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 mating

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

3   success. Thus, the model is adequate for any population where mating among distinct

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

5   preference model. It is shown that the concept of mating propensity permits to express

6   the observed change in the mating frequencies as the gain in information with respect to

7   random mating. This information framework provides the connection between mate

8   choice and the exact mathematical partition of the choice effects. Namely sexual

9   isolation, sexual selection and a mixed effect. The sexual selection component is the

10 sum of the intrasexual male and female selection. Interestingly, the information partition

11 is composed of log-likelihood ratios providing a baseline for defining adequate null

12 hypotheses for the distinct aspects of the mate choice problem. The utility of the

13 proposed framework is shown by analyzing real data to compare previous estimates of

14 intra and intersexual effects. On the other hand, some toy-models are also studied

15 showing how different mating schemes (e.g. by similarity or by preference-display)

16 correspond to different proportions of intra- and intersexual selection information. We

17 outline that when the effect of the phenotype onto the mating propensity is

18 multiplicative the intersexual selection effects cannot appear. Thus, sexual isolation

19 occurs as a deviation from multiplicativity in the phenotypic or trait effects over mate

20 choice. The preference-display models are also easily interpreted in terms of

21 information and we have inspected models of full isolation, full intrasexual selection

22 and mixed effect models. It is concluded that the new framework permits testing the

23 different choice effects. Additionally, it provides a new setting for exploring different

24 mating models and their consequences.

25   *Introduction*

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

27   been a bunch of controversy regarding this concept in part because is a significant

28   element for fields so diverse as population genetics, evolutionary-ecology, animal

29   behavior, sociology, or psychology. By other side, there has been an excess of verbal

30   models and imprecise terminology regarding different aspects of mate choice (Edward,

31   2015). Mate choice can be broadly described as the effect of some expressed traits

32   leading to non-random mating. Under this broad definition there are various aspects of

33   mate choice that can be considered. Yet Darwin (1871) distinguishes between

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

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

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

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

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

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

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

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

42   selection), which is the deviation from random mating in mated individuals (Rolán-

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

44   intrasexual and intersexual selection.

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

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

47   tests. Unfortunately, little effort has been made to discuss different theoretical models in

48 the light of the observations, and the empirical tests have been rarely interpreted from

49 the modeling side (Roff, 2015).

50 A related problem is the question about the adequate null hypothesis to confront the

51 evolution of mate choice. The Lande-Kirpatrick (L-K) model has been proposed as a

52 null model (Kirkpatrick, 1982; Lande, 1981; Prum, 2010; Roff and Fairbairn, 2014).

53 This model assumes neutral genetic variation for the preference but the target trait can

54 be under natural selection. Hence, L-K fails as a null model when the preference is by

55 similarity (preference and target trait coincide) and the target trait is "magic" sensu

56 Gavrilets (2004) because in this case the preference trait is already under selection

57 (Hughes, 2015).

58 Therefore, there is a need for both null models and a general framework where the key

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

60 formalism provided by the information theory is the right tool to do so.

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

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

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

64 due to mate choice. As far as I know there is not a previous attempt of describing mate

65 choice from the point of view of the information theory. Although the potential of the

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

67 2005).

68 I begin with the definition of a general model that only requires an abstract functional

69 relationship connecting the observed mating frequencies with the expected by random

70 mating from the population gene or phenotype frequencies. This suffices for developing

71 a general information equation for mate choice that can be adequately partitioned into

72   intrasexual and intersexual information components plus a mixed term provoked by the

73   confounding effect of the marginal frequencies when the propensity effects are

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

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

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

77   provides the baseline for solving the mate choice null hypothesis problem since the null

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

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

80   The utility of this framework is shown by analyzing a real data example. Additionally,

81   some a priori defined mating functions are tested to explore the importance that the

82   implementation of different mating preferences can have on the intra- and intersexual

83   selection partition. A deeper study on the outcomes of different forms of the mating

84   preference functions is out of the scope of the present article and is left for future work.

85

86   *Model of Mate Choice*

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

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

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

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

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

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

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

94   intrasexual and intersexual selection effects.

95

96   **GENERAL MODEL**

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

98   phenotype X with K different classes having values $X_1, X_2 \dots X_k$, the frequency of the

99   phenotype X_i in the female population is $p_{1i} = n_{1X_i} / n_1$, i.e. the number of females with

100   that phenotypic value divided by the total number of females. Similarly for the male

101   phenotype Y with K' classes the frequency of Y_j in the male population is $p_{2j} = n_{2Y_j} / n_2$.

102   In this way, using the frequency of the phenotype for each sex we compute the expected

103   mating frequencies if mating is at random

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

105   The observed mating frequencies in a given environment e can be expressed as

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

107   $\qquad M = \sum_{i,j} q_{ij} m_{ij}(x,y,e),$

108   where $m_{ij}(x,y,e)/M$ is the relative propensity linked to female phenotype X_i paired with

109   male phenotype Y_j, for successfully mating in the environment e.

110   Therefore, the observed mating frequencies are the result of the aprioristic functions

111   $m_{ij}(x,y,e)$ (hereafter noted as m_{ij}) that can be any kind of composition of the preference

112   of female X_i for male Y_j, and vice versa, in the environment e. Note that random mating

113   is a particular case of the model in (1) when the propensities are equal for every mating

114   pair. In general, because each m_{ij} can be composed of female and male preferences,

115   mutual mate choice models (Bergstrom and Real, 2000) are not discarded under this

116   setting. These propensity functions can also represent intrasexual mating propensity, or

117   indeed several kinds of functions can be defined, empirical or analytical as for example

118   the Gaussian-like preference functions (reviewed in Carvajal-Rodriguez and Rolán-

119   Alvarez, 2014). Moreover, the model should be able to account for functions describing

120   more complex and general mate-choice scenarios (Kuijper et al., 2012; Roff, 2015).

