The information theory formalism unifies the detection of the patterns of sexual selection and assortative mating for both discrete and quantitative traits.

A. Carvajal-Rodríguez*

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

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

email: acraaj@uvigo.es

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

Abstract

Sexual selection plays a crucial role in modern evolutionary theory, offering valuable insight into evolutionary patterns and species diversity. Recently, a comprehensive definition of sexual selection has been proposed, defining it as any selection that arises from fitness differences associated with nonrandom success in the competition for access to gametes for fertilization. Previous research on discrete traits demonstrated that non-random mating can be effectively quantified using Jeffreys (or symmetrized Kullback-Leibler) divergence, capturing information acquired through mating influenced by mutual mating propensities instead of random occurrences. This novel theoretical framework allows for detecting and assessing the strength of sexual selection and assortative mating.

In this study, we aim to achieve two primary objectives. Firstly, we demonstrate the seamless alignment of the previous theoretical development, rooted in information theory and mutual mating propensity, with the aforementioned definition of sexual selection. Secondly, we extend the theory to encompass quantitative traits. Our findings reveal that sexual selection and assortative mating can be quantified effectively for quantitative traits by measuring the information gain relative to the random mating pattern. The connection of the information indices of sexual selection with the classical measures of sexual selection is established.

Additionally, it is shown that under the normal distribution, the measure capturing the underlying information of assortative mating is a function of the square of the correlation coefficient, taking values within the non-negative real number set $[0, +\infty)$.

It is worth noting that the same divergence measure captures information acquired through mating for both discrete and quantitative traits. This is interesting as it provides a common context and can help simplify the study of sexual selection patterns.

Introduction

Sexual selection is a fundamental concept in modern evolutionary theory, offering valuable insights into various evolutionary patterns and the diversity of species. Originally proposed by Darwin in (1871), sexual selection describes the competition among individuals of one sex to secure mates from the other sex. However, the concept of sexual selection has been a subject of controversy since its inception (Alonzo and Servedio, 2019; Andersson, 1994; Lehtonen, 2022; Parker, 2014; Parker and Pizzari, 2015; Prum, 2012; Roughgarden et al., 2015; Vries and Lehtonen, 2023). There is ongoing debate surrounding its precise definition (Fitze et al., 2011), and its role as a

key component of modern evolutionary biology has even faced challenges (Roughgarden et al., 2006; Parker and Pizzari, 2015; but see Shuker, 2010).

Recently, Shuker and Kvarnemo (2021) put forth a comprehensive definition of sexual selection, characterizing it as "any selection that arises from fitness differences associated with nonrandom success in the competition for access to gametes for fertilization". In essence, a trait falls under sexual selection when variations in that trait are nonrandomly associated with variations in access to gametes, which serve as a limiting resource. From an evolutionary perspective, this process generates a discernible pattern of change in gene frequency, influencing the frequencies of corresponding genotypes and phenotypes. It is important to emphasize the use of the term "pattern of change" when discussing sexual selection, as it helps to clarify whether we are referring to the dynamic process or to the recognizable pattern in genetic or phenotypic changes.

The pattern of sexual selection is caused mainly by two biological mechanisms: mate competition and mate choice (Arnold and Wade, 1984; Endler, 1986; Lewontin et al., 1968; Rolán-Alvarez et al., 2015; Rolán-Alvarez and Caballero, 2000).

The process of mate competition refers, in a broad sense, to access to mating through courtship, intrasexual aggression and/or competition for limited reproductive resources (Andersson, 1994; Kokko et al., 2012; Wacker and Amundsen, 2014). Mate competition may generate a pattern of sexual selection (a change in frequencies of the trait under study) in the sex that competes.

Much work has been done to quantify sexual selection, reviewed in (Henshaw et al., 2018, 2016; Jones, 2009). Almost all measures currently used require estimates of individual mating success and reproductive success. In this work I focus on mating and fertilization success, rather than reproductive success (Shuker and Kvarnemo, 2021).

The process of mate choice refers to the effects of certain traits expressed in one sex that leads to the non-random allocation of reproductive effort with members of the opposite sex (Edward, 2015; Rosenthal, 2017). Mate choice may be mediated by phenotypic (sensorial or behavioral) properties that affect the propensity of individuals to mate with certain phenotypes (Jennions and Petrie, 1997). The observed pattern driven by mate choice can be a change in trait frequency in the other sex (sexual selection) and/or assortative mating where similar phenotypes or genotypes mate with one another more or less frequently than would be expected under a random mating pattern i.e. it produces a deviation from random mating in mated individuals (Carvajal-Rodríguez, 2018a; Rolán-Alvarez and Caballero, 2000). When the observed mating pattern between similar phenotypes is more frequent than expected by chance, we refer to positive assortative mating and when it is less frequent we refer to negative assortative mating. Sometimes in the literature, positive assortative mating is just referred to as assortative mating and negative assortative mating as disassortative mating. Mate choice when it produces positive assortative mating can have important evolutionary effects as it alters the variance of quantitative traits (Fisher, 1918), can generate sexual selection (Carvajal-Rodríguez, 2018a; de Cara et al., 2008) and under certain conditions, may facilitate local adaptation and speciation even in the presence of gene flow (Cotto and Servedio, 2017; Coyne and Orr, 2004; Fernández-Meirama et al., 2022; Gavrilets, 2004; Kirkpatrick and Ravigné, 2002; Rettelbach et al., 2013; Sachdeva and Barton, 2017; Yukilevich, 2023).

When examining phenotypes involving discrete traits, sexual selection can be identified through mating data using the pair sexual selection statistic (PSS), similarly, assortative mating can be identified by PSI, the pair sexual isolation statistic (Carvajal-Rodríguez and Rolan-Alvarez, 2006; Rolán-Alvarez and Caballero, 2000). For quantitative traits,

measuring sexual selection involves functions of the variance in mating or reproductive success (reviewed in Henshaw et al., 2016). On the other side, assessing assortative mating can be achieved by computing the Pearson correlation coefficient within mated pairs (Jiang et al., 2013). However, it is important to note that this measure comes with known problems and limitations (Clancey et al., 2022; Fernández-Meirama et al., 2022).

In a previous studies (Carvajal-Rodríguez, 2019, 2018a), it was demonstrated that non-random mating can be effectively quantified using the Jeffreys (Kullback-Leibler symmetrized) divergence. This measure captures the information acquired when mating is influenced by mutual mating propensities, rather than occurring randomly. By employing this theoretical framework, it becomes possible to detect and assess the strength of sexual selection and assortative mating (Carvajal-Rodríguez, 2020; Estévez et al., 2020; Lau et al., 2021).

The use of information theory to describe evolutionary processes is not new as it has a long tradition in evolutionary ecology, see for example (Sherwin, 2018; Sherwin et al., 2017; Sherwin and Prat i Fornells, 2019) and population genetics (Frank, 2012; Hledík et al., 2022; Kimura, 1961). Previous work on information theory and non-random mating was done on discrete traits. Here we extend that work to quantitative traits to describe patterns of sexual selection and assortative mating in terms of information.

The objective of this work is twofold. Firstly, we aim to demonstrate that the previous theoretical development, which is rooted in information theory and the concept of mutual mating propensity (Carvajal-Rodríguez, 2018a, 2020), seamlessly aligns with the sexual selection definition put forth by Shuker and Kvarnemo (2021). In this context, sexual selection emerges as a consequence of variations in the mutual mating propensity, without requiring specific assumptions about the genetic basis of the

involved traits. Secondly, we aim to illustrate that, for quantitative traits, sexual selection is also measured by Jeffreys divergence, which in turn can also be connected to classical metrics such as the opportunity for sexual selection and the standardized mating differential (see below). Additionally, we emphasize that the measure capturing the underlying information of assortative mating is not the correlation itself, but rather a function of the square of the correlation coefficient, that takes values within the non-negative real number set [0, +∞).

Fitness and sexual selection

Fitness, defined as an organism's ability or propensity to survive and reproduce relative to others in the same population drives natural selection by leading to changes in gene frequencies (Hartl, 2020; Hedrick, 2005). Identifying natural selection relies on recognizing the patterns of change it produces in frequencies.

Consider a population with various types, each representing a set of individuals with specific properties (traits, genotypes, etc.). Let N_i be the number of individuals of type *i*, and suppose a selection episode changes this number to N'_i. The absolute fitness, or growth rate, of type *i* during this episode is denoted as $W_i = N'_i/N_i$. To compare different types' fitness fairly, we compute the relative fitness, w_i, as the ratio of their absolute fitness to the mean population fitness. Thus, for a given type *i* with frequency p_i, the new frequency p'_i after a selection episode will be given by (Bürger, 2000; Hansen, 2018)

$$p_i' = p_i w_i \quad (1).$$

Recently, a simple theoretical framework, similar to the model presented in (1), has been developed to describe the influence of mating competition and mate choice on the emergence of sexual selection and assortative mating patterns (Carvajal-Rodríguez,

2018a, 2019, 2020). This theoretical framework has enabled the development of new statistical tests for detecting sexual selection and assortative mating. Moreover, by linking variation in mating ability (i.e., gamete access for fertilization) to the resulting frequency patterns, this framework facilitates the construction of predictive models and supports multi-model inference based on observed data patterns (Carvajal-Rodríguez, 2020).

In the following sections, I will briefly review and elucidate this theoretical framework, demonstrating its compatibility with Shuker and Kvarnemo's (SK hereafter) definition of sexual selection ("any selection that arises from fitness differences associated with nonrandom success in the competition for access to gametes for fertilization"; Shuker and Kvarnemo 2021).

Fitness for mating

We will focus on the change in frequencies due to fitness differences associated with access to gametes for fertilization. First, we must specify the concept of individual fitness for mating. Secondly, we will express for the discrete case, the SK definition of sexual selection in terms of information and then extend the definition to the continuous case.

Let be a female character X with a total of k_1 discrete possible trait values and a male character Y with k_2 discrete values. Characters X and Y can be the same or not. We define M_{ij} as the mutual ability or propensity to access gametes for fertilization between a female with value i for X and a male with value j for Y. Let p_{1i} be the population frequency of type i females and p_{2j} the frequency of type j males so that $q_{ij} = p_{1i}p_{2j}$ is the probability of random pairing of gametes from type i females with gametes from type j males for fertilization. The mean propensity is

$$M=\sum_{i=1}^{k1}\sum_{j=1}^{k2} q_{ij} M_{ij}$$

and the relative mutual propensity $m_{ij}=\frac{M_{ij}}{M}$.

