the

463    outcome in (Rolán-Alvarez and Caballero, 2000).

464    The value of $JZ_{PTI}$ multiplied by the number of matings can be approximated by a chi-

465    square variable with 3 degrees of freedom under the expectation of $JZ_{PTI} = 0$, the $p$-

466    value obtained was below 0.00001 which indicates non-random mating. The test against

467    $JZ_{PSI} = 0$ with 1 degree of freedom, also had a $p$-value below 0.00001. The test against

468    $JZ_{PSS} = 0$ was also below 0.0001. However, testing separately the female and male

469    sexual selection cases (with one degree of freedom each) produced a $p$-value below

470    0.0001 for the female case but a $p$-value of 0.77 for males.

471    Thus, we detected significant sexual isolation and selection effects as previously

472    reported by (Rolán-Alvarez and Caballero, 2000). The sexual selection component is

473    caused by a significant intrasexual effect in females. The mixed term $E_0$ is positive thus

474    indicating that not all the information is recovered by the $PSS$ and $PSI$ coefficients. This

475    is due to the confounding effect which explains as far as the 5% from the total

476    information.

477

**TABLE 2. Analysis using the mate choice information model (Table 1 and equations 7) on *D. melanogaster* mating data from (Hollocher et al., 1997). The number of observed copulating pairs is $t = 1704$.**

|  |  | Females Z | Females M |  |
| --- | --- | --- | --- | --- |
|  |  | $0.5 \times 1440$ | $0.5 \times 1440$ |  |
| Males Z | $0.5 \times 1440$ | $0.3585 \times 1704$ | $0.145 \times 1704$ | $0.5035 \times 1704$ |
| Males M | $0.5 \times 1440$ | $0.051 \times 1704$ | $0.4455 \times 1704$ | $0.4965 \times 1704$ |
|  |  | $0.4095 \times 1704$ | $0.5905 \times 1704$ |  |
| $JZ_{PTI}$ | 0.526 |  |  |  |
| $JZ_{PSI}$ $(I_{PSI})$ | 0.468 (0.63) |  |  |  |
| $JX_{S1}+JY_{S2}$ | $0.033 + 0.00005$ |  |  |  |
| $ZE_0$ | 0.024 |  |  |  |
| $E_{PTI}$ | 0 |  |  |  |

Number of females in the population: $n_1 = 1440$; number of males in the population: $n_2 = 1440$; From Table 1, $p'_{1i}$: observed relative frequency of type $i$ in mating females; $p'_{2i}$: observed relative frequency of type $i$ in mating males; $q'_{ij}$: observed relative frequency of copulating pair $i, j$.

*4.1 Exploring models*

In the analysis performed above we used the information partition for testing if the observations can be explained by random mating, in a similar way as we do when using the $I_{PSI}$ statistic for testing sexual isolation (Carvajal-Rodriguez and Rolan-Alvarez, 2006; Rolán-Alvarez and Caballero, 2000).

However, the proposed theoretical framework permits going further than just testing random mating. We can rely on the described properties of mutual propensities under

492    sexual selection and isolation, for defining different effects models. If we can define

493    models from which we can predict the effects, then we can try to fit and infer significant

494    parameters from the available data.

495    As an example, I have used the software InfoMating (Carvajal-Rodriguez, 2017) to

496    estimate the mutual mating propensity parameters associated to the data in Table 2. The

497    software uses the $J$ information framework to a priori construct (before data) different

498    effects models, and then compare the fitting of random mating, sexual selection and

499    sexual isolation models to the data. There are models having sexual selection only in

500    females, only in males or in both. The models with sexual isolation will have or not

501    sexual selection depending on the frequencies (the conditions on marginal propensities

502    for sexual selection are frequency dependent). The most complex model is also

503    considered. Under this model the mutual mating propensities are estimated by the $PTI$s

504    that are indeed the maximum likelihood estimates.

505    I have considered BIC (Schwarz, 1978) and AIC (Akaike, 1973) selection criteria. Both

506    gave similar results. The best fit model was a two parameter model with sexual isolation

507    and female sexual selection effects. The model uses two parameters $a$ and $b$ to define

508    the four mating propensity values as $m_{ZZ} = a$, $m_{ZM} = 1-b$, $m_{MZ} = 1$, $m_{MM} = a+b$.

509    The obtained estimates under the BIC criterion were $a = 2.47$ and $b = 0.64$ which after

510    normalization, provide the mutual mating propensity estimates as they appear in Table

511    3.