121   The standardized m_{ij} functions could also be estimated a posteriori from the data. In this

122   case they coincide with the pair total index (PTI Rolán-Alvarez and Caballero, 2000)

123   which becomes an observed realization of the relative mating propensity for the

124   observed phenotypes (see below).

125   Once we have the observed mating frequencies as defined in (1), the change with

126   respect to random mating is

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

128   The mean population change for a combined phenotype Z= X ∘ Y is

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

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

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

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

132   which in the logarithmic scale becomes

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

134   Thus, if we take the logarithm of the propensity as the couple combined phenotype Z

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

136   can measure the mean population change ΔL in relative propensity as

137
$$\Delta L = \sum_{i,j} \Delta q_{ij} l_{ij} = \sum_{i,j} \Delta q_{ij} \, log\left(\frac{q'_{ij}}{q_{ij}}\right) = J(q', q) = J_{PTI} \quad (2)$$

138   which is the Kullback-Leibler symmetrized divergence (noted as Jeffreys inFrank,

139   2012), that measures the gain in information when the differential mating propensity

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

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

142   minimum information value since J cannot be negative.

143   From equation (1) recall that each m_{ij}/M is the ratio of the frequency of the observed

144   types divided by the expected pair types calculated from the total frequencies. Such

145   ratio of frequencies is, by definition, the pair total index PTI (Rolán-Alvarez and

146   Caballero, 2000) and then the logarithmic term in ΔL is the logarithm of PTI values.

147   Therefore $J(q',q)$ measures the gain in information as captured by the PTI coefficients,

148   confronting the hypothesis of mate choice against random mating. Hereafter we note

149   this J as J_{PTI}. Interestingly enough the Jeffreys' divergence computed as J_{PTI} (by taking

150   the natural logarithm and multiplying by the total number of matings) can be

151   approximated by a chi-square for the null hypothesis of random mating with KK'-1

152   degrees of freedom (Evren and Tuna, 2012).

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

154   as classes for classifying the couples (because we equated $log(m)$ and Z), when the

155   classes are based upon the phenotypes rather than in propensities we are conveying a

156   specific meaning for the change in frequencies. Therefore, the phenotype can be viewed

157   as other scale on which we can measure this information (Frank, 2013). Of course

158   different kinds of phenotypes can be more or less involved in mate choice and so,

159   different scales are more or less useful for measuring the mating choice information.

160

161   **RELATIVE PROPENSITY AND PHENOTYPES**

162   When we observe any mating pair (i,j) we need to identify that copula by a given

163   characteristic since we cannot in general classify the mating by the value of the

164   propensity function m_{ij} or by a phenotype that matches it perfectly as we did above

165   (each phenotypic pair was perfectly differentiated by specific m_{ij} mating propensity).

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

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

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

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

170    $$\Delta_m Z = \sum_{i,j} \Delta q_{ij} Z_{ij} = \sum_{ij} q_{ij} \left(m_{ij} - M \right) \frac{Z_{ij}}{M} = \frac{cov(Z,m)}{M} \qquad (3)$$

171   Note that the covariance in (3) would also account for the expected genetic correlation,

172   if any, between trait and preference in assortative mating cases (Lande, 1981). The

173   covariance $cov(m,Z)$ is the regression $\beta(Z,m)$ multiplied by the variance $V(m)$. The

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

175   propensities. So, if we take again Z equal to the logarithm of m, then by substituting in

176   (3) we obtain

177    $$\Delta L = cov(m,l) / M = \beta(l,m) V(m) / M$$

178   remembering from (2) that $\Delta L = J_{PTI}$ then $V(m) / M = J_{PTI} / \beta(l,m)$ so that

179 $$\Delta_m Z = \beta(Z,m)\frac{V(m)}{M} = \alpha_z J_{PTI}.$$

180 The term $\alpha_z = \frac{\beta(Z,m)}{\beta(l,m)}$ changes the scale from mating propensity to phenotype.

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

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

183 computing

184 $$JZ_{PTI} = \alpha_z J_{PTI} \text{ so}$$

185 $$\Delta_m Z = JZ_{PTI}$$

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

187 mating propensities.

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

189 by mate choice is computed as JZ_{PTI}, a value of zero could means that *i)* $\alpha_z = 0$ i.e. the

190 trait Z do not covariate with the differential propensities so that the mating is random

191 with regard to Z or, alternatively *ii)* $J_{PTI} = 0$ meaning that there is no differential mating

192 propensity at all, i.e. the mating is random independently of the trait we focused on. In

193 any other case, when $JZ_{PTI} \neq 0$ it means that the non-random mating is correlated with

194 the trait Z i.e. $cov(m,Z) \neq 0$.

195 If we have an estimate or a computable proxy for the propensity function m as for

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

197 Gaussian functions (Carvajal-Rodriguez and Rolán-Alvarez, 2014) then the term α_z can

198 be separated from J_{PTI}. In this case we could obtain J_{PTI} by means of $J(q', q)$ using the

199 estimated mating propensities to classify the frequencies and we still can use the

200 phenotypes Z and our proxy for m to compute α_z as the ratio of the corresponding

201   regressions. In this way, we have kept apart the information J from the scaling α. The

202   product of information and scale gives $\Delta_m Z$.