The probability q'_{ij} of mating or gamete access for fertilization between any pair having such a combination of traits is (Carvajal-Rodríguez, 2018a)

$$q'_{ij}=q_{ij} m_{ij} \qquad (2).$$

Equation (2) represents the expected frequencies of mating between types *i* and *j* as a function of the expected frequencies per random gamete encounter and the relative values of mutual propensity. The equation clearly resembles equation (1) for the change in frequencies because of selection. In fact, the absolute value M_{ij} can be expressed in a similar way to absolute fitness i.e., as the ratio of the number N'_{ij} of matings between types *i* and *j* after selection over the expected number N_{ij} if there were no selection (random mating).

$$M_{ij}=\frac{N'_{ij}}{N_{ij}}.$$

Our focus is on identifying the individual propensity to access gametes for fertilization, rather than the mutual propensity of pairs. We refer to this individual propensity as the fitness for mating. In this context, we define the absolute marginal propensity M_{Fi} of the female of type *i* as

$$M_{Fi}=\sum_{j=1}^{k2} p_{2j} M_{ij}.$$

The relative marginal propensity or mating fitness m_{Fi} is obtained by dividing by the mean propensity *M*

$$m_{Fi}=\frac{M_{Fi}}{M} \qquad (3).$$

Similarly, the absolute marginal propensity M_{Mj} of the male of type j is

$$M_{Mj}=\sum_{i=1}^{k1} p_{1i} M_{ij}.$$

and the relative marginal propensity or mating fitness of males of type j is

$$m_{Mj}=\frac{M_{Mj}}{M}.$$

Thus, the relative mating fitness of a type is the average relative ability of individuals of that type to access gametes for fertilization.

While different mutual propensities shape mate choice, different mating fitness within a sex will produce a pattern of sexual selection (see Figure1 in Carvajal-Rodríguez, 2020). Sexual selection arises due to the unequal ability to access the gametes of the opposite sex for fertilization. Consequently, this sexual selection aligns perfectly with SK's definition.

Importantly, the concepts of mutual propensity and mating fitness, as defined, do not presuppose any particular mating preference function.

Having formalized the concepts of mutual propensity and mating fitness it is then possible to model mate competition and choice and the patterns of sexual selection and assortative mating they produce (see Carvajal-Rodríguez, 2018a, 2020).

The model in (2) facilitates the development of new statistical tests, based on information theory, to detect patterns of sexual selection and assortative mating (Carvajal-Rodríguez, 2018a). Moreover, it makes it possible to formalize the necessary and sufficient conditions for random mating in terms of mating propensities. Once these

conditions are defined, we can generate different mating fitness scenarios that produce the intended patterns of sexual selection and assortative mating, allowing the application of powerful model inference techniques (Carvajal-Rodríguez, 2020).

The formalization of the mate choice and competition processes from the model presented in (2) have been carried out only for discrete traits and here we extend the mathematical framework to the continuous case.

Sexual selection and assortative mating in quantitative traits

Consider two continuous traits in a population, X in females and Y in males, and let be the mating probability distribution $Q'(x,y)$ with probability density $q'(x,y)$ representing the mating probability for pairs with values in the infinitesimal interval ($[x,x+dx]$, $[y,y+dy]$). Alternatively consider the probability distribution $Q(x,y)$ of random mating from the product of densities $q(x,y)=f(x)g(y)$ of X and Y, respectively. Where $f(x)$ and $g(y)$ are the population probability densities for traits X and Y, respectively.

Note that (2) still holds so that $q'(x,y)$ depends on the density $q(x,y)$ and the infinitesimal mutual mating propensity m_{xy} which is the relative mutual propensity to access gametes for fertilization between a female with value in the infinitesimal interval $[x,x+dx]$ and a male with value in the infinitesimal interval $[y,y+dy]$.

In earlier work, Carvajal-Rodríguez (2018b) showed for discrete traits, that non-random mating can be characterized as the divergence between the mating distribution, Q', derived from mutual mating propensities, and the distribution of random mating, Q. Following (Carvajal-Rodríguez, 2018a; Frank, 2012), the average change in female and/or male traits caused by non-random mating when we take the logarithm of mutual propensity as a trait, is given by the Jeffreys divergence (or symmetric Kullback-Leibler divergence).

$$J=\int_{-a}^{+a}\int_{-a}^{+a}(q'(x,y)-q(x,y))\log\frac{q'(x,y)}{q(x,y)}dxdy \qquad (4),$$

where $q(x,y)=f(x)g(y)$.

For simplicity and without loss of generality we assume that the range is the same for X and Y so that, $X,Y\in[-a,a]$.

In this way, J captures the gain in information obtained when using Q' instead of Q and vice versa. If the information is not significantly different from 0 we can assume that the distribution of matings Q' is the same as that expected by random mating Q (Kullback, 1997). Note that the choice of J is not ad hoc, arising when we measure the average change in the logarithm of mutual mating fitness caused by the same mutual mating fitness. The relationship of J to the average change in any trait Z caused by mutual mating fitness, is (Frank, 2012)

$$\Delta_s Z=\frac{\beta_{Z,m}}{\beta_{L,m}}J$$

where $\beta_{Z,m}$ is the regression of the trait Z on the mutual mating propensity m and $\beta_{L,m}$ is the regression of log(m) on m.

For continuous traits and small changes, the average change in any trait Z, caused by mutual mating fitness reduces to (Frank, 2020)

$$\Delta_s Z=\beta_{Z,m}J$$

We will see that, just as in the discrete case (Carvajal-Rodríguez, 2018a), J can be decomposed into information due to sexual selection patterns in females and/or males ($J_{PSS}=J_{S1}+J_{S2}$) and assortative mating (J_{PSI}). So, $J=J_{PSS}+J_{PSI}+E$ (see below).

The distribution function of X in the population

$$F(x)=\int_{-a}^{x} f(u)\,du$$

and Y

$$G(y)=\int_{-a}^{y} g(v)\,dv,$$

where $f(u)$ and $g(v)$ are the respective probability densities.

From the probability density $q'(x,y)$, the marginal densities for X and Y in the matings are

$$f_1(x)=\int_{-a}^{+a} q'(x,y)\,dy$$

$$f_2(y)=\int_{-a}^{+a} q'(x,y)\,dx$$

Sexual selection

The difference $q'(x,y)$-$q(x,y)$ in (4) can be partitioned as follows

$$q'(x,y)-q(x,y)=f_1(x)f_2(y)-q(x,y)+q'(x,y)-f_1(x)f_2(y),$$

similarly, the logarithm

$$\log\frac{q'(x,y)}{q(x,y)}=\log\left(\frac{f_1(x)f_2(y)}{q(x,y)}\frac{q'(x,y)}{f_1(x)f_2(y)}\right)=\log\frac{f_1(x)f_2(y)}{q(x,y)}+\log\frac{q'(x,y)}{f_1(x)f_2(y)}$$

Recall that the pattern of sexual selection can be quantified by comparing the expected mating types resulting from random mating among mated individuals with those calculated using the population frequencies (Hartl and Clark, 1997; Rolán-Alvarez and Caballero, 2000). In the continuous scenario, this is formalized by the Jeffreys divergence

$$J_{PSS}=\int_{-a}^{+a}\int_{-a}^{+a}(f_1(x)f_2(y)-q(x,y))\log\frac{f_1(x)f_2(y)}{q(x,y)}dxdy \qquad (5)$$

and because

$$\int_{-a}^{+a} f_1(x)dx=\int_{-a}^{+a} f_2(y)dy=1 \text{ and } \int_{-a}^{+a} f(x)dx=\int_{-a}^{+a} g(y)dy=1$$

we can separate by sex

$$J_{PSS}=J_{S1}+J_{S2} \text{ where}$$

$$J_{S1}=\int_{-a}^{+a}(f_1(x)-f(x))\log\frac{f_1(x)}{f(x)}dx$$

$$J_{S2}=\int_{-a}^{+a}(f_2(y)-g(y))\log\frac{f_2(y)}{g(y)}dy.$$

Therefore, similar to the approach applied in the discrete case (Carvajal-Rodríguez, 2018a), J_{PSS} quantifies sexual selection for quantitative traits as the change in phenotype distribution resulting from differential mating. The information captured in J_{PSS} is the sum of the sexual selection within each sex.

Normally distributed traits

Assume that $q'(x,y)$ is a bivariate normal density and traits X and Y are normally distributed. Then, the marginal density function for the trait in females within matings is $f_1(x) \sim N(\mu_1,\sigma_1^2)$, and in the population is $f(x) \sim N(\mu_x,\sigma_x^2)$. Similarly, the marginal density function for the trait in males within matings is $f_2(y) \sim N(\mu_2,\sigma_2^2)$ and in the population is $g(y) \sim N(\mu_y,\sigma_y^2)$. Then, J_{S1} and J_{S2} can be expressed in closed form as (Belov and Armstrong, 2011; Kullback, 1997)

$$J_{S1}=\frac{1}{2}\left(\frac{\Phi_1{}^2+1}{\Phi_1}+\frac{\Phi_1+1}{\Phi_1}\frac{(\mu_1-\mu_x)^2}{\sigma_x{}^2}-2\right) \text{ where } \Phi_1=\sigma_1{}^2/\sigma_x{}^2.$$

$$J_{S2}=\frac{1}{2}\left(\frac{\Phi_2{}^2+1}{\Phi_2}+\frac{\Phi_2+1}{\Phi_2}\frac{(\mu_2-\mu_y)^2}{\sigma_y{}^2}-2\right) \text{ where } \Phi_2=\sigma_2{}^2/\sigma_y{}^2 \qquad (6).$$

Information statistics for sexual selection

With some sligth abuse of notation, consider now that J_{S1} and J_{S2} correspond to the values obtained using maximum likelihood estimators for the multivariate normal distribution. Then, for a random sample of n matings, nJ_{S1} (nJ_{S2}) is asymptotically χ^2 distributed with 2 degrees of freedom (Evren and Tuna, 2012; Kullback, 1997) under the null hypothesis that the females (males) within matings are distributed with mean μ_x (μ_y) and variance σ_x^2 (σ_y^2) i.e. absence of sexual selection.

Note that in the above expressions, the term for the difference of the means is the square of the standardized sexual selection intensity (SSI) index (Caballero, 2020; Erlandsson and Rolán-Alvarez, 1998; Ng et al., 2019) so that

$$J_{S1}=\frac{1}{2}\left(\frac{\Phi_1{}^2+1}{\Phi_1}+\frac{\Phi_1+1}{\Phi_1}SSI_1{}^2-2\right)$$

$$J_{S2}=\frac{1}{2}\left(\frac{\Phi_2{}^2+1}{\Phi_2}+\frac{\Phi_2+1}{\Phi_2}SSI_2{}^2-2\right)$$

where SSI_1 is the SSI index for females and SSI_2 for males.