512    **TABLE 3. Mutual-propensity estimates from multimodel inference.**

| Female | Z | M |
|--------|---|---|
| **Male** | | |

| | | |
|---|---|---|
| **Z** | 1.42 | 0.58 |
| **M** | 0.21 | 1.79 |

513

514  The obtained estimates are almost identical to the corresponding *PTI* values but we have

515  only needed two parameters instead of three for defining the model. Therefore, the two

516  parameter model may provide some insight into the biology of the mating relationships.

517  The obtained estimates imply positive assortative mating because the homotype mutual

518  propensities (main diagonal in Table 3) are higher than the heterotype ones

519  (antidiagonal, $m_{ZM}$ and $m_{MZ}$). If we compare the mean homotype versus the mean

520  heterotype mating propensities, the difference is $a + b$ -1. The value 1 is the value under

521  random mating so, the increase of homotype mating with respect to random mating is $a$

522  $+ b$.

523  Moreover, the chosen model has no male sexual selection effect. This is clear when we

524  measure the mean effect of changing the male type in the matings. We see that the

525  effect is 0 i.e. $(m_{MM} - m_{MZ} + m_{ZM} - m_{ZZ}) / 2 = 0$. On the contrary, the mean effect of

526  changing female Z by M is $b$.

527  Thus, the deviation from random mating in the data from Table 2 is composed of a

528  sexual isolation effect captured by the parameter $a$ plus an effect $b$ of sexual selection

529  focused on the M females which may imply that this females are more receptive to

530  mating in general.

531

532  **5. Female preference and male display models**

533    The example we have considered involves the same trait in female and male. However,

534    there are several situations where the female preference is for a male display trait

535    (Pomiankowski and Iwasa, 1998). In this case, the female trait is the exerted preference

536    and the male trait is the target phenotype. In the preference-display context, the traits

537    involved are different between sexes so that the crosses cannot be classified in

538    homotypic versus heterotypic, which prevents the calculation of $I_{PSI}$ and other similar

539    indices that are only applicable to mating models in which the female and male

540    phenotype is the same (similarity/dissimilarity models).

541    The mutual mating propensity framework can easily capture the preference-display

542    scenario to express the components of mate choice in terms of information.

543    In Table 4 we appreciate three examples of such preference-display models. There are

544    two types of females which have preference for males displaying phenotypic values $A$,

545    $B$ or $C$. The frequencies for the different phenotypes are equal. The mating propensies

546    have been defined with only one parameter and three possible values, namely $a$, $a/2$ or

547    virtually 0 ($\varepsilon$). In the first column the female preference generates a situation of

548    complete isolation; in the second column the resultant effect of the female preference is

549    of full intrasexual selection in males and the third column corresponds to a mixed

550    scenario were both sexual selection and isolation occur with a mixed effect of -24%

551    than indicates an strong overlap between both effects.

552

553    **TABLE 4. Mating propensity models of female preference for male display traits.**

554    **Two types of females '0' or '1' might have different preferences for males**

555    **presenting distinct values for some secondary trait ($a$ = 1, $a/2$ or $\varepsilon$). Females are the**

556 **choosy sex so that the generic model implies only the female acceptance (or**

557 **preference) function $f_1$.**

| $m_{female,male}$ | Isolation | Sexual selection | Mixed | Generic |
|---|---|---|---|---|
| $m_{0A}$ | $a$ | $a$ | $a$ | $f_1(0,A)$ |
| $m_{0B}$ | $a/2$ | $a/2$ | $\varepsilon$ | $f_1(0,B)$ |
| $m_{0C}$ | $\varepsilon$ | $\varepsilon$ | $\varepsilon$ | $f_1(0,C)$ |
| $m_{1A}$ | $\varepsilon$ | $a$ | $\varepsilon$ | $f_1(1,A)$ |
| $m_{1B}$ | $a/2$ | $a/2$ | $\varepsilon$ | $f_1(1,B)$ |
| $m_{1C}$ | $a$ | $\varepsilon$ | $a$ | $f_1(1,C)$ |
| $JZ_{PTI}$ | 13 | 13 | 26 | |
| $JZ_{PSI}/ JZ_{PTI}$ | 100% | 0% | 75% | |
| $(JX_{S1}+JY_{S2}) / JZ_{PTI}$ | 0% | 100% (0% + 100%) | 49% (0% + 100%) | |
| $ZE_0 / JZ_{PTI}$ | 0% | 0% | -24% | |

558 $\varepsilon$: represents an infinitesimal value for which the quantity $\varepsilon\log(\varepsilon)$ will be zero.

559

560 However, upon inspecting the propensities in the Table 4, the effects (isolation,

561 selection, and mixed) of the preference-display scenarios are not so intuitive, which

562 stresses the usefulness of the information partition. For example, the column "Mixed"

563 can be represented in a two-way table (Table 5).