203   Suppose that the estimate of J_{PTI} is different from zero while the scaling $\alpha_z = 0$, mate

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

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

206   J_{PTI}. It seems that if we are able of having good proxies for mating propensity, this

207   could pave the way for testing the impact of different traits on mate choice.

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

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

210   values, $\Delta_m Z$ and ΔZ , for the change in Z, the discrepancy between them gives an

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

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

213   Thus the total change in mean Z is

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

215   The mate choice mediated by the differences in mating propensity would produce a

216   deviation from random mating. At the same time, this may cause two different effects,

217   namely sexual isolation and, sexual selection.

218

219   **SEXUAL SELECTION**

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

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

222   Caballero, 2000). This change can be studied using the frequencies within each sex i.e.

223   intrasexual selection, or considering jointly the both sexes by using the pair sexual

224   selection coefficient (*PSS*, Rolán-Alvarez and Caballero, 2000). I will show that when

225   the *PSS* coefficients are aprioristically considered as the marginal propensities for the

226   mating types, the information gained due to sexual selection is the sum of the

227   information from each sex. When the focus is on the phenotypes, the above continue to

228   be true provided that the same phenotypic scale is applied when computing *PSS* and the

229   intrasexual components.

230   *Intrasexual selection*

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

232   observed frequency of X_i in the matings, p'_{1i}, is computed as the sum of the frequencies

233   of matings involving a female X_i

234
$$p'_{1i} = \sum_j^{males} q'_{ij} = p_{1i} \sum_j p_{2j} \frac{m_{ij}}{M} = p_{1i} \frac{m'_{fi}}{M}$$

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

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

237   type *j* is

238
$$p'_{2j} = p_{2j} \frac{m'_{mj}}{M}$$

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

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

241   the female marginal propensity (female intrasexual selection)

242
$$\Delta_m L_x = \sum_i^{females} \Delta p_{1i} X_i = \sum_{ij} p_i \left(m'_{fi} - M \right) \frac{X_i}{M} = J(p'_1, p_1) = J_{S1}$$

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

244 $$\Delta_m L_y = \sum_j^{males} \Delta p_{2j} Y_j = J(p'_2, p_2) = J_{S2}$$

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

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

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

248 corresponding (female or male) marginal m'.

249 The change to the scale of phenotypes produces

250 $$\Delta_m \bar{X} = \frac{\beta_{xm}}{\beta_{lm}} J_{S1} = JX_{S1}$$

251 $$\Delta_m \bar{Y} = \frac{\beta_{ym}}{\beta_{lm}} J_{S2} = JY_{S2}$$

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

253 intrasexual selection measured on the combined phenotypic scale Z.

254 *Pair sexual selection*

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

256 under random mating calculated from mates with the expected pair types from total

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

258 can be viewed as an aprioristic expression of the *PSS* coefficients. Again, the difference

259 between the observed and the expected distribution can be expressed as

260 $$\Delta_{PSS} L = \sum_{i,j} \Delta(p_{1i} p_{2j}) log\left(\frac{p'_{1i} p'_{2j}}{p_{1i} p_{2j}}\right) = J(p'_1 p'_2, p_1 p_2) = J_{PSS},$$

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

262 In the scale of phenotypes

263 $$\Delta_{PSS} \bar{Z} = \frac{\beta_{zpss}}{\beta_{lpss}} J_{PSS} = JZ_{PSS}$$

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

265   definition of *PSS* and is expressed in term of the information accumulated and rescaled

266   from *PSS* to *Z*.

267   *Intrasexual selection and pair sexual selection*

268   The relationship between intrasexual selection and pair sexual selection measured by

269   *PSS* is, in terms of the information

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

271   Recall that J_{PSS} is the sum of products $\Delta(p_{1i}p_{2j}) \times log((p'_{1i}\,p'_{2j})/(p_{1i}p_{2j}))$. Then note that

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

273   and that

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

275   because each summatory is 1. Then, after some algebraic rearrangement we obtain

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

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

278   And in the scale of phenotypes is

279    $$JZ_{PSS} = JX_{S1} + JY_{S2} \quad (4)$$

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

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

282   couples is the same).

283   The information captured in the *PSS* coefficients is the sum of the intrasexual selection

284   within each sex.

285

286   **SEXUAL ISOLATION**

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

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

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

290   of our model this is the ratio of frequencies

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

292   The term δ refers to an aprioristic (depends on the m's from the model) definition of the

293   PSIs. The joint isolation index for PSI can be expressed as

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

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

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

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

298   observed and expected pair types in terms of J.

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

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

301   In the scale of phenotypes

302    $$\Delta_{PSI}\bar{Z} = \frac{\beta_{z\delta}}{\beta_{l\delta}}J_{PSI} = JZ_{PSI}.$$

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

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

305   formalism allow us to contemplate some facts that are not obvious from the a posteriori

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

307   the propensity of each pair is the product of the marginal types of each partner then $\delta =$

308   1 and so, both the values of I_{PSI} and J_{PSI} are zero indicating no sexual isolation at all.

309   Thus, in any model in which the mate propensity is multiplicative the only possible

310   outcome from mate choice is intrasexual selection (see below).