If we want to test only the mean value of the female trait X in the mating sample, we set Φ_1=1 so that

$$J_{S1\Phi_1=1}=\frac{(\mu_1-\mu_x)^2}{\sigma_1{}^2}$$

and with a sample size of n matings we have $(nJ_{S1\Phi=1})^{0.5} \sim t_{n-1}$. Similarly, for the males we have $(nJ_{S2\Phi=1})^{0.5} \sim t_{n-1}$ with

$$J_{S2\Phi_2=1}=\frac{(\mu_2-\mu_y)^2}{\sigma_2{}^2}.$$

For large sample sizes both types of tests (χ^2 or t) work similar, for a smaller sample size the χ^2 test might be slightly liberal and the t-test should be preferred.

More generally, the χ^2 test should also detect differences in the variances, i.e., stabilizing or diversifying selection, or combinations of these forms of selection with directional selection (differences in means).

Relationship of sexual selection information to other measures

There are several measures for the strength of sexual selection in quantitative traits (reviewed in Henshaw et al., 2016). Many of them are defined in terms of variation in reproductive success which is actually a much broader concept, representing an organism's direct fitness (Shuker and Kvarnemo, 2021). Here we will make the connection in terms of mating success as a proxy for the mating fitnesses m_F and m_M as defined above. We will use male sexual selection as an example, but the approach for female sexual selection is analogous. Recall that we have defined the information due to the difference in the distribution of males within the matings with respect to the population distribution of males as

$$J_{S2}=\int_{-a}^{+a}(f_2(y)-g(y))\log\frac{f_2(y)}{g(y)}dy.$$

Also, the marginal density for Y in the matings was

$$f_2(y)=\int_{-a}^{+a}q'(x,y)dx=\int_{-a}^{+a}m_{xy}f(x)g(y)dx=g(y)\int_{-a}^{+a}m_{xy}f(x)dx=g(y)m_{My}$$

where m_{My} is the mating fitness of males with value for trait Y in the interval [y,y+dy].

The mean change in male trait caused by sexual selection is (Frank, 2012; Price, 1970; Taylor, 1996),

$$\Delta_s \bar{y} = \int_{-a}^{a} (f_2(y) - g(y)) \cdot y\, dy = \int_{-a}^{a} (g(y) \frac{M_{My}}{M} - g(y)) \cdot y\, dy = \int_{-a}^{a} g(y) (\frac{M_{My} - M}{M}) \cdot y\, dy = cov(Y, m_M)$$

and if we take as character Y the logarithm of mating fitness, L_M=log(m_M), we get J_{S2}, i.e.

$$\Delta_s \bar{L}_M = cov(L_M, m_M) = \beta_{LM,mM} V_{mM} = J_{S2}$$ and in general,

$$\Delta_s \bar{y} = cov(Y, m_M) = \beta_{Y,mM} V_{mM} = \frac{\beta_{Y,mM}}{\beta_{LM,mM}} J_{S2}$$

where V_{mM} is the variance in mating fitness and $\beta_{Y,mM}$, $\beta_{LM,mM}$ the regression coefficients of trait Y and log(m_M) on fitness m_M, respectively.

If changes are small and continuous (Frank, 2020, 2017) then $\beta_{LF,mF}$ => 1 and

$$\Delta_s \bar{L}_M = V_{mM} = J_{S2}$$

Opportunity for sexual selection, I_s

For a given sex, the opportunity for sexual selection, I_s, is equal to the variance in mating success divided by the square of mean mating success (Wade and Arnold, 1980). Considering relative mating success as the individual mating fitness, m_M, for males, we get

$$I_{sM} = V_{mM}$$

so for small continuous changes we have

$$I_{sM} = J_{S2}$$

and in the general case

$$I_{sM} = \frac{J_{S2}}{\beta_{LM,mM}}$$

Standardized mating differential, s_m

The mating differential (noted as m' in Jones, 2009) is the covariance between standardized trait values and relative mating success, i.e.

$$s_{mM} = cov(Y, m_M)/\sigma_Y = \beta_{Y,mM} V_{mM}/\sigma_Y = \frac{\beta_{Y,mM}}{\beta_{LM,mM}} J_{S2}/\sigma_Y$$

Bateman gradient and Jones index

The Bateman gradient β_{ss} is the slope of least-squares regression of relative reproductive success (*R*) on relative mating success (Arnold and Duvall, 1994; Bateman, 1948), i.e. for males $\beta_{ssM} = \beta_{R,mM}$. The product of the Bateman gradient and the standardized mating differential is the standardized selection differential *s*' (Jones, 2009) here s'_M for males, i.e. $s'_M = \beta_{R,mM}\, s_{mM}$. The Jones index is the maximum standardized sexual selection differential i.e., for males

$$s'_{Mmax} = \beta_{ssM}\sqrt{I_{sM}} = \beta_{ssM}\sqrt{\frac{J_{S2}}{\beta_{LM,mM}}}$$

and similarly for females.

It is clear that the information measures, J_{S1} and J_{S2}, developed here only refer to mating success, while the connection to reproductive success is part of other work that is ongoing.

Assortative mating

A mating pattern can be described as the a posteriori deviation from random mating among mated individuals, resulting in positive assortative mating when similar

phenotypes mate more frequently than expected, and negative assortative mating when the opposite occurs (Lewontin et al., 1968; Merrell, 1950; Spieth and Ringo, 1983).

Therefore, the assortative mating pattern corresponds to the divergence that compares the observed matings (q') with those expected from random mating among mated individuals ($f_1(x) \times f_2(y)$)

$$J_{PSI} = \int_{-a}^{+a} \int_{-a}^{+a} (q'(x,y) - f_1(x) f_2(y)) \log \frac{q'(x,y)}{f_1(x) f_2(y)} dxdy \qquad (7).$$

Normally distributed traits

As before, suppose that $q'(x,y)$ is a bivariate normal density and that traits X and Y are normally distributed. The divergence for assortative mating in (7) is the Jeffreys divergence between the joint distribution and the product of the marginals and serves as a measure of the relationship between X and Y that can be expressed as a function of the correlation coefficient (see Appendix A and Kullback, 1997) so,

$$J_{PSI} = \int_{-a}^{+a} \int_{-a}^{+a} (q'(x,y) - f_1(x) f_2(y)) \log \frac{q'(x,y)}{f_1(x) f_2(y)} dxdy = \frac{\rho^2}{1-\rho^2} \qquad (8).$$

Thus, as long as the quantitative traits we are measuring are normally distributed and also normally distributed within mating pairs, the information measure of assortative mating is a function of the square of correlation coefficient that takes values within the set of nonnegative real numbers $[0, +\infty)$.

The statistical significance of $J_{PSI}>0$ can be tested since nJ_{PSI} is asymptotically distributed as χ^2 with 1 degree of freedom (Kullback 1997). To distinguish between positive and negative assortative mating, we only need to consider the sign of the Pearson correlation coefficient ρ.

Total information

Finally, the total divergence in (4) can be expressed as the sum of sexual selection (5) and assortative mating (7) divergences plus a factor E

$$J = J_{S1} + J_{S2} + J_{PSI} + E$$

where (see Appendix B)

$$E = \int_{-a}^{+a} \int_{-a}^{+a} \left(f_1(x) f_2(y) - q(x,y)\right) \log \frac{q'(x,y)}{f_1(x) f_2(y)} dxdy \neq 0 \Leftrightarrow J_{PSS} \neq 0 \wedge J_{PSI} \neq 0.$$

So the E component only appears when both sexual selection ($J_{PSS} \neq 0$) and assortative mating ($J_{PSI} \neq 0$) patterns are present.

Carvajal-Rodríguez (2020) showed that from (2) we can define models where the mutual propensity to mate, m_{ij}, is not multiplicative, that is, it is not equal to the product of the female and male marginals, $m_{ij} \neq m_{Fi} \times m_{Mj}$, and these types of models correspond to mate choice models that generate specific mating patterns. Moreover, in addition to the assortative mating pattern, these models can also generate a frequency-dependent pattern of sexual selection. When this occurs, the increase in information reflected in both sexual selection and assortative mating patterns also includes a non-additive component that is captured by E.

For normally distributed traits, the total divergence J in (4) can be obtained in closed form and the non-additive component can be estimated by the difference of the additive components with the total (Appendix C)

$$E = J - \left(J_{S1} + J_{S2} + J_{PSI}\right)$$

Furthermore, for normally distributed traits, it can be shown that the sum $J_{S1} + J_{S2}$ corresponds to equation (4) when the covariance in the pairings is 0 and J_{PSI} corresponds

to equation (4) when the means and variances of both distributions (Q' and Q) are equal (see Appendix C).

Simulations

Detection of sexual selection

We will utilize the program MateSim (Carvajal-Rodríguez, 2018b) to simulate the mating distribution for quantitative traits using a logistic model (Xie et al., 2015). This model represents an open-ended preference function, capable of generating a pattern of sexual selection in both females and males.

The simulation procedure consists of two main steps. First a population of size N is generated, comprising $N/2$ females and $N/2$ males. The individuals are randomly sampled from a standard normal distribution with a mean of 0 and a standard deviation of 1, $Z(0,1)$. Second, a sample of n ($n<N/2$) matings is obtained as the individuals interact to form pairs for mating. The mating probability of a male j with phenotype Z_j of mating with any female F is evaluated as follows:

$$P(F,j)=\exp(-1+\alpha Z_j)/[1+\exp(-1+\alpha Z_j)]$$

and the same applies for a female i with phenotype Z_i to mate with any male M.

$$P(i,M)=\exp(-1+\alpha Z_i)/[1+\exp(-1+\alpha Z_i)]$$

Therefore, the mating probability after encounter for a pair $i \times j$ will be

$$p_{ij}=P(i,M)\times P(F,j).$$

The parameter α (≥0) accounts for the strength of sexual selection, if α=0 there is random mating, the higher the value of α, the greater the strength of sexual selection.

The tests in (6) are able of distinguishing between random mating and sexual selection for different sample sizes and sexual selection intensities. Not surprisingly, the greater the sexual selection and the size of the sample, the greater the power of detection and the value of the information recovered by the J_{S1} and J_{S2} indexes (Table 1). For a large sample size, n=500, the correlation between the strength of sexual selection α and the J indexes was 0.99. For smaller sample size, n=50, the correlation was 0.97, indicating that J_{S1} and J_{S2} indices are good proxies of the strength of sexual selection.