564

565 **Table 5. Mating preferences involved in the mixed model from Table 4.**

| Males | A | B | C |
|---|---|---|---|

| **Females** | | | |
| --- | --- | --- | --- |
| 0 | a | ε | ε |
| 1 | ε | ε | a |

566

567  The pattern in Table 5 is a clear case of isolation that splits females 0 and males A from

568  females 1 and males C. Recall that a mixed model implies isolation+ sexual selection.

569  The model is mixed because there is strong sexual selection against B males that

570  virtually do not mate. At this stage, we do not care if this is because A and C have more

571  vigour than B in the searching for mates, or because females in general do not like B

572  males. The result is male sexual selection (against B males), so the model is mixed

573  because the preferences in the model produce both sexual isolation and selection.

574  We can perform a similar exercise with the other models in Table 4 and see, for

575  example, that the isolation model provokes isolation because females 0 prefer A while

576  skip C, and vice versa, females 1 skip A and prefer C (both female phenotypes have the

577  same preference for B).

578  Under uniform frequencies in both sexes, this isolation model does not generate sexual

579  selection. The marginal propensity of females 0 and 1 is the same, $m'_{f0} = m'_{f1} = (a + a/2$

580  $+ \varepsilon) / 3$ so there is no sexual selection in females. In males, the marginal propensity of A

581  and C is $(a + \varepsilon)/2$ while is $a/2$ for B males; they are equal except for the addition of the

582  factor $\varepsilon/2$ which is virtually 0 and therefore there is no detectable effect of sexual

583  selection.

584

585  *Discussion*

586  The mate choice model defined in (1) is valid for phenotypes and genotypes, and it only

587  requires the abstract representation of any kind of relative mutual mating propensity.

588  The model in (1) is similar to the model for the mating pattern predicted from

589  encounter-mating (EM) scenarios when the availability of individuals is not affected by

590  the matings that have already occurred (equation 19 in Gimelfarb, 1988). The latter

591  happens in polygamous species, or even with monogamous, when only a small fraction

592  of individuals of both sexes successfully mate (i.e. the process of the encounter

593  corresponds to sampling with replacement).

594  On the contrary, when the species are monogamous and the population size is small, the

595  mating pattern will depend on the kind of pair formation process (Gimelfarb, 1988). In

596  the latter case, the information framework should still be valid but the equations must be

597  updated after each mating round. Therefore, the pair formation process without

598  replacement, would introduce some noise in the obtained mating patterns. The

599  application of the proposed methodology in such situations is left for future work.

600  At the same time, (1) is analogous to the Wright's selection equation for the change in

601  gene frequencies so, from the viewpoint of that analogy, the relative propensity would

602  play the role of fitness referred to each mating couple. By defining the relationship

603  between observed and expected mating frequencies as a function of relative mating

604  propensity, the choice is expressed as a potentiality which is also a key characteristic of

605  fitness (Wagner, 2010).

606  As with the fitness concept, the mate propensity faces two main aspects, namely the

607  measurement of differences between couples, and the intrinsic causes that provokes the

608  propensity values. By expressing the equation of change in terms of the choice

609  information and its components, this work focused in the first aspect.

610    I have connected the cause of mating choice, which is modeled by the abstract concept

611    of mutual mating propensity, with the different possible outcomes. Notably, the

612    connection between mate choice and its consequences appears in terms of information.

613    The general equation ($J_{PTI}$) represents the information gained by mate choice with

614    respect to random mating. This general information is the sum of the information due to

615    sexual isolation and sexual selection, plus a mixed effect term that can be computed

616    separately from the others. The mixed term measures the adjustment of the partition

617    components with respect to the total mate choice information. In addition, the

618    information from sexual selection is the sum of the male and female intrasexual

619    selection information.

620    Although the model has been constructed assuming discrete phenotypes, it is possible to

621    estimate the Kullback-Leiblerg divergence for the continuous case (Pérez-Cruz, 2008)

622    in order to apply a similar mate choice information partition for quantitative traits.

623    The information framework also provides a baseline for defining adequate null

624    hypotheses for the distinct aspects of the mate choice problem. In fact, the information

625    terms are mean log-likelihood ratios, so we can apply them for contrasting the different

626    null hypothesis about random mating, sexual selection, and isolation.

627    Therefore, the statistical test defined as $nJ$ (total number of matings $n$, multiplied by the

628    Jeffreys' divergence) is similar to a $G$-test. In fact, if we note $G$ for the $G$-test with $nq$

629    expected counts, and $G'$ for the $G$-test with $nq'$ expected counts, then $nJ = (G + G') / 2$.

630    Indeed, it has been shown that the $G$-test $G$, is highly correlated (0.99) with the Jeffreys'

631    statistic (Evren and Tuna, 2012).