311

312   *Relationship between Mate Choice, Sexual Selection and Sexual Isolation*

313   The information as captured by the *PTI* coefficients can be partitioned in terms of *PSS*

314   and *PSI*. Recall the expression (2) for J_{PTI}

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

316   The term Δq_{ij} can be expressed as the sum of the frequency changes for sexual selection

317   and isolation

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

319   The logarithmic term is also partitioned in the sexual selection and isolation

320   components

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

322   Therefore

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

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

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

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

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

328   that can also be expressed as

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

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

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

332   depending on the weights.

333   The total information is separated into the intrasexual selection, J_{PSS}, and isolation, $J_{PSI,}$

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

335   selection and sexual isolation effects occur.

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

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

338   is not the total information from mating choice. On the other side, when E_0 is negative

339   there is some overlap between sexual selection and sexual isolation information.

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

341   classification is applied when computing the different measures

342          $JZ_{PTI} = JZ_{PSS} + JZ_{PSI} + ZE_0$ (6)

343   where ZE_0 is the value of E_0 in the phenotypic scale.

344   For any given logarithmic base, the amount of the total information, JZ_{PTI}, will depend

345   on the magnitude of the differences among the population mating propensity values.

346   The higher the differences encountered in the propensities the higher the value of JZ_{PTI}.

347   Without loss of generality we consider the natural logarithm because this facilitates

348   testing against the null hypothesis of no information by means of the chi-square

349   distribution.

350   Provided that JZ_{PTI} is not zero, the relationships between the quantities in (6) can be

351   resumed in three mating information statistics, the sexual isolation information (SII) and

352   sexual selection information (SSI) measures

353          $SII = 100 \times JZ_{PSI} / JZ_{PTI}$ (7-a)

354          $SSI = 100 \times JZ_{PSS} / JZ_{PTI}$ (7-b)

355   These terms cannot be negative since they come in the form of the Jeffrey's divergence

356   which is non-negative. An additional mixed term that can have negative values is the

357   mixed sexual selection isolation information ($MSSII$)

358          $MSSII = 100 \times ZE_0 / JZ_{PTI}$ (7-c)

359   These expressions measure the proportion of information that is obtained in terms of

360   sexual isolation or intrasexual selection (recall from equation 4 that JZ_{PSS} is the sum of

361   the intrasexual indexes) or the confounded effect of both.

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

363   the same sample, the sum in (6) is exact so that the statistics in (7) recover the whole

364   information gathered from mate choice. On the contrary, if the computations has been

365   performed using different samples, it could be a remaining part of mate choice

366   information that is non-explained by the above statistics but that can be recovered by

367   the error term

368          $E_{PTI} = 100 - (SII + SSI + MSSII)$ (7-d)

369   that gives (in %) how much information may be lost due to differences in the

370   measurement of the involved phenotypes when computing from separate samples the

371   different information components.

372

373   *Real Data Application*

374   The mating model I have presented so far has been defined in a quite general way for

375   any number of male and female phenotypic classes and for any kind of mating

376   propensities. The application of the statistics *SII*, *SSI* and *MSSII* to a data sample of

377   dimorphic traits (two classes) is immediate. For clarity I will use the same model that

378   appears in the pairwise statistics original article (Rolán-Alvarez and Caballero, 2000).

379   Therefore, the two phenotypic types are noted as *A* and *B*, the total number of observed

380   matings is *t* and the number of type *A* females (A' in Rolán-Alvarez and Caballero,

381   2000) becomes, under our notation, $p_{1A}n_1$, and so B' is $p_{1B}n_1$; the number of males *A*,

382   becomes $p_{2A}n_2$ and males *B* are $p_{2B}n_2$. The observed absolute number for each pair (*i,j*)

383   would be $q'_{ij}t$ with $i,j \in \{A, B\}$ (see Table 1). The total number of expected copulating

384   pairs from population frequencies is n_1n_2 corresponding to the quantity *S* in (Rolán-

385   Alvarez and Caballero, 2000).

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

387   ***B*. The number of observed copulating pairs is *t*. The quantities in the cells**

388   **correspond to absolute numbers.**

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

$$p_{2B}n_2 \quad q'_{AB}\,t \quad q'_{BB}\,t \quad p'_{2B}\,t$$

$$p'_{1A}\,t \quad p'_{1B}\,t$$

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

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

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

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

393

394   The data to be analyzed correspond to the same example utilized in (Rolán-Alvarez and

395   Caballero, 2000) concerning a multiple-choice experiment involving two different lines

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

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

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

399   selection. They also suggested a fitness advantage of females versus males but were not

400   able of distinguishing between female mate propensity (sexual selection) and male

401   preference for *M* females.

402   To perform the analysis, we can express the observed data from that experiment in

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

404   observed number of copulating pairs was $t = 1704$ we obtain the necessary quantities in

405   terms of our model (Table 2). By convenience, the computations in Table 2 and

406   hereafter were performed using the natural logarithms.