Table 1. Mating under a logistic model. The parameter α accounts for the intensity of sexual selection. A value of $\alpha = 0$ corresponds to random mating. Mating is with replacement. N is the population size and n the mating sample size. The quantitative trait distribution is $Z(0,1)$. Number of runs: 10,000. % sig: The % of tests with p-value ≤0.05. The values in parentheses correspond to the average value of the statistic for the total number of significant runs.

N	***n***	***α***	**% sig. (J_{S1})**	**%sig. (J_{S2})**
10^4	500	0	5.3 (0.016)	4.3 (0.016)
10^4	500	0.1	28.5.0 (0.019)	30.0 (0.019)
10^4	500	0.25	96.6 (0.039)	96.1 (0.038)
10^4	500	0.5	100 (0.126)	100 (0.128)
10^4	500	1	100 (0.40)	100 (0.41)
10^4	500	1.5	100 (0.710)	100 (0.701)
10^4	500	2	100 (0.981)	100 (0.985)
500	50	0	5.0 (0.146)	5.1 (0.141)
500	50	0.1	9.5 (0.155)	8.6 (0.15)
500	50	0.25	25.9 (0.168)	28.2 (0.179)
500	50	0.5	64.3 (0.215)	66.3 (0.219)
500	50	1	99.9 (0.586)	99.5 (0.476)
500	50	1.5	100 (0.845)	100 (0.918)
500	50	2	100 (1.107)	100 (1.044)

Detection of assortative mating: J_{PSI} versus correlation

We will utilize the program MateSim (Carvajal-Rodríguez, 2018b) to simulate the mating distribution for quantitative traits using a FND Gaussian function (Carvajal-Rodríguez and Rolán-Alvarez, 2014). The FND function with parameter C>0 generates positive assortative mating patterns that can be measured by the Pearson correlation coefficient ρ and also by J_{PSI} as given in (8).

The simulation procedure is as before but the preference is evaluated following the FND function

$$FND = e^{-\left(\frac{C^2 D^2}{s^2 D^2_{max}}\right)}.$$

If C=0 the mating is random, if C>0 there is mate choice that generates positive assortative mating. The parameter D represents the phenotypic difference between male and female in the pair. If the D is zero the preference is the maximum. The parameter s is the tolerance to mate with a partner that does not correspond to the preference optimum. i.e. s= 0.08 implies eight times more tolerance for non-optimal mating than s=0.01. D_{max} is the maximum phenotypic difference in the population between any two individuals, regardless of sex. For a phenotypic difference D/D_{max} between a pair, the strength of the choice depends on the ratio between the choice and tolerance parameters, C/s.

For a sample of n matings, the significance of ρ can be computed as $\frac{\rho\sqrt{(n-2)}}{\sqrt{(1-\rho^2)}}$ that follows a t-distribution with n-2 degrees of freedom. We have already seen that nJ_{PSI} is asymptotically distributed as χ^2 with 1 degree of freedom.

In Table 2 both types of tests are performed for mating distributions generated under different choice and tolerance values. When the population and sample size are large, 10,000 and 500, respectively, from choice values of 0.2, both the correlation and the J_{PSI} have greater than 97% power to detect assortative mating. The difference is that the correlation value already reaches its maximum for choice values of 0.4.

When the population and sample sizes are smaller, specifically 500 and 50, respectively, we observe a few noteworthy points. Firstly, it is not surprising that J_{PSI} tends to be somewhat liberal in these cases, as the test nJ_{PSI} is only asymptotically distributed as χ^2, and its behavior improves with higher sample sizes. Secondly, both methods demonstrate approximately 40% power when the choice is 0.2 and the tolerance is 0.08. However, they exhibit almost 100% power in other cases, such as when the tolerance is 0.01 or the choice is from 0.4 and beyond. The difference between ρ and J_{PSI} is again the saturation of the value of ρ as the strength of choice increases.

Table 2. One sex is choosy. Choice implies preference for similarity. Mating is with replacement. *N* is the population size and *n* the sample size of matings. The quantitative trait distribution is *Z*(0,1). Number of runs: 10,000. % sig: The % of tests with *p*-value ≤0.05. The values in parentheses correspond to the average value of the statistic for the total number of significant runs.

N	***n***	***Choice***	***s***	**% sig. (ρ)**	**%sig. ($\rho^2/(1-\rho^2)$)**
10^4	500	0	--	5.1 (0.01)	5.2 (0.01)
10^4	500	0.2	0.08	97.9 (0.18)	97.9 (0.03)
10^4	500	0.4	0.08	100 (0.55)	100 (0.43)
10^4	500	0.8	0.08	100 (0.85)	100 (2.60)
10^4	500	1	0.08	100 (0.89)	100 (3.72)
10^4	500	0.2	0.01	100 (0.95)	100 (9.3)
10^4	500	0.4	0.01	100 (0.99)	100 (59.0)
10^4	500	0.8	0.01	100 (1.0)	100 (194.0)

10^4	500	1	0.01	100 (1.0)	100 (413.4)
500	50	0	--	5.1 (0.03)	6.2 (0.12)
500	50	0.2	0.08	38.6 (0.37)	41.7 (0.16)
500	50	0.4	0.08	99.95 (0.61)	99.97 (0.64)
500	50	0.8	0.08	100 (0.90)	100 (4.59)
500	50	1	0.08	100 (0.93)	100 (6.68)
500	50	0.2	0.01	100 (0.96)	100 (13.54)
500	50	0.4	0.01	100 (0.99)	100 (56.68)
500	50	0.8	0.01	100 (1.0)	100 (183.08)
500	50	1	0.01	100 (1.0)	100 (403.27)

J_{PSI} achieves higher resolution when the strength of choice is sufficiently high to yield correlation values close to 1. For instance, as demonstrated in Table 2, a choice C of 0.2 with a low tolerance of s=0.01 produces a mating correlation of 0.95. Consequently, for values exceeding C>0.2 under a tolerance of 0.01, J_{PSI} will more effectively discriminate between varying degrees of assortative mating.The greater the sample size and the choice strength, the greater the power to detect assortative mating. In Figure 1, the correlation of the values in Table 1 i.e., between the choice strength (C/s) and both statistics, can be appreciated. For the ρ statistic the correlation with choice strength is 0.6 for both large and small sample size, for J_{PSI} the correlation with the choice strength is 0.97.

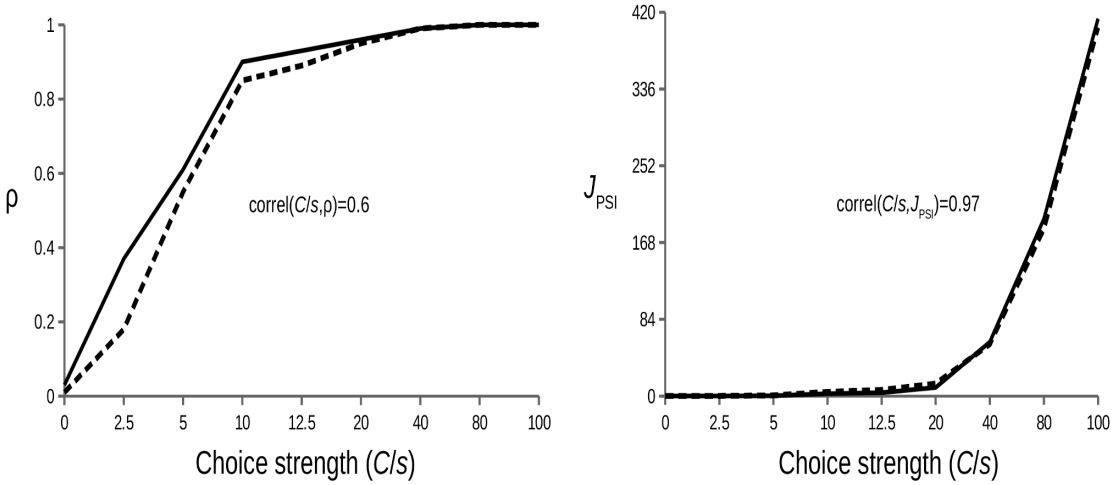

Figure 1. Graphic representation of values of the rho statistics (left panel) and J_{PSI} (right panel) with respect to the strength of the choice (*C/s*). The value of the correlation between each statistic and the strength of the choice is given. Continuous line: population size *N*=10,000, sample size *n*=500. Dashed line: *N*=500, *n*=50. The values of ρ and J_{PSI} are those in Table 1 ordered by increasing *C/s*.

The results were almost identical (Appendix D Table S1) when we consider a bias for the mating preference, i.e. the choosy males preferring females 1.5 times bigger than themselves (Lau et al., 2021).

We were also interested in evaluating the performance of the J_{PSI} index across different functions and mating scenarios in which there was competition for mating (which generates sexual selection patterns) but no mate choice (no assortative mating pattern). To achieve this, we employed the logistic function with α =2 which implies sexual selection without mate choice. The mating process was implemented with replacement, where each individual can mate more than once, that is, the availability of individuals is not affected by matings that have already occurred. Additionally, mating without replacement was also considered, where the proportion of individuals available for mating must be updated after each mating event. In the case of no replacement, the encounters can be individual or massive (Gimelfarb, 1988). Individual encounters imply that only one encounter occurs at a time, while when mating occurs with mass encounters, more than one pair can be formed simultaneously (see Appendix D Table

S2). In the case of large population and sample sizes, both ρ and J_{PSI} exhibited the expected false positive rate of 5%. However, with lower sample sizes, J_{PSI} showed a slightly liberal false positive rate of 6%.

We also simulate a mate choice scenario for a bimodal population where two more or less extreme phenotypes coexist (Appendix D Table S3). The power for the detection of assortative mating was similar to the unimodal case and the correlation of the statistics with the strength of choice was greater the larger the sample size, being about 0.58-0.65 for ρ and 0.95-0.97 for J_{PSI} (Figure 2).