632    We can perform the test against random mating by considering a chi-square distribution

633    with $KK'$-1 degrees of freedom (Evren and Tuna, 2012; Sokal and Rohlf, 1981), where

634     $K \times K'$ is the number of different mating categories. The intrasexual selection

635     components correspond to $K$-1 and $K'$-1 degrees of freedom for $K$ female and $K'$ male

636     traits respectively. In addition, the sexual isolation component corresponds to $(K-1)(K'-$

637     1) degrees of freedom.

638     Of course, we may also use randomization tests if we prefer to rely on the empirical

639     distribution approach.

640     Therefore, if we want to contrast mate choice for a given trait $Z$, we test deviations from

641     zero information in $JZ_{PTI}$ and its components. However, if we want to contrast mate

642     choice in general, we must test deviations from zero information in $J_{PTI}$ which should be

643     the same that testing a flat preference function across all trait values (Edward, 2015).

644     In addition to contrasting the null hypothesis of random mating, we may take advantage

645     of the informational partition of mate choice effects to develop different kind of general

646     models defined by their effects. This is possible because the developed relationships

647     expose and clarify useful general properties, such as the requirement of non-

648     multiplicative mutual propensity functions for obtaining sexual isolation effects and the

649     connection of the marginal propensities at each sex with sexual selection.

650     As an example of the possible insight that can be gained relying in the informational

651     framework, I reanalyzed the well-known example of *D. melanogaster* mating data from

652     (Hollocher et al., 1997) and besides confirming previous results on the components of

653     sexual isolation and selection effects, I have been able to fit a simple two-parameter

654     model that explains the data by means of a component of sexual isolation plus a sexual

655     selection component favoring the mating of the M-type females.

656     In addition to the similarity models in which the same phenotype is involved in both

657     sexes, the preference-display models are also easily interpreted in terms of information

658    and we have been able of inspecting models of full isolation, full intrasexual selection,

659    and mixed effect models.

660    We have also seen an example with multiplicative mutual propensity by means of a

661    simple preference-display model based on the bird sage grouse (*Centrocercus*

662    *urophasianus*) in which the traits 'acoustic broadcast' and 'display rate', act

663    multiplicatively over the preference.

664    To conclude, it is worth mentioning that the concept of mate choice is important in the

665    evolutionary theory and other disciplines. It has been approached from a diversity of

666    fields and inference methodologies, which has provoked that the terminology has not

667    always been very precise. This may have contributed to some confusion in terms of

668    causes and effects jointly with plenty discussion (Ah-King and Gowaty, 2016; Edward,

669    2015; Janicke et al., 2016; Roughgarden et al., 2015).

670    Here, I have shown that the mean change in the mating phenotypes can be expressed as

671    the information gained due to mate choice. Overall, the obtained results lead to the

672    suggestion that the information interpretation of mate choice is an interesting avenue

673    that may help to improve the study of the causes as well as the effects of this important

674    evolutionary phenomenon.

675

**Appendix A. Relative propensity and phenotypes**

677    Let $T$ the trait that is the target of the choice while $Z$ is any other trait that can be more

678    or less related to the choice.

679    We call $J_{PTI}$ to the change in the number of matings when these matings were classified

680    by $T$ (equation 2 in the main text). On the other hand, the change in the number of

681    matings when they were classified by $Z$ is $JZ_{PTI}$.

682    If we cannot measure directly the values of $m$ (trait $T$) then we simply compute $J$ based

683    on trait $Z$ and therefore we are really computing

684              $JZ_{PTI} = \alpha_z J_{PTI}$

685    The scaling factor $\alpha_z$ is

686    $\alpha_z = (\beta(m_z, l_z) \times D_z) / (\beta(m,l) \times D)$ if $J_{PTI} > 0$; or 1 otherwise.

687    The values $D_m = V(m) / M$ and $D_z = V(m_z)/M_z$ are the indexes of dispersion over $T$ and $Z$

688    respectively; the subscript $z$ indicates that the matings were classified by phenotype Z

689    instead of by $T$ (see Appendix C for more details in the scaling formulae).

690    The distinction between $JZ_{PTI}$ and $J_{PTI}$ matters because when the information produced

691    by mate choice is computed as $JZ_{PTI}$, a value of zero could means that $i$) $cov(m_z, l_z) = 0$

692    so $\alpha_z = 0$ i.e. the trait $Z$ do not covariate with the differential propensies (the mating is

693    random with regard to $Z$) or, alternatively $ii$) $J_{PTI} = 0$ meaning that there is no

694    differential mating propensity at all, i.e. the mating is random independently of the trait

695    we focused on.