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

408   isolation ($JZ_{PSI} = 0.47$; $I_{PSI} = 0.63$), 6% of sexual selection and 5% of mixed effects

409   which explains the 100% of JZ_{PTI}. The information coming from sexual isolation is 14

410   times the intrasexual information, result that matches pretty well the outcome in (Rolán-

411   Alvarez and Caballero, 2000). The value of JZ_{PTI} multiplied by the number of matings

412 can be approximated by a chi-square variable with 3 degrees of freedom under the

413 expectation of $JZ_{PTI} = 0$, the p-value obtained is below 0.00001 which indicates non-

414 random mating. We may now test against the $JZ_{PSI} = 0$ with 1 degree of freedom and the

415 p-value is again below 0.00001. We may also test against $JZ_{PSS} = 0$ which is also below

416 0.0001 and so it makes sense to test both the intrasexual female and male cases (with

417 one degree of freedom each). The p-value for the female case is below 0.0001 while is

418 0.77 in the males. Thus we detect significant sexual isolation and selection effects as

419 previously reported by (Rolán-Alvarez and Caballero, 2000). The sexual selection

420 component is caused by a significant intrasexual effect in females. The mixed term E_0 is

421 positive thus indicating that not all the information is recovered by the *PSS* and *PSI*

422 coefficients. This is due to the confounding effect which explains as far as the 5% from

423 the total information.

424

425 **TABLE 2. Analysis using the mate choice information model (Table 1 and**

426 **equations 7) on *D. melanogaster* mating data from (Hollocher et al., 1997). The**

427 **number of observed copulating pairs is $t = 1704$.**

	Females Z	Females M		
		0.5×1440	0.5×1440	
Males Z	0.5×1440	0.3585×1704	0.145×1704	0.5035×1704
Males M	0.5×1440	0.051×1704	0.4455×1704	0.4965×1704
		0.4095×1704	0.5905×1704	
JZ_{PTI}	0.53			
SII (JZ_{PSI} , I_{PSI})	89% (0.47, 0.63)			
SSI ($JX_{S1} + JY_{S2}$)	6% (0.033 + 0.00005)			

MSSII	5%
E_{PTI}	0%

428   Number of females in the population: $n_1 = 1440$; number of males in the population: $n_2 = 1440$; From

429   Table 1, p'_{1i}: observed relative frequency of type i in mating females; p'_{2i}: observed relative frequency of

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

431

Relative Propensity Mate Choice Models

433   In the analysis performed above we have used the information partition for testing if the

434   observations can be explained from random mating. Since the expectation was

435   computed using the population phenotypic frequencies this computation for each

436   copulating pair corresponds to the PTI_{ij} statistics. Thus, each PTI_{ij} is an estimation of

437   what we have called the mating propensity m_{ij}/M (see equation 1). The more correlated

438   is the phenotype with the propensity the more precise would be the estimate.

439   The aprioristic modeling of mating propensity permits to interpret the deviations from

440   random mating as caused by some intrinsic biological property among the copulating

441   phenotypes. There are several ways in which these mating propensities or preferences

442   can be modeled (Carvajal-Rodriguez and Rolán-Alvarez, 2014; Edward, 2015;

443   Gavrilets, 2014). By studying the effect that different kind of functions may have on the

444   observed mating distribution we would gain insight on the different mechanisms of

445   mate choice and their consequences. In what follows we just take a brief look on some

446   examples though a more in deep study on mating propensities is left for future work.

447   We consider a population with equal sex ratio and equal frequencies between

448   phenotypes. The number of phenotypic classes was fixed to 3 just because this allow the

449 inspection of a MHC (major histocompatibility complex) population genetics choice

450 model (p. 195 Hedrick, 2005). The relative observed frequencies are the result of the

451 aprioristic definition of the corresponding mating propensity model. The different

452 assayed models are particular realizations of a generic model. The generic model

453 implies the composition $\circ$ of the female acceptance (or preference) function f_1 with the

454 male acceptance function f_2. For example, $f_1(A',B) \circ f_2(B,A')$ involves the acceptance

455 function from female with phenotype A' for the male with phenotype B combined with

456 the acceptance from male B for the female A' (Table 3).

457 **TABLE 3. Mating propensity models. Values of *m* are already expressed relative to**

458 **the mean. The contribution of each phenotype to the specific models is noted by**

459 **lowercase.**

$m_{\text{female,male}}$	Additive	Multiplicative	Positive	Negative	MHC	Generic
$m_{A'A}$	$a' + a$	$a' \times a$	$a' \times a$	10^{-17}	$1 - s$	$f_1(A',A) \circ f_2(A,A')$
$m_{A'B}$	$a' + b$	$a' \times b$	10^{-17}	$a' \times b$	$1 - hs$	$f_1(A',B) \circ f_2(B,A')$
$m_{A'C}$	$a' + c$	$a' \times c$	10^{-17}	$a' \times c$	1	$f_1(A',C) \circ f_2(C,A')$
$m_{B'A}$	$b' + a$	$b' \times a$	10^{-17}	$b' \times a$	$1 - s$	$f_1(B',A) \circ f_2(A,B')$
$m_{B'B}$	$b' + b$	$b' \times b$	$b' \times b$	10^{-17}	$1 - s$	$f_1(B',B) \circ f_2(B,B')$
$m_{B'C}$	$b' + c$	$b' \times c$	10^{-17}	$b' \times c$	$1 - s$	$f_1(B',C) \circ f_2(C,B')$
$m_{C'A}$	$c' + a$	$c' \times a$	10^{-17}	$c' \times a$	1	$f_1(C',A) \circ f_2(A,C')$
$m_{C'B}$	$c' + b$	$c' \times b$	10^{-17}	$c' \times b$	$1 - hs$	$f_1(C',B) \circ f_2(B,C')$
$m_{C'C}$	$c' + c$	$c' \times c$	$c' \times c$	10^{-17}	$1 - s$	$f_1(C',C) \circ f_2(C,C')$

460 Positive: positive assortative mating. Negative: negative assortative mating. MHC: negative assortative

461 female mate choice model for MHC as defined in (Hedrick, 2005).