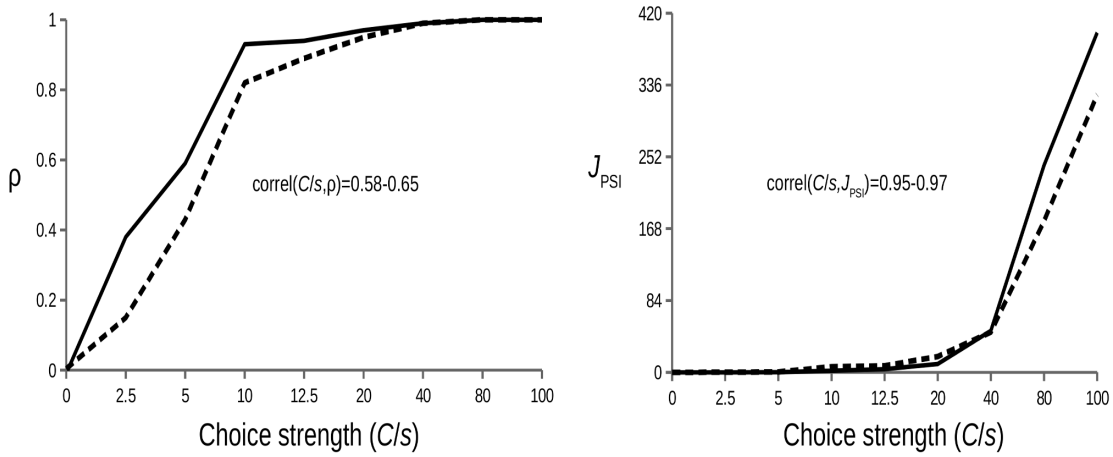

Figure 2. Graphic representation of values of the rho statistics (left panel) and J_{PSI} (right panel) with respect to the strength of the choice (*C*/*s*). Bimodal population with mixture proportion π=0.5, μ_2-μ_1=3 and σ_1+σ_2 = 2. Continuous line: population size *N*=10,000, sample size *n*=500. Dashed line: *N*=500, *n*=50. The values of ρ and J_{PSI} are those in Table S3 ordered by increasing *C*/*s*.

Also, we examined how being choosy in one or both sexes affects the ρ and J_{PSI} indexes and found no differences (compare Table S4 in Appendix D with Table 1).

Lastly, we check that J_{PSI} still performs well for smaller choice strength values (Table S5 and Figure S1 in Appendix D).

5. Example of application

Echinolittorina malaccana is a marine intertidal snail commonly found on rocky shores throughout the Indo-West Pacific region (Reid, 2007). The primary mechanism of mate choice in this species appears to be male preference for females slightly larger than themselves. Assortative mating for size, measured by pairwise correlation, has been estimated to be around 0.5 (López-Cortegano et al., 2020; Ng et al., 2019). In a previous study, size (shell length, a continuous trait) has been transformed into a qualitative trait (discrete size classes) enabling the use of multimodel inference techniques. These analyses provided deeper insights into mate choice and confirmed that the most suitable model involves mate choice with bias, resulting in both assortative mating and sexual selection for size (Lau et al., 2021).

We will use the same onshore data from mating pairs of *E. malaccana* used in Lau et al. (Lau et al., 2021) and available from Ng et al. (Ng et al., 2019; Rolán-Alvarez et al., 2021) and Rolán-Alvarez (Rolán-Alvarez et al., 2021) to apply the new indices J_{PSS} and J_{PSI} directly to the shell length trait (Table 3).

Table 3. Analysis of *Echinolittorina malaccana* data.

Test	***N***	***n***	J_{S1} **(pval)**	J_{S2} **(pval)**	**ρ (pval)**	J_{PSI} **(pval)**
Chi^2	876	228	0.11 ($<10^{-5}$)	0.03 (0.031)	0.57 ($<10^{-5}$)	0.49 ($<10^{-5}$)

Data from Ng et al 2019.

Sexual selection was observed in both sexes, although it appeared to be weaker in males. This finding aligns with previous research, indicating that sexual selection in *E. malaccana* females is likely driven by male preference for slightly larger females, while in males, it may result from male-male competition (Lau et al., 2021; Ng et al., 2019). As for assortative mating, both the Pearson correlation coefficient and the new J_{PSI} index supported and validated previous findings.

6. Discussion

There is a vast amount of literature exploring mate choice, competition, assortative mating, and sexual selection as influential forces in the evolution of traits that may not always be directly favoured by natural selection (Andersson, 1994; Darwin, 1871; reviewed in Lindsay et al., 2019). These concepts are traditionally grouped under the term 'theory of sexual selection'. Sexual selection theory stands as one of the most active areas of evolutionary research, engaging diverse fields and inference methodologies, given its relevance in population genetics, evolutionary ecology, animal behavior, sociology, and psychology. Two recent important reviews were published on the concept and definition of sexual selection (Alonzo and Servedio, 2019; Shuker and Kvarnemo, 2021). Alonzo and Servedio discuss the challenges in achieving a consensus definition, while Shuker and Kvarnemo propose an integrative definition for sexual selection.

In this study, we demonstrate that the SK definition of sexual selection can be effectively applied within a modeling framework that utilizes information theory to describe mate choice and competition processes, leading to patterns of sexual selection and assortative mating. Under the information theory formalism, these patterns of sexual selection and assortative mating are described in terms of Jeffreys divergence.

Importantly, this novel framework, initially developed for discrete traits, is general and doesn't assume a priori whether the choice is exercised by males, females, or both, nor does it make assumptions about the sex that competes. Furthermore, it is agnostic concerning the genetic basis or evolutionary mechanisms underlying complex mate choice and competition processes. The informational framework starts with a concept of mutual mating fitness or mutual mating propensity (Carvajal-Rodríguez, 2020, sensu 2018a), where the marginal values correspond to individual mating fitness. These

mating fitnesses allow us to measure the pattern of sexual selection according to the SK definition.

In addition, we have extended the informational framework to encompass quantitative traits. For both discrete and quantitative traits, sexual selection is detected by comparing the distribution of mating phenotypes with that of the overall population. Similarly, assortative mating is detected by comparing, within mating couples, the observed joint distribution of mating traits to that expected under random mating.

When the traits are normally distributed, the sexual selection indexes J_{S1} (females) and J_{S2} (males) can be expressed as a function of the standardized sexual selection intensity index and the ratio of sample and population variances (6). Simulations have shown that J_S indexes have a correlation of 0.99 with the strength of sexual selection.

When we compare sexual selection information indices with other measures of sexual selection for quantitative traits, we see that if we consider mating success as a proxy for mating fitness, the sexual selection information index coincides with the opportunity for sexual selection (Wade and Arnold, 1980), and from here we can establish the relationship with other measures such as the standardized mating differential (Jones, 2009). Therefore, in this work, we have demonstrated that the average change in a quantitative trait resulting from differential mating fitness corresponds to the increase in information quantified by the sexual selection information indexes J_{S1} and J_{S2}. Additionally, we have established a connection between $J_{S1}+J_{S2,}$ and the statistic for discrete traits *PSS* (Rolán-Alvarez and Caballero, 2000), as well as with measures of quantitative traits based on mating success.

Furthermore, the assortative mating index J_{PSI}, when the traits are normally distributed, is a transformation of ρ and has as much statistical power as ρ, with the added

advantage of being highly correlated with the strength of mate preference, which is not generally true for the correlation coefficient (Clancey et al., 2022; Fernández-Meirama et al., 2022).

Finally, we applied the quantitative trait information indices developed in this work to a previously published dataset on size assortative mating and sexual selection (Lau et al., 2021; Ng et al., 2019). We confirmed previous findings and validate the quantitative approach for the new indices of sexual selection and assortative mating.

In conclusion, the application of information theory to describe patterns of sexual selection and assortative mating (Carvajal-Rodríguez, 2020, 2019, 2018a), has paved the way for extending these developments to quantitative traits. This study demonstrates that sexual selection and assortative mating can be effectively quantified as information gain relative to the random mating pattern. Just like the previous developments for discrete traits, the results obtained with quantitative traits indicate that employing information theory to describe mating processes and patterns holds great promise as a valuable approach to understanding both the causes and effects of sexual selection.

Declaration of competing interest

None

Acknowledgements

Dedicated to my sister Paci. I thank to Emilio Rolán-Alvarez and two anonymous reviewers for their useful comments. This work was supported by Xunta de Galicia (Grupo de Referencia Competitiva, ED431C 2020/05), Ministerio de Ciencia e Innovación (PID2022-137935NB-I00) and by Fondos FEDER (“Unha maneira de facer Europa”). Funding for open access charge: Universidade de Vigo/CISUG.

Appendix

A. Assortative mating with normally distributed traits

The general formulation is

$$J_{PSI}=\int_{-a}^{+a}\int_{-a}^{+a}\left(q'(x,y)-r'(x,y)\right)\log\frac{q'(x,y)}{r'(x,y)}dxdy$$

where $r'(x,y)= f_1(x)f_2(y)$

If q' is bivariate normal and f_1 and f_2 are normally distributed we have

$$q'(x,y)=\frac{1}{|2\Pi\Sigma_1|^{0.5}}\exp\left[-\frac{1}{2}(z-\mu_1)'\Sigma_1^{-1}(z-\mu_1)\right]$$

where Σ_1 is the variance-covariance matrix (see below), $|\Sigma_1|$ is the determinant, z is the column vector of the two variables x,y and z' is the row vector of x,y and μ_1 is the column vector (μ_{1x},μ_{1y}).

Similarly, the product of the two marginals is

$$r'(x,y)=\frac{1}{|2\Pi\Sigma_2|^{0.5}}\exp\left[-\frac{1}{2}(z-\mu_2)'\Sigma_2^{-1}(z-\mu_2)\right]$$

where μ_2 is the column vector (μ_{2x},μ_{2y}).

Note that in our case, using males and females from matings (joint distribution versus random mating distribution obtained from mating data) implies that mean and variances are equal between distributions ($\mu_1=\mu_2$, $\sigma_1=\sigma_2$), i.e. $\mu_{1x}=\mu_{2x}$, $\mu_{1y}=\mu_{2y}$ and $\sigma_{1x}=\sigma_{2x}$, $\sigma_{1y}=\sigma_{2y}$.