696    Let's see an example of the first situation i.e. there is mate choice but the trait $Z$ is not

697    involved in the mate choice process. Thus, assume that some unknown trait $X$ that is

698    involved in an assortative mating process exists. There are two phenotypic classes '1'

699    and '2' so that $m_{11} = 2$, $m_{12} = 1$, $m_{12} = 1$, $m_{22} = 2$; the phenotype frequencies are uniform

700    in males and females, $p = 0.5$, and mean propensity $M = 1.5$. This results in $J_{PTI} = J_{PSI} =$

701    0.1155.

702    However, when counting the matings, we evaluated a phenotype $Z$ with classes $A/B$ that

703    are independent of the mating choice process. If the trait responsible of the mate choice

704    is uniformly distributed over the phenotypes $A/B$ (i.e. half of $A$ individuals have trait

705    value '1' and the other half have value '2' and the same is true for $B$ individuals) then the

706    expected preference for the phenotype pairs are

707    $m_{AA} = m_{AB} = m_{BA} = m_{BB} = (m_{11} + m_{12} + m_{21} + m_{22}) / 4 = 1.5 = M = M_z$.

708    Thus it is clear that the normalized preferences are 1 and $JZ_{PTI} = 0$.

709    Consider now a different case in which $JZ_{PTI} \neq 0$, this means that the non-random

710    mating is correlated to some extent with the trait $Z$. For example, consider the same

711    mate choice scenario as above with $J_{PTI} = J_{PSI} = 0.1155$ but now the phenotype under

712    study is partially linked to the mate choice so $m_{AA} = 1.7$, $m_{AB} = 1.2$, $m_{BA} = 1.2$, $m_{BB} =$

713    1.7.

714    Recall that the frequencies are uniform. If we compute directly the information index

715    over the phenotypes $Z$, we get $JZ_{PTI} = 0.03$. The mean propensity for these phenotypes

716    is $M_z = 1.45$ and $cov(m_z, l_z) = 0.0435$. However, $M = 1.5$ and $cov(m,l) = 0.1733$ for the

717    real mate choice trait ($T$). The scaling is $\alpha_z = [cov (m_z, l_z) /M_z]$ / $[cov (m, l) /M] = 0.2597$

718    so $J_{PTI} = JZ_{PTI} / \alpha_z = 0.03/0.2597 = 0.1155$, as expected.

719     If we have an estimate or a computable proxy for the propensity function *m*, as for

720     example, a measure of distance between female and male traits |D|, or a model with

721     Gaussian functions (Carvajal-Rodriguez and Rolán-Alvarez, 2014), then $JZ_{PTI}$ and $J_{PTI}$

722     can be estimated separately. We obtain $J_{PTI}$ by means of $J(q', q)$ using the estimated

723     mating propensities to classify the frequencies, and we still can use the phenotypes *Z* to

724     compute $JZ_{PTI}$. The relationship between both measures may give an idea about the

725     linkage between the phenotypes *Z* and the mate choice.

726     Suppose that the estimate of $J_{PTI}$ is different from zero while $JZ_{PTI} = 0$, then mate choice

727     do exist but it is not linked with the phenotype *Z*. An interested researcher could

728     compare different traits looking for the ones having the best scaling for the information

729     $J_{PTI}$, i.e. the one that is more involved in the mate choice. It seems that if we are able of

730     having good proxies for mating propensity, this could pave the way for testing the

731     impact of different traits on mate choice.

732     Additionally, we still can compute directly $\Delta Z = Z' - Z$, i.e. the difference in phenotype

733     frequencies between observed and expected by random mating. Therefore, we have two

734     values, $\Delta_m Z$ and $\Delta Z$, for the change in *Z*, the discrepancy between them gives an

735     estimate of the change in *Z* caused by other factors than mating propensity (e.g.

736     predators) so $e_z = \Delta Z - \Delta_m Z$.

737     Thus the total change in mean *Z* is

738         $$\Delta Z = \alpha_z J_{PTI} + e_z$$

**Appendix B**

739    The relationship between sexual selection measured within sex and the pair sexual

740    selection measured by *PSS* is

741        $J_{PSS} = J_{S1} + J_{S2}$

742    To see this, recall that $J_{PSS}$ is the sum of products $\Delta( p_{1i}p_{2j}) \times log((p'_{1i}\, p'_{2j})/ (p_{1i}p_{2j}))$.