462

463   **ADDITIVE AND MULTIPLICATIVE MODELS**

464   In the additive model each phenotype adds its contributing effect to the value of m,

465   similarly under the multiplicative model each phenotype contributes multiplicatively to

466   m. In both kind of models the contribution of each phenotype does not depend on the

467   partner phenotype i.e. the contribution a' from female A' is the same when mating with

468   male A or B. Obviously, if the contribution of every phenotype is the same (a' $= a = b$'

469    $= b = c$' $= c$) there is no deviation from random mating ($JZ_{PTI} = 0$). The assayed

470   contributions were $a'=a= 1$; $b'=b=5$; $c'=c=10$.

471   When the model is additive, the occurrence of non-random mating is detected as a

472   composition of both intrasexual selection and sexual isolation (Table 4). Under the

473   effects considered most of the information comes from sexual selection equally

474   distributed in both sexes. These proportions change if other magnitudes of effects are

475   considered (not shown).

476   On the contrary, if the model is multiplicative the deviation from random mating only

477   produces intrasexual selection whatever the phenotypic effects. This happens because

478   under this model, the *PSI* coefficients are the product of the two marginal mating

479   propensities from the phenotypes in the copula.

480   **TABLE 4. Results in terms of mating information statistics for distinct mating**

481   **propensity models.**

	JZ_{PTI}	SII (I_{PSI})	SSI ($J_{S1}+J_{S2}$)	$MSSII$	E_{PTI}
Additive	0.30	7% (-0.13)	83% (50% + 50%)	10%	0%
Multiplicative	1.28	0% (0)	100% (50% + 50%)	0%	0%

Positive	29.5	48% (1)	11% (50% + 50%)	40%	0%
Negative	14.8	118% (-1)	4% (50% + 50%)	-22%	0%
MHC (h=0)	0.12	48% (-0.22)	54% (82% + 18%)	-2%	0%
MHC (h=0.25)	0.10	57% (-0.2)	46% (93% + 7%)	-3%	0%
MHC (h=0.5)	0.09	65% (-0.18)	38% (100% + 0%)	-3%	0%
MHC (h=0.75)	0.09	71% (-0.15)	34% (87% + 13%)	-5%	0%
MHC (h=1)	0.1	70% (-0.11)	36% (50% +50%)	-6%	0%

482   Phenotypic effects from Table 3: $a'=a=1$; $b'=b=5$; $c'=c=10$. MCH: $s=0.5$ from (Hedrick, 2005). E_{PTI}:

483   error due to scaling.

484

485   **ASSORTATIVE POSITIVE AND NEGATIVE MODELS**

486   We have also defined two extreme assortative models with three different possible

487   mating types with asymmetric effects. The assortative positive model consists on

488   multiplicative effects except for the heterotypic crosses that have virtually 0 mating

489   acceptance (see Positive column in Table 3). From the total information recovered in

490   J_{ZPTI}, 48% was due to isolation while 11% was intrasexual selection and another 41%

491   was due to confounding effects. As expected the value of I_{PSI} was 1 (Table 4).

492   The assortative negative model (see column noted as Negative in Table 3) is also a

493   multiplicative model except for the homotypic crosses that have virtually 0 mating

494   acceptance. The value of I_{PSI} was -1 which is not surprising but the percentage of 118%

495   linked to the isolation information index was somewhat striking. The highest value of

496   the statistic *SII* is indicating that the information recovered by the *PSI* and *PSS*

497   coefficients is up biased by the confounding effect from marginal frequencies. The

498 excess obtained in the *SII* (+18) plus that in the *SSI* (+4) coefficients is recognized in the

499 negative sign of the *MSSII* statistic (-22).

500 The observed bias is expected for the *PSI* coefficients when the mate choice is not

501 symmetrical (Rolán-Alvarez and Caballero, 2000). We have seen that it requires both

502 sexual isolation and selection effects detected. We have also seen that the sign will

503 depend on the weights (*PSS* - 1)/ *PTI*. In our case it disappears when we define equally

504 weighted mating effects $a' = a = b' = b = c' = c$ for the heterotypic crosses under the

505 negative model; in this case the whole information is recovered by the sexual isolation

506 component with null sexual selection and mixed components (*SSI* = *MSSII* = 0).

507

508 *MHC-based negative assortative*

509 So far we have studied phenotypic models; however, the proposed framework can be

510 applied to a general class of models including population genetic ones. Different models

511 have been proposed to explain the maintenance of diversity in the major

512 histocompatibility complex. One of the hypotheses suggests negative assortative mate

513 choice for MHC. Thus, it is assumed that females preferentially mate males that differ

514 genetically from themselves (p. 196 Hedrick, 2005). The model is defined for two

515 alleles giving the genotypes A_1A_1, A_1A_2 and A_2A_2 that under our notation become *A'*, *B'*

516 and *C'* for females and *A*, *B* and *C* for males. Therefore, we can express this model in

517 terms of the information equations. The default selective and dominance coefficients

518 were $s = h = 0.5$ as suggested in (Hedrick, 2005). However a range of different selective

519 and dominance coefficients were also checked.