Let

$$\Sigma_1=\begin{pmatrix}\sigma_{xx} & \sigma_{xy}\\ \sigma_{xy} & \sigma_{yy}\end{pmatrix},\ \Sigma_1^{-1}=\frac{1}{S}\begin{pmatrix}\sigma_{yy} & -\sigma_{xy}\\ -\sigma_{xy} & \sigma_{xx}\end{pmatrix}\text{ with } S=\sigma_{xx}\sigma_{yy}-\sigma_{xy}^2$$

and

$$\Sigma_2 = \begin{pmatrix} \sigma_{xx} & 0 \\ 0 & \sigma_{yy} \end{pmatrix}, \ \Sigma_2^{-1} = \frac{1}{\sigma_{xx}\sigma_{yy}} \begin{pmatrix} \sigma_{yy} & 0 \\ 0 & \sigma_{xx} \end{pmatrix}$$

In this case the Kullback-Leibler divergences are (c.f. Kullback, 1997 (1.6) p. 190)

$$KL(q' \| r') = \frac{1}{2} \log \frac{|\Sigma_2|}{|\Sigma_1|} - 1 + \frac{1}{2} tr(\Sigma_1 \Sigma_2^{-1}) = \frac{1}{2} \log \frac{\sigma_{xx}\sigma_{yy}}{S}$$

and

$$KL(r' \| q') = \frac{1}{2} \log \frac{|\Sigma_1|}{|\Sigma_2|} - 1 + \frac{1}{2} tr(\Sigma_2 \Sigma_1^{-1}) = \frac{1}{2} \log \frac{S}{\sigma_{xx}\sigma_{yy}} - 1 + \frac{\sigma_{xx}\sigma_{yy}}{S}$$

where *tr* is the trace (sum of diagonal elements) of a square matrix.

Therefore,

$$J_{PSI} = KL(q' \| r') + KL(r' \| q') = \frac{\sigma_{xx}\sigma_{yy}}{S} - 1 = \frac{\sigma_{xy}{}^2}{\sigma_{xx}\sigma_{yy} - \sigma_{xy}{}^2} = \frac{\rho^2}{1-\rho^2}.$$

B. General formula for non-random mating information

Consider two continuous traits, X in females and Y in males from a population and let the probability distribution Q'(x,y) with probability density $q'(x,y)$ that represents the mating probability for pairs with values in the infinitesimal interval ([x,x+dx],[y,y+dy]). Consider alternatively the probability distribution $Q(x,y)$ of random mating with the product of densities $q(x,y)=f(x)g(y)$ from X and Y, respectively.

Following (Carvajal-Rodríguez, 2018a; Frank, 2012), the mean change in female and/or male traits caused by non-random mating when we take as trait the logarithm of the mutual fitness, is

$$J=\int_{-a}^{+a}\int_{-a}^{+a}(q'(x,y)-q(x,y))\log\frac{q'(x,y)}{q(x,y)}dxdy,\ \text{where } q(x,y)=f(x)g(y) \qquad \text{(B1).}$$

The difference $q'(x,y)$-$q(x,y)$ can be partitioned as follows

$$q'(x,y)-q(x,y)=q'(x,y)-f_1(x)f_2(y)+f_1(x)f_2(y)-q(x,y),$$

where $f_1(x)$ and $f_2(y)$ are the marginal densities for X and Y

$$f_1(x)=\int_{-a}^{+a}q'(x,y)dy$$

$$f_2(y)=\int_{-a}^{+a}q'(x,y)dx \qquad \text{(B2).}$$

Similarly, the logarithm

$$\log\frac{q'(x,y)}{q(x,y)}=\log\left(\frac{q'(x,y)}{f_1(x)f_2(y)}\frac{f_1(x)f_2(y)}{q(x,y)}\right)=\log\frac{q'(x,y)}{f_1(x)f_2(y)}+\log\frac{f_1(x)f_2(y)}{q(x,y)}.$$

Now note that the densities $f(x)$ and $g(y)$ depend on the population distribution, while the marginal densities $f_1(x)$ and $f_2(y)$ depend on the mating distribution so they are not necessarily equal. Then we have

$$J_{PSS}=\int_{-a}^{+a}\int_{-a}^{+a}(f_1(x)f_2(y)-q(x,y))\log\frac{f_1(x)f_2(y)}{q(x,y)}dxdy$$

and

$$J_{PSI}=\int_{-a}^{+a}\int_{-a}^{+a}(q'(x,y)-f_1(x)f_2(y))\log\frac{q'(x,y)}{f_1(x)f_2(y)}dxdy$$

therefore, as in the discrete case, the measure of non-random mating can be divided into

$$J=J_{PSS}+J_{PSI}+E \qquad \text{(B3).}$$

The component E is

$$E=\int_{-a}^{+a}\int_{-a}^{+a}(A+B)dxdy=\int_{-a}^{+a}\int_{-a}^{+a}Adxdy+\int_{-a}^{+a}\int_{-a}^{+a}Bdxdy=\int_{-a}^{+a}\int_{-a}^{+a}Adxdy$$

$$A=(f_1(x)f_2(y)-q(x,y))\log\frac{q'(x,y)}{f_1(x)f_2(y)}$$

$$B=(q'(x,y)-f_1(x)f_2(y))\log\frac{f_1(x)f_2(y)}{q(x,y)}.$$

We will show that

$$\int_{-a}^{+a}\int_{-a}^{+a}Bdxdy=\int_{-a}^{+a}\int_{-a}^{+a}[(q'(x,y)-f_1(x)f_2(y))\log\frac{f_1(x)f_2(y)}{q(x,y)}]dxdy=0 \qquad \text{(B4)}$$

so that,

$$E=\int_{-a}^{+a}\int_{-a}^{+a}(f_1(x)f_2(y)-q(x,y))\log\frac{q'(x,y)}{f_1(x)f_2(y)}\neq 0\Leftrightarrow J_{PSS}\neq 0\wedge J_{PSI}\neq 0 \qquad \text{(B5).}$$

Now, first recall that $q(x,y)=f(x)g(y)$ and then

$$\log\frac{f_1(x)f_2(y)}{q(x,y)}=\log\frac{f_1(x)}{f(x)}+\log\frac{f_2(y)}{g(y)}.$$

Also,

$$\int_{-a}^{+a} f_1(x)\,dx=\int_{-a}^{+a}\int_{-a}^{+a} q'(x,y)\,dxdy=\int_{-a}^{+a} f_2(y)\,dy=1$$

so that,

$$\int_{-a}^{+a}\int_{-a}^{+a}[f_1(x)f_2(y)\log\frac{f_1(x)}{f(x)}]\,dxdy=\int_{-a}^{+a} f_1(x)\log\frac{f_1(x)}{f(x)}\,dx\int_{-a}^{+a} f_2(y)\,dy=\int_{-a}^{+a} f_1(x)\log\frac{f_1(x)}{f(x)}\,dx$$

(B6),

and similarly

$$\int_{-a}^{+a}\int_{-a}^{+a}[f_1(x)f_2(y)\log\frac{f_2(y)}{g(y)}]\,dxdy=\int_{-a}^{+a} f_2(y)\log\frac{f_2(y)}{g(y)}\,dy \qquad \text{(B7).}$$

Also using the marginal density definitions from (A2)

$$\int_{-a}^{+a}\int_{-a}^{+a}[q'(x,y)\log\frac{f_1(x)}{f(x)}]\,dxdy=\int_{-a}^{+a}\log\frac{f_1(x)}{f(x)}\,dx\int_{-a}^{+a} q'(x,y)\,dy=\int_{-a}^{+a} f_1(x)\log\frac{f_1(x)}{f(x)}\,dx$$

(B8)

and

$$\int_{-a}^{+a}\int_{-a}^{+a}[q'(x,y)\log\frac{f_2(y)}{g(y)}]\,dxdy=\int_{-a}^{+a} f_2(y)\log\frac{f_2(y)}{g(y)}\,dy \qquad \text{(B9).}$$

Finally, noting that (B6) equals (B8) and (B7) equals (B9) and rearranging and substituting in (B4) we obtain

$$\int_{-a}^{+a}\int_{-a}^{+a} B dxdy = \int_{-a}^{+a}\int_{-a}^{+a} [(q'(x,y) - f_1(x)f_2(y))\log\frac{f_1(x)f_2(y)}{q(x,y)}]dxdy = (A6)+(A7)-(A8)-(A9)=0$$

C. Total *J* with normally distributed traits

$$J = \int_{-a}^{+a}\int_{-a}^{+a} (q'(x,y) - q(x,y))\log\frac{q'(x,y)}{q(x,y)}dxdy,$$ where $q(x,y)=f(x)g(y)$

If q' is $N(\mu_1, \Sigma_1)$ and q $N(\mu_2, \Sigma_2)$ where Σ_i is the variance-covariance matrix, we have that the KL divergence has the following closed form (Pardo, 2018)

$$KL(q'\|q) = \frac{1}{2}\left(\log\frac{|\Sigma_2|}{|\Sigma_1|} - 2 + tr(\Sigma_2^{-1}\Sigma_1) + (\mu_2-\mu_1)'\Sigma_2^{-1}(\mu_2-\mu_1)\right) \qquad \text{(C1)}$$

where *tr* is the trace (sum of diagonal elements) of a square matrix, $|\Sigma|$ is the determinant, μ_i is the column vector (μ_{ix}, μ_{iy}), μ' is the row vector.

Therefore,

$$\Sigma_1 = \begin{pmatrix} \sigma_{1xx} & \sigma_{1xy} \\ \sigma_{1xy} & \sigma_{1yy} \end{pmatrix},\ |\Sigma_1| = \sigma_{1xx}\sigma_{1yy} - \sigma_{1xy}^2$$

and

$$\Sigma_2 = \begin{pmatrix} \sigma_{2xx} & \sigma_{2xy} \\ \sigma_{2xy} & \sigma_{2yy} \end{pmatrix},\quad \Sigma_2^{-1} = \frac{1}{S_2}\begin{pmatrix} \sigma_{2yy} & -\sigma_{2xy} \\ -\sigma_{2xy} & \sigma_{2xx} \end{pmatrix}$$

where

$$|\Sigma_2| = S_2 = \sigma_{2xx}\sigma_{2yy} - \sigma_{2xy}^2 = \sigma_{2xx}\sigma_{2yy} \text{ because } \sigma_{2xy} = 0$$

Now, let

$$T = \sigma_{1xx}\sigma_{2yy} + \sigma_{1yy}\sigma_{2xx}$$

then

$$tr(\Sigma_2^{-1}\Sigma_1)=T/S_2=\frac{\sigma_{1xx}}{\sigma_{2xx}}+\frac{\sigma_{1yy}}{\sigma_{2yy}}$$

and,

$$(\mu_2-\mu_1)'\Sigma_2^{-1}(\mu_2-\mu_1)=\frac{(\mu_{2xx}-\mu_{1xx})^2}{\sigma_{2xx}}+\frac{(\mu_{2yy}-\mu_{1yy})^2}{\sigma_{2yy}}$$

The other divergence is

$$KL(q\|q')=\frac{1}{2}\left(\log\frac{|\Sigma_1|}{|\Sigma_2|}-2+tr(\Sigma_1^{-1}\Sigma_2)+(\mu_1-\mu_2)'\Sigma_1^{-1}(\mu_1-\mu_2)\right) \qquad \text{(C2)}$$

$$\Sigma_1^{-1}=\frac{1}{S_1}\begin{pmatrix}\sigma_{1yy} & -\sigma_{1xy}\\ -\sigma_{1xy} & \sigma_{1xx}\end{pmatrix} \text{ with } S_1=|\Sigma_1|$$

$$tr(\Sigma_1^{-1}\Sigma_2)=T/S_1=\frac{\sigma_{1xx}\sigma_{2yy}+\sigma_{1yy}\sigma_{2xx}}{\sigma_{1xx}\sigma_{1yy}-\sigma_{1xy}^2}$$

$$(\mu_1-\mu_2)'\Sigma_1^{-1}(\mu_1-\mu_2)=\frac{\sigma_{1yy}(\mu_{1xx}-\mu_{2xx})^2+\sigma_{1xx}(\mu_{1yy}-\mu_{2yy})^2-2\sigma_{1xy}(\mu_{1xx}-\mu_{2xx})(\mu_{1yy}-\mu_{2yy})}{S_1}$$

Finally,

$$J=KL(q'\|q)+KL(q\|q')$$

with nJ asymptotically χ^2 distributed with 5 degrees of freedom where n is the sample size of matings.