743    Then note that

744        $log((p'_{1i}p'_{2j}) / (p_{1i}p_{2j})) = log(p'_{1i} / p_{1i}) + log(p'_{2j} / p_{2j})$

745    and that

746        $\Sigma_{ij}\, \Delta( p_{1i}p_{2j}) = \Sigma_{ij}(p'_{1i}p'_{2j} - p_{1i}p_{2j}) = \Sigma_i p'_{1i}\, \Sigma_j p'_{2j} - \Sigma_i p_{1i}\, \Sigma_j p_{2j} = 0$

747    because each summation is 1. Then, after some algebraic rearrangement we obtain

748        $J_{PSS} = \Sigma_{ij}\, \Delta(p_{1i}p_{2j})log((p'_{1i}p'_{2j})/(p_{1i}p_{2j})) = \Sigma_i p'_{1i}log(p'_{1i}/p_{1i}) - \Sigma_i p_{1i}log(p'_{1i}/p_{1i}) +$

749        $\Sigma_j p'_{2j}log(p'_{2j}/p_{2j}) - \Sigma_j p_{2j}log(p'_{2j}/p_{2j}) = J_{S1} + J_{S2}.$

## Appendix C. Scaling factors

750    We can compute the scaling factors that translate the information between different

751    phenotypic scales.

752    We have used the notation $J_{PTI}$, $J_{PSS}$, $J_{PSI}$ and $E_0$ for indicating the information when

753    measured from phenotypes that are the choice targets i.e. the phenotypes that the mates

754    care about in choosing each other. On the other hand, we note $JZ_{PTI}$, $JZ_{PSS}$, $JZ_{PSI}$ and

755    $ZE_0$ when the phenotypes may or may not be related with the choice.

756    Therefore, it is interesting to shown how the information changes between one measures

757    or others. So that

758    $JZ_{PTI} = \alpha_z J_{PTI}$; $JZ_{PSS} = \alpha_{pss} J_{PSS}$; $JX_{S1} = \alpha_x J_{S1}$; $JY_{S2} = \alpha_y J_{S2}$; $ZE_0 = \alpha_E E_0$ and $JZ_{PSI} = \alpha_z J_{PTI} -$

759    $(\alpha_{pss} J_{PSS} + \alpha_E E_0)$

760    The scalings are as follows.

761    $\alpha_z = [cov(m_z, l_z)/M_z] / [cov(m, l)/M]$ with $l_z = log(m_z)$ and $l = log(m)$ if $J_{PTI} > 0$

762    or $\alpha_z = 1$ otherwise ($J_{PTI} = 0$).

763    However, we can also express $cov(m_z, l_z)/M_z$ as $\beta(m_z, l_z) \times D_z$ which is the regression of

764    the propensity under the trait Z over its logarithm multiplied by the index of dispersion.

765    Then if $D_m = V(m)/M$ and $D_z = V(m_z)/M_z$ are the indexes of dispersion over the choice

766    and Z traits respectively, we obtain

767        $(cov(m_z, l_z)/M_z) / (cov(m, l)/M) = (\beta(m_z, l_z) \times D_z) / (\beta(m, l) \times D)$

768    Then if if $J_{PTI} > 0$ define

769    $\alpha_z = (\beta(m_z, l_z) \times D_z) / (\beta(m, l) \times D)$

770    where $l_z = log(m_z)$ and $l = log(m)$

771    or $\alpha_z = 1$ if $J_{PTI} = 0$

772    Similarly,

773    $\alpha_x = [cov(m'_{zf}, l_{zf})/M_z] / [cov(m'_f, l_f)/M] = (\beta(m'_{zf}, l_{zf}) \times D_{zf}) / (\beta(m'_f, l) \times D_f)$

774    or 1 if $J_{PS1} = 0$

775    where $l_{zf} = log(m'_{zf})$, $D_{zf} = V(m'_{zf})/M_z$, $l_f = log(m'_f)$, $D_f = V(m'_f)/M$

776    $\alpha_y = [cov(m'_{zm}, l_{zm})/M_z] / [cov(m'_m, l_m)/M] = (\beta(m'_{zm}, l_{zm}) \times D_{zm}) / (\beta(m'_m, l) \times D_m)$ or 1 if

777    $J_{PS2} = 0$

778     where $l_{zm} = log(m'_{zm})$ , $D_{zm} = V(m'_{zm})/M_z$ .

779     $\alpha_{pss} = [cov(m'_{zf} m'_{zm}, l'_z) /M^2_z] \; / \; [cov(m'_f m'_m, l') /M^2] = (\beta(m'_z, l'_z) \times D'_z) / (\beta(m', l') \times D')$

780     or 1 if $J_{PSS} = 0$

781     where $m'_z = m'_{zf} \times m'_{zm}$, $m' = m'_f m'_m$, ,$D'_z = V(m'_z)/ M^2_z$, $l'_z = log(m'_z)$, $l' = log(m')$, $D' =$

782     $V(m')/ M^2_z$.