520 The results for the different dominance coefficients are shown in Table 4. In any case,

521 negative assortative mating is detected ($I_{psi} \in [-0.11, -0.22]$) with the percentage of

522   information expressed as intersexual selection (SII) increasing with the augment of the

523   dominance effect. The maximum information JZ_{PTI} and the maximum isolation (I_{psi}) do

524   coincide with the case of $h = 0$. Note that this is not the situation having the maximum

525   percentage on the SII statistic just because under the $h = 0$ scenario is also when the

526   highest female intrasexual selection occurs. In addition, the intrasexual partition also

527   varies with h; under codominance ($h = 0.5$) the full intrasexual component is due to

528   females while under absolute dominance ($h = 1$) it is equally partitioned between both

529   sexes. The outcome of varying s (not shown) is equivalent to varying the effects

530   between phenotypes. Small s implies less information but also lower confounding

531   effect. Higher s increases the information jointly with the confounding effect.

532   From Table 4 it seems that when negative assortative mating occurs due to asymmetric

533   effects, the I_{PSI} and the mixed term signs coincide and in fact both types of values

534   correlated well ($r = 0.95$).

535   Finally, it should be noted that the error term E_{PTI} has always been 0 indicating that the

536   partition of the total mate choice information was exact as expected because we have

537   used the same phenotypic classification when computing all the indexes.

538

539   **FEMALE PREFERENCE AND MALE DISPLAY MODELS**

540   So far we have considered examples with the same trait in female and male. However,

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

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

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

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

545   homotypic versus heterotypic so preventing the calculation of I_{PSI} and other similar

546 indices. Our mating propensity model can easily capture this type of situation to express

547 the components of mate choice in terms of information. This is an improvement with

548 respect to other sexual isolation indexes that by requiring a classification in homotypic

549 versus heterotypic mates, are only applicable to mating models in which the female and

550 male phenotype is the same (similarity/dissimilarity models).

551 In Table 5 we appreciate three examples of such preference-display models. There are

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

553 B or C. The mating propensities have been defined with only three possible values,

554 namely $a = 1$, $a/2$ or virtually 0 (10^{-17}). In the first column the female preference

555 generates a situation of complete isolation; in the second column the resultant effect of

556 the female preference is of full intrasexual selection in males and the third column

557 corresponds to a mixed scenario were both sexual selection and isolation occur with a

558 mixed effect of -24%. Thus, again we appreciate that when both sexual selection and

559 strong sexual isolation (negative) appear, the sign of the mixed term indicates the

560 direction of the isolation.

561 **TABLE 5. Mating propensity models of female preference for male display traits.**

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

563 **presenting distinct values for some secondary trait ($a = 1$, $a/2$ or 10^{-17}). Only the**

564 **females choose so that the generic model implies only the female acceptance (or**

565 **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	10^{-17}	$f_1(0,B)$

m_{0C}	10^{-17}	10^{-17}	10^{-17}	$f_1(0,C)$
m_{1A}	10^{-17}	a	10^{-17}	$f_1(1,A)$
m_{1B}	a/2	a/2	10^{-17}	$f_1(1,B)$
m_{1C}	a	10^{-17}	a	$f_1(1,C)$
JZ_{PTI}	13	13	26	
SII	100%	0%	75%	
SSI ($JX_{S1}+JY_{S2}$)	0%	100% (0% + 100%)	49% (0% + 100%)	
$MSSII$	0%	0%	-24%	

566

567

Discussion

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

570   requires the abstract representation of any kind of relative mating propensity. At the

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

572   frequencies so, from the point of view of that analogy, the relative propensity would

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

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

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

576   fitness (Wagner, 2010).

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

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

579   propensity values. In this work by expressing the equation of change in terms of the

580   choice information and its components I have focused in the first aspect.

581 I have connected the cause of mating choice, modeled by the abstract concept of

582 propensity, with the different possible outcomes. Notably, the connection between mate

583 choice and its consequences appears in terms of information. The general equation

584 represents the information gained by mate choice with respect to random mating. This

585 general information is the sum of the information due to sexual isolation and sexual

586 selection plus a mixed effect term that can be computed separately from the others and

587 measures the adjustment of the partition components with respect to the total mate

588 choice information. In addition, the information from sexual selection is the sum of the

589 male and female intrasexual selection information.

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

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

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

593 has been left for future work.

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

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

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

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

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

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

600 $K \times K'$ is the number of different mating categories. The intrasexual selection

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

602 traits respectively. And the sexual isolation component corresponds to $(K-1)(K'-1)$

603 degrees of freedom. Of course, we may also use randomization tests if we prefer to rely

604 on the empirical distribution approach.

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

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

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

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

609   We have also gained some intuition about the effects of choice by defining different

610   preference models and studying the information outcome. In doing so, we have seen

611   that multiplicative effects of the phenotype onto the mating propensity function do not

612   generate any kind of intersexual selection. Thus, sexual isolation can be viewed as a

613   deviation from multiplicativity in the phenotypic or trait effects over mate choice.

614   Interestingly, the preference-display models are also easily interpreted in terms of

615   information and we have been able of inspecting models of full isolation, full

616   intrasexual selection and mixed effect models.

617   We have also seen that the asymmetry in the phenotypic effects can bias the information

618   within the intra- and intersexual components provoking overrated *PSI* and/or *PSS*

619   information that becomes exposed by the negative values in the mixed component from

620   the total information partition. In other cases, the asymmetry provokes that the

621   information recovered in the intra- and intersexual components is less than the total

622   mate choice information. The bias disappears when the effects are symmetric. The total

623   mate choice information is not affected in any case.