C.1 Mating covariance greater than 0 with equal means and variances

Note that from (C1) and (C2), if we assume that the means and variances between the two distributions are the same, i.e. $\mu_1=\mu_2$, $\sigma_{1xx}=\sigma_{2xx}$, $\sigma_{1yy}=\sigma_{2yy}$ but $\sigma_{1xy}>0$ and $\sigma_{2xy}=0$ then

$$J=KL(q'\|q)+KL(q\|q')=0+\frac{\sigma_{xy}{}^2}{\sigma_{xx}\sigma_{yy}-\sigma_{1xy}{}^2}=\frac{\rho^2}{1-\rho^2}=J_{PSI}$$

which is the assortative mating component (J_{PSI}) obtained in the Appendix A.

C.2 No covariance within matings

On the other side, if we assume $\sigma_{1xy}=\sigma_{2xy}=0$ then from C1 and C2 we get

$$J=-2+\frac{1}{2}\left(\frac{\sigma_{1xx}}{\sigma_{2xx}}+\frac{\sigma_{2xx}}{\sigma_{1xx}}+\frac{\sigma_{1yy}}{\sigma_{2yy}}+\frac{\sigma_{2yy}}{\sigma_{1yy}}\right)+\frac{1}{2}(\mu_{1x}-\mu_{2x})^2\left(\frac{1}{\sigma_{1xx}}+\frac{1}{\sigma_{2xx}}\right)+\frac{1}{2}(\mu_{1y}-\mu_{2y})^2\left(\frac{1}{\sigma_{1yy}}+\frac{1}{\sigma_{2yy}}\right)$$

which can be expressed as

$$J=-1+\frac{1}{2}\left(\frac{\sigma_{1xx}}{\sigma_{2xx}}+\frac{\sigma_{2xx}}{\sigma_{1xx}}\right)+\frac{1}{2}(\mu_{1x}-\mu_{2x})^2\left(\frac{1}{\sigma_{1xx}}+\frac{1}{\sigma_{2xx}}\right)-1+\frac{1}{2}\left(\frac{\sigma_{1yy}}{\sigma_{2yy}}+\frac{\sigma_{2yy}}{\sigma_{1yy}}\right)+\frac{1}{2}(\mu_{1y}-\mu_{2y})^2\left(\frac{1}{\sigma_{1yy}}+\frac{1}{\sigma_{2yy}}\right)$$

and by taking $\Phi_1=\sigma_{1xx}/\sigma_{2xx}$ and $\Phi_2=\sigma_{1yy}/\sigma_{2yy}$ and noting that

$$\left(\frac{1}{\sigma_{1xx}}+\frac{1}{\sigma_{2xx}}\right)=\frac{\Phi_1+1}{\sigma_{2xx}\Phi_1} \text{ and } \left(\frac{1}{\sigma_{1yy}}+\frac{1}{\sigma_{2yy}}\right)=\frac{\Phi_2+1}{\sigma_{2yy}\Phi_2}$$

then

$J=J_{S1}+J_{S2}$ as defined in (6).

C.3 No covariance and equal means

Even if we assume only differences in variances, we obtain the information gain due to the pattern of sexual selection as

$$J=-1+\frac{1}{2}\left(\frac{\sigma_{1xx}}{\sigma_{2xx}}+\frac{\sigma_{2xx}}{\sigma_{1xx}}\right)-1+\frac{1}{2}\left(\frac{\sigma_{1yy}}{\sigma_{2yy}}+\frac{\sigma_{2yy}}{\sigma_{1yy}}\right)$$

that corresponds to (6) when the means are assumed to be equal.

D. Simulation results tables

Table S1. One sex is choosy. Choice implies preference for similarity with a bias of 1.5. Mating is with replacement. *N* is the population size and *n* the sample size of matings. The quantitative trait distribution is *Z*(0,1). Number of runs: 10,000. % sig: The % of tests with *p*-value ≤0.05. The values in parentheses correspond to the average value of the statistic for the total number of significant runs.

N	***n***	***Choice***	***s***	**% sig. (ρ)**	**%sig. ($\rho^2/(1-\rho^2)$)**
10^4	500	0	--	4.8 (0.004)	4.9 (0.01)

10^4	500	0.2	0.08	99.9 (0.22)	99.9 (0.05)
10^4	500	0.4	0.08	100 (0.54)	100 (0.41)
10^4	500	0.8	0.08	100 (0.87)	100 (3.19)
10^4	500	1	0.08	100 (0.89)	100 (3.99)
500	50	0	--	5 (-0.025)	5.9 (0.12)
500	50	0.2	0.08	44.7 (0.37)	48.2 (0.17)
500	50	0.4	0.08	100 (0.67)	100 (0.90)
500	50	0.8	0.08	100 (0.84)	100 (2.54)
500	50	1	0.08	100 (0.90)	100 (4.43)
500	50	0.2	0.01	100 (0.97)	100 (64.72)
500	50	0.4	0.01	100 (0.99)	100 (41.97)
500	50	0.8	0.01	100 (1)	100 (115.87)
500	50	1	0.01	100 (1)	100 (3935.1)

Table S2. Mating under a logistic model with α=2. There is no preference for similarity. *N* is the population size and *n* the sample size of matings. The quantitative trait distribution is *Z*(0,1). Number of runs: 10,000. % sig: The % of tests with *p*-value ≤0.05. The values in parentheses correspond to the average value of the statistic for the total number of significant runs.

N	***n***	**Mating**	**% sig. (ρ)**	**%sig. ($\rho^2/(1-\rho^2)$)**
10^4	500	replacement	5.3 (0.003)	5.4 (0.01)
10^4	500	individual	4.9 (0.003)	5.0 (0.01)
10^4	500	mass-encounter	4.7 (0.004)	4.8 (0.01)
500	50	replacement	5.0 (-0.01)	6.0 (0.12)
500	50	individual	5.2 (0.02)	6.3 (0.12)
500	50	mass-encounter	5.4 (0.03)	6.4 (0.12)

Table S3. Bimodal populations with mixture proportion π=0.5, μ_2-μ_1-=3 and σ_1+σ_2 = 2. One sex is choosy. Choice implies preference for similarity. Mating is with replacement. *N* is the population size and *n* the sample size of matings. The quantitative trait distribution is *Z*(0,1). Number of runs: 10,000. % sig: The % of tests with *p*-value ≤0.05. The values in parentheses correspond to the average value of the statistic for the total number of significant runs.

N	***n***	***Choice***	***s***	**% sig. (ρ)**	**%sig. ($\rho^2/(1-\rho^2)$)**
10^4	500	0	--	5.1 (0.004)	5.2 (0.01)
10^4	500	0.2	0.08	90 (0.15)	90.1 (0.03)
10^4	500	0.4	0.08	100 (0.43)	100 (0.22)
10^4	500	0.8	0.08	100 (0.82)	100 (1.98)
10^4	500	1	0.08	100 (0.89)	100 (3.79)
10^4	500	0.2	0.01	100 (0.95)	100 (9.99)
10^4	500	0.4	0.01	100 (0.99)	100 (48.67)
10^4	500	0.8	0.01	100 (1.0)	100 (242.35)
10^4	500	1	0.01	100 (1.0)	100 (397.16)
500	50	0	--	5.1 (-0.01)	6.1 (0.12)
500	50	0.2	0.08	43.2 (0.38)	46.2 (0.18)
500	50	0.4	0.08	99.7 (0.59)	99.7 (0.58)
500	50	0.8	0.08	100 (0.93)	100 (6.58)
500	50	1	0.08	100 (0.94)	100 (7.74)
500	50	0.2	0.01	100 (0.97)	100 (18.57)
500	50	0.4	0.01	100 (0.99)	100 (47.17)
500	50	0.8	0.01	100 (1.0)	100 (177.0)
500	50	1	0.01	100 (1.0)	100 (324.56)

Table S4. Both sexes are choosy. Mating with replacement. *N* is the population size and *n* the sample size of matings. Choice implies preference for similarity. The quantitative trait distribution is *Z*(0,1). Number of runs: 1,000. % sig: The % of tests with *p*-value ≤0.05. The values in parentheses correspond to the average value of the statistic for the total number of significant runs.

N	***n***	***Choice***	***s***	**% sig. (ρ)**	**%sig. ($\rho^2/(1-\rho^2)$)**
10^4	500	0	--	4.4 (0.03)	5.4 (0.06)
10^4	500	0.2	0.08	24.6 (0.25)	26.1 (0.07)
10^4	500	0.4	0.08	100 (0.47)	100 (0.3)
10^4	500	0.8	0.08	100 (0.75)	100 (1.39)
10^4	500	0.2	0.01	100 (0.93)	100 (7)
10^4	500	0.4	0.01	100 (0.98)	100 (26)
10^4	500	0.8	0.01	100 (1)	100 (106)
500	50	0	--	4.5 (0.017)	5.7 (0.12)
500	50	0.2	0.08	36.3 (0.36)	38.5 (0.16)
500	50	0.4	0.08	99.8 (0.58)	99.9 (0.57)
500	50	0.8	0.08	100 (0.81)	100 (2.1)
500	50	0.2	0.01	100 (0.96)	100 (12.7)
500	50	0.4	0.01	100 (0.99)	100 (56.7)
500	50	0.8	0.01	100 (1.0)	100 (206)

Table S5. Comparison of ρ and J_{PSI} for lower choice values. One sex is choosy. Choice implies preference for similarity. Mating is with replacement. *N* is the population size and *n* the sample size of matings. The quantitative trait distribution is *Z*(0,1). Number of runs: 10,000. % sig: The % of tests with *p*-value ≤0.05. The values in parentheses correspond to the average value of the statistic for the total number of significant runs.