783     $\alpha_E = [cov (m'_{zf}m'_{zm}, log(PSI_z)) / M_z^{\;2}] / [cov(m'_f m'_m, log(PSI)) / M^2] = (\beta(m'_z, l_{zpsi}) \times D'_z) /$

784     $(\beta(m', l_{psi}) \times D')$ or 1 if $E_0 = 0$

785     where $l_{zpsi} = log(PSI_z)$, $l_{psi} = log(PSI)$.

786     Finally

787     if $J_{PSI} > 0$

788     $\alpha_\delta = \alpha_z$ when $J_{PSS} = 0$ or in general

$$\alpha_\delta = \frac{\alpha_T J Z_{PSI}}{\alpha_{pss}\alpha_E J Z_{PTI} - \alpha_z(\alpha_E J Z_{PSS} + \alpha_{pss} Z E_0)}$$

789     with $\alpha_T = \alpha_z \times \alpha_{pss} \times \alpha_E$; so that $J Z_{PSI} = \alpha_\delta J_{PSI}$ .

## Appendix D. Multiplicative preference example

790     Consider two male traits, *B/b* for acoustic broadcast and *D/d* for display rate, where in

791     both cases the upper case refers to the higher value of the trait; consider also one female

792     trait *X* with a single phenotypic class. The females are the choosers and so we may

793     define multiplicative preferences as appear in Table S1.

794

795    **Table S1. Mating preferences for acoustic broadcast and display rate.**

| | Males Bd | BD | bD | bd |
|---|---|---|---|---|
| **Females** | | | | |
| $X$ | α | αβ | β | 1 |

796

797    The model assumes a single female phenotypic class and so the frequency is 1. Let the

798    frequencies of the different male classes be $p_{Bd}$, $p_{BD}$, $p_{bD}$ and $p_{bd}$. Then the mean

799    preference is $M = \alpha p_{Bd} + \alpha\beta p_{BD} + \beta p_{bD} + p_{bd}$. There is only one female marginal

800    preference, that in fact coincides with the mean preference, $m'_{fX} = M$. There are four

801    male marginal preferences ($m'_{mBd}$, $m'_{mBD}$, $m'_{mbD}$, $m'_{mbd}$) that match the corresponding

802    male propensity with the single female phenotype i.e. $m'_{mBd} = \alpha$, $m'_{mBD} = \alpha\beta$, $m'_{mbD} = \beta$

803    and $m'_{mbd} = 1$.

804    In (5) we have given an aprioristic expression (δ) of the pair sexual isolation (*PSI*)

805    coefficients in terms of the preferences so that $\delta_{ij} = (m_{ij} /M) / (m'_{fi} m'_{mj} / M^2)$. Therefore,

806    $\delta_{Bd} = (m_{Bd} /M) / (m'_{fX} m'_{mBd} / M^2) = (\alpha /M) / (M \alpha / M^2) = 1$ and similarly for the other

807    phenotypes so finally $\delta_{Bd} = \delta_{BD} = \delta_{bD} = \delta_{bd} = 1$, which implies no sexual isolation.

On the other hand, the model predicts male sexual selection whenever α and/or β $\neq$ 1.

**Appendix E**

808    *Proposition* 1

809        $\Sigma_{ij} \Delta(p'_{1i} p'_{2j}) log(PSS_{ij}) = 0$

810    then

811 $\quad E_0 = \Sigma_{ij}(\Delta(p_{1i}p_{2j})log(PSI_{ij}) + \Delta(p'_{1i}p'_{2j})log(PSS_{ij})) = \Sigma_{ij}\,\Delta(p_{1i}p_{2j})log(PSI_{ij}).$

812 First, recall that

813 $\quad \Sigma_{ij}\,\Delta(p'_{1i}p'_{2j})log(PSS_{ij}) = \Sigma_{ij}(q'_{ij} - p'_{1i}p'_{2j})log(PSS_{ij})$

814 and also that by definition of *PSS*

815 $\quad log(PSS_{ij}) = log((p'_{1i}p'_{2j}) / (p_{1i}p_{2j}))$

816 that can be expressed as

817 $\quad log(PSS_{ij}) = log(p'_{1i} / p_{1i}) + log(p'_{2j} / p_{2j})$

818 then by simple substitution and rearranging the terms

819 $\quad \Sigma_{ij}\,\Delta(p'_{1i}p'_{2j})log(PSS_{ij}) =$

820 $\quad \Sigma_{ij}(q'_{ij} - p'_{1i}p'_{2j})log(PSS_{ij}) = \Sigma_{ij}q'_{ij}log(p'_{1i}/p_{1i}) + \Sigma_{ij}q'_{ij}log(p'_{2j} / p_{2j}) -$
821 $\quad \Sigma_{ij}(p'_{1i}p'_{2j})log(p'_{1i} / p_{1i}) - \Sigma_{ij}(p'_{1i}p'_{2j})log(p'_{2i} / p_{2i})$