624   In addition to the phenotypic models already commented we have also analyzed a

625   population genetic model of mate choice for MHC. Although the support for MHC-

626   based negative assortative mating is contentious (Hedrick, 2005), the model suffices for

627   showing the application of the choice information framework in the context of

628   population genetics. To convert the model to our framework we simply needed to

629   consider each genotype as a type and the mating preference in the original model as a

630   relative propensity that depends on the selective and dominance coefficients (see

631   Hedrick, 2005). The original model just try to represent female negative assortative

632   mating by favoring matings in which the males shares less alleles with the female

633   partner. Because the mating preferences are built from the side of the female

634   convenience (less shared alleles with the male partner) there is a priori no male

635   intrasexual selection in the model. However, intrasexual selection emerges as an effect

636   in one or both sexes depending on the dominance coefficient. These different outcomes

637   simply occur because changing h is equivalent to change the relative mating propensity

638   relationships among the different couples.

639   To conclude, it is worth mention that the concept of mate choice is important in the

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

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

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

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

644   2015; Janicke et al., 2016; Roughgarden et al., 2015).

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

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

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

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

649   evolutionary phenomenon.

650

APPENDIX A

651   *Proposition* 1

652 $\quad \Sigma_{ij} \Delta(p'_{1i} p'_{2j}) log(PSS_{ij}) = 0$

653 then

654 $\quad E_0 = \Sigma_{ij}(\Delta(p_{1i} p_{2j}) log(PSI_{ij}) + \Delta(p'_{1i} p'_{2j}) log(PSS_{ij})) = \Sigma_{ij} \Delta(p_{1i} p_{2j}) log(PSI_{ij}).$

655 First, recall that

656 $\quad \Sigma_{ij} \Delta(p'_{1i} p'_{2j}) log(PSS_{ij}) = \Sigma_{ij}(q'_{ij} - p'_{1i} p'_{2j}) log(PSS_{ij})$

657 and also that by definition of *PSS*

658 $\quad log(PSS_{ij}) = log((p'_{1i} p'_{2j}) / (p_{1i} p_{2j}))$

659 that can be expressed as

660 $\quad log(PSS_{ij}) = log(p'_{1i} / p_{1i}) + log(p'_{2j} / p_{2j})$

661 then by simple substitution and rearranging the terms

662 $\quad \Sigma_{ij} \Delta(p'_{1i} p'_{2j}) log(PSS_{ij}) =$

663 $\quad \Sigma_{ij}(q'_{ij} - p'_{1i} p'_{2j}) log(PSS_{ij}) = \Sigma_{ij} q'_{ij} log(p'_{1i} / p_{1i}) + \Sigma_{ij} q'_{ij} log(p'_{2j} / p_{2j}) -$

664 $\quad \Sigma_{ij}(p'_{1i} p'_{2j}) log(p'_{1i} / p_{1i}) - \Sigma_{ij}(p'_{1i} p'_{2j}) log(p'_{2i} / p_{2i})$

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

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

667 = 1 we note that

668 $\quad \Sigma_{ij}(p'_{1i} p'_{2j}) log(p'_{1i} / p_{1i}) = \Sigma_i(p'_{1i}) log(p'_{1i} / p_{1i}) \Sigma_j p'_{2j} = \Sigma_i p'_{1i} log(p'_{1i} / p_{1i})$

669 and similarly

670 $\quad \Sigma_{ij}(p'_{1i} p'_{2j}) log(p'_{2i} / p_{2i}) = \Sigma_j p'_{2j} log(p'_{2i} / p_{2i})$

671 so we have

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

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

674   Now note that

675      $\Sigma_{ij}q'_{ij}log(p'_{1i}/p_{1i}) = \Sigma_{i}log(p'_{1i}/p_{1i})\Sigma_{j}q'_{ij}$

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

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

678   have $\Sigma_{i}q'_{ij} = p'_{2j}$. Then

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

680   and

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

682   therefore

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

684      $\Sigma_{i}log(p'_{1i}/p_{1i})p'_{1i} - \Sigma_{i}p'_{1i}log(p'_{1i}/p_{1i}) + \Sigma_{j}log(p'_{2j}/p_{2j})p'_{2j} - \Sigma_{j}p'_{2j}log((p'_{2i}/p_{2i}) = 0$

685   and so the proposition is true

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

687

688   *Proposition* 2

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

690   where

691 $\qquad p' = p'_1 p'_2$

692 $\qquad w_{ij} = (PSS_{ij} - 1) / PTI_{ij}$

693 $\qquad D'_{KL}(w, q' \| p') = \Sigma_{ij} w_{ij} q'_{ij} log(q'_{ij} / (p'_{1i} p'_{2j}))$

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

695 $\qquad (p_{1i} p_{2j}) = (p'_{1i} p'_{2j}) / PSS_{ij}$

696 $\qquad (p'_{1i} p'_{2j}) = q'_{ij} / PSI_{ij}$

697 therefore

698 $\qquad \Delta(p_{1i} p_{2j}) = (p'_{1i} p'_{2j}) - (p_{1i} p_{2j}) = (q'_{ij} / PSI_{ij}) - (q'_{ij} / PTI_{ij}) = q'_{ij}[(1 / PSI_{ij}) - (1 / PTI_{ij})]$

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

700 $\qquad \Delta(p_{1i} p_{2j}) = q'_{ij}(PSS_{ij} - 1) / PTI_{ij}$

701 and so

702 $\qquad E_0 = \Sigma_{ij}(\Delta(p_{1i} p_{2j})) log(PSI_{ij}) = \Sigma_{ij} w_{ij} q'_{ij} log(PSI_{ij}) = D'_{KL}(w, q' \| p')$

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

704

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