822 Now recall that the *i* subscript refers to females and subscript *j* to males, then the double

823 summary is the sum through females and males, thus by reminding that $\Sigma_j p'_{2j} = \Sigma_i p'_{1i}$

824 = 1 we note that

825 $\quad \Sigma_{ij}(p'_{1i}p'_{2j})\,log(p'_{1i}/p_{1i}) = \Sigma_i(p'_{1i})log(p'_{1i}/p_{1i})\,\Sigma_j p'_{2j} = \Sigma_i\,p'_{1i}log(p'_{1i}/p_{1i})$

826 and similarly

827 $\quad \Sigma_{ij}(p'_{1i}p'_{2j})log(p'_{2i}/p_{2i}) = \Sigma_j\,p'_{2j}log(p'_{2i}/p_{2i})$

828 so we have

829 $\quad \Sigma_{ij}\,\Delta(p'_{1i}p'_{2j})log(PSS_{ij}) =$

830 $\Sigma_{ij}q'_{ij}log(p'_{1i}/p_{1i}) + \Sigma_{ij}q'_{ij}log(p'_{2j} / p_{2j}) - \Sigma_i p'_{1i}log(p'_{1i}/p_{1i}) - \Sigma_j p'_{2j}log((p'_{2i} / p_{2i})$

831 Now note that

832   $\Sigma_{ij}q'_{ij}log(p'_{1i}/p_{1i}) = \Sigma_i \, log(p'_{1i}/p_{1i}) \, \Sigma_j q'_{ij}$

833 and that for each female $i$ the sum through males of the observed mating frequencies

834 involving female $i$ is, by definition, $p'_{1i}$ i.e. $\Sigma_j q'_{ij} = p'_{1i}$ and similarly for each male $j$ we

835 have $\Sigma_i q'_{ij} = p'_{2j}$. Then

836   $\Sigma_{ij}q'_{ij}log(p'_{1i}/p_{1i}) = \Sigma_i \, log(p'_{1i}/p_{1i}) p'_{1i}$

837 and

838   $\Sigma_{ij}q'_{ij}log(p'_{2j}/p_{2j}) = \Sigma_j log(p'_{2j}/p_{2j}) p'_{2j}$

839 therefore

840   $\Sigma_{ij} \, \Delta(p'_{1i}p'_{2j})log(PSS_{ij}) =$

841 $\Sigma_i \, log(p'_{1i}/p_{1i}) p'_{1i} - \Sigma_i p'_{1i}log(p'_{1i}/p_{1i}) + \Sigma_j log(p'_{2j}/p_{2j}) p'_{2j} - \Sigma_j p'_{2j}log((p'_{2i}/p_{2i}) = 0$

842 and so the proposition is true

843   $E_0 = \Sigma_{ij}(\Delta(p_{1i}p_{2j})log(PSI_{ij})$

844

845 *Proposition* 2

846   $E_0 = D'_{KL}(w, q' \| p')$

847 where

848   $p' = p'_1 p'_2$

849   $w_{ij} = (PSS_{ij} - 1) / PTI_{ij}$

850 $\quad\quad D'_{KL}(w, q' \| p') = \Sigma_{ij} w_{ij} q'_{ij} log(q'_{ij} / (p'_{1i} p'_{2j}))$

851 From the model (1) and the partitions (4) and (5) in the main text we know that

852 $\quad\quad (p_{1i} p_{2j}) = (p'_{1i} p'_{2j}) / PSS_{ij}$

853 $\quad\quad (p'_{1i} p'_{2j}) = q'_{ij} / PSI_{ij}$

854 therefore

855 $\quad\quad \Delta(p_{1i} p_{2j}) = (p'_{1i} p'_{2j}) - (p_{1i} p_{2j}) = (q'_{ij} / PSI_{ij}) - (q'_{ij} / PTI_{ij}) = q'_{ij}[(1/ PSI_{ij}) - (1 / PTI_{ij})]$

856 and since $PTI_{ij} = PSI_{ij} \times PSS_{ij}$ we obtain

857 $\quad\quad \Delta(p_{1i} p_{2j}) = q'_{ij}(PSS_{ij} - 1) / PTI_{ij}$

858 and so

859 $\quad\quad E_0 = \Sigma_{ij}(\Delta(p_{1i} p_{2j})) log(PSI_{ij}) = \Sigma_{ij} w_{ij} q'_{ij} log(PSI_{ij}) = D'_{KL}(w, q' \| p')$

860 which is Kullback–Leibler-like divergence with weights $w_{ij}$ in the observations $q'$.

861

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