N	***n***	***Choice***	***s***	**% sig. (ρ)**	**%sig. ($\rho^2/(1-\rho^2)$)**
500	50	0.05	0.08	5.1 (0.05)	6.2 (0.12)
500	50	0.1	0.08	11 (0.32)	13 (0.13)

500	50	0.2	0.08	38.6 (0.37)	41.7 (0.16)
500	50	0.3	0.08	86 (0.44)	88 (0.27)
500	50	0.4	0.08	99.95 (0.61)	99.97 (0.64)
500	50	0.5	0.08	100 (0.71)	100 (1.1)
500	50	0.05	0.01	99.9 (0.64)	100 (0.78)
500	50	0.1	0.01	100 (0.90)	100 (4.6)
500	50	0.2	0.01	100 (0.96)	100 (13.54)
500	50	0.3	0.01	100 (0.99)	100 (47.6)
500	50	0.4	0.01	100 (0.99)	100 (56.68)
500	50	0.5	0.01	100 (1.0)	100 (188.6)

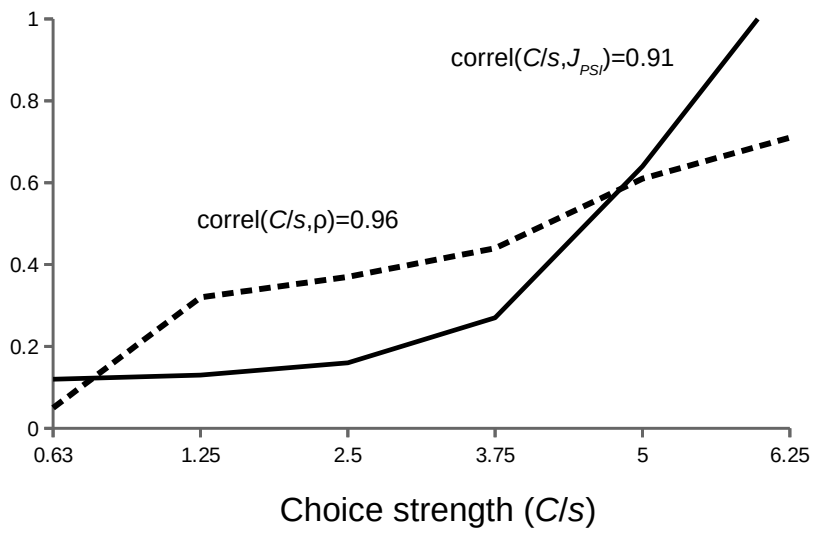

Figure S1. Graphic representation of values of the rho (dashed line) and J_{PSI} (continuous line) statistics with respect to the strength of the choice. The value of the correlation between each statistic and the strength of the choice is given. Population size N=500, sample size n=50. The values of ρ and J_{PSI} are those in Table S5 ordered by increasing C/s.

References

Alonzo, S.H., Servedio, M.R., 2019. Grey zones of sexual selection: why is finding a modern definition so hard? Proc. R. Soc. B Biol. Sci. 286, 20191325. https://doi.org/10.1098/rspb.2019.1325

Andersson, M., 1994. Sexual selection, Monographs in behavior and ecology. Princeton University Press, Princeton, N.J.

Arnold, S.J., Duvall, D., 1994. Animal Mating Systems: A Synthesis Based on Selection Theory. Am. Nat. 143, 317–348.

Arnold, S.J., Wade, M.J., 1984. On the measurement of natural and sexual selection: applications. Evolution 720–734.

Bateman, A.J., 1948. Intra-sexual selection in Drosophila. Heredity 2, 349. https://doi.org/10.1038/hdy.1948.21

Belov, D.I., Armstrong, R.D., 2011. Distributions of the Kullback–Leibler divergence with applications. Br. J. Math. Stat. Psychol. 64, 291–309.

Bürger, R., 2000. The Mathematical theory of selection, recombination, and mutation, Wiley series in mathematical and computational biology. John Wiley, Chichester.

Caballero, A., 2020. Quantitative Genetics. Cambridge University Press.

Carvajal-Rodríguez, A., 2020. Multi-model inference of non-random mating from an information theoretic approach. Theor. Popul. Biol. 131, 38–53. https://doi.org/10.1016/j.tpb.2019.11.002

Carvajal-Rodríguez, A., 2019. A generalization of the informational view of non-random mating: Models with variable population frequencies. Theor. Popul. Biol. 125, 67–74. https://doi.org/10.1016/j.tpb.2018.12.004

Carvajal-Rodríguez, A., 2018a. Non-random mating and information theory. Theor. Popul. Biol. 120, 103–113. https://doi.org/10.1016/j.tpb.2018.01.003

Carvajal-Rodríguez, A., 2018b. MateSim: Monte Carlo simulation for the generation of mating tables. Biosystems 171, 26–30.

Carvajal-Rodríguez, A., Rolán-Alvarez, E., 2014. A comparative study of Gaussian mating preference functions: a key element of sympatric speciation models. Biol. J. Linn. Soc. 113, 642–657.

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

Clancey, E., Johnson, T.R., Harmon, L.J., Hohenlohe, P.A., 2022. Estimation of the strength of mate preference from mated pairs observed in the wild. Evolution 76, 29–41. https://doi.org/10.1111/evo.14397

Cotto, O., Servedio, M.R., 2017. The Roles of Sexual and Viability Selection in the Evolution of Incomplete Reproductive Isolation: From Allopatry to Sympatry. Am. Nat. 190, 680–693. https://doi.org/10.1086/693855

Coyne, J.A., Orr, H.A., 2004. Speciation. Oxford University Press, Oxford, New York.

Darwin, C., 1871. The descent of man, and selection in relation to sex. Murray.

de Cara, M.A., Barton, N.H., Kirkpatrick, M., 2008. A model for the evolution of assortative mating. Am. Nat. 171, 580–596.

Edward, D.A., 2015. The many facets of mate choice: a response to comments on Edward. Behav. Ecol. https://doi.org/10.1093/beheco/arv021

Endler, J.A., 1986. Natural selection in the wild, Monographs in population biology ; 21. Princeton University Press, Princeton, N.J.

Erlandsson, J., Rolán-Alvarez, E., 1998. Sexual selection and assortative mating by size and their roles in the maintenance of a polymorphism in Swedish Littorina saxatilis populations. Hydrobiologia 378, 59–69. https://doi.org/10.1023/A:1003277202763

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

Evren, A., Tuna, E., 2012. On some properties of goodness of fit measures based on statistical entropy. Int. J. Res. Rev. Appl. Sci. 13, 192–205.

Fernández-Meirama, M., Rolán-Alvarez, E., Carvajal-Rodríguez, A., 2022. A Simulation Study of the Ecological Speciation Conditions in the Galician Marine Snail Littorina saxatilis. Front. Genet. 13. https://doi.org/10.3389/fgene.2022.680792

Fisher, R.A., 1918. The correlations between relatives on the supposition of Mendelian inheritance. Trans. R. Soc. Edinb. 52, 399–433.

Fitze, P.S., Le Galliard, J.-F., xe, ois, Associate Editor: Suzanne, H.A., Editor: Ruth, G.S., 2011. Inconsistency between Different Measures of Sexual Selection. Am. Nat. 178, 256–268.

Frank, S.A., 2020. Simple unity among the fundamental equations of science. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190351. https://doi.org/10.1098/rstb.2019.0351

Frank, S.A., 2017. Universal expressions of population change by the Price equation: Natural selection, information, and maximum entropy production. Ecol. Evol. 7, 3381–3396. https://doi.org/10.1002/ece3.2922

Frank, S.A., 2012. Natural selection. V. How to read the fundamental equations of evolutionary change in terms of information theory. J Evol Biol 25, 2377–96.

Gavrilets, S., 2004. Fitness landscapes and the origin of species, Princeton paperbacks. Princeton University Press, Princeton, N.J.

Gimelfarb, A., 1988. Processes of Pair Formation Leading to Assortative Mating in Biological Populations: Encounter-Mating Model. Am. Nat. 131, 865–884. https://doi.org/10.1086/284827

Hansen, T.F., 2018. Fitness in Evolutionary Biology. https://doi.org/10.20944/preprints201804.0271.v1

Hartl, D.L., 2020. A Primer of Population Genetics and Genomics. Oxford University Press. https://doi.org/10.1093/oso/9780198862291.001.0001

Hartl, D.L., Clark, A.G., 1997. Principles of Population Genetics, Third. ed. Sinauer Associates, Inc., Sunderland, MA.

Hedrick, P.W., 2005. Genetics of Populations, 3rd ed. Jones & Bartlett Publishers, Boston.

Henshaw, J.M., Jennions, M.D., Kruuk, L.E.B., 2018. How to quantify (the response to) sexual selection on traits. Evolution 72, 1904–1917. https://doi.org/10.1111/evo.13554

Henshaw, J.M., Kahn, A.T., Fritzsche, K., 2016. A rigorous comparison of sexual selection indexes via simulations of diverse mating systems. Proc. Natl. Acad. Sci. 113, E300–E308. https://doi.org/10.1073/pnas.1518067113

Hledík, M., Barton, N., Tkačik, G., 2022. Accumulation and maintenance of information in evolution. Proc. Natl. Acad. Sci. 119, e2123152119. https://doi.org/10.1073/pnas.2123152119

Jennions, M.D., Petrie, M., 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biol. Rev. 72, 283.
Jiang, Y., Bolnick, D.I., Kirkpatrick, M., 2013. Assortative Mating in Animals. Am. Nat. 181, E125–E138. https://doi.org/10.1086/670160
Jones, A.G., 2009. On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. Evolution 63, 1673–1684. https://doi.org/10.1111/j.1558-5646.2009.00664.x
Kimura, M., 1961. Natural selection as the process of accumulating genetic information in adaptive evolution. Genet. Res. 2, 127–140. https://doi.org/10.1017/S0016672300000616
Kirkpatrick, M., Ravigné, V., 2002. Speciation by natural and sexual selection: models and experiments. Am. Nat. 159 Suppl 3, S22-35. https://doi.org/10.1086/338370
Kokko, H., Klug, H., Jennions, M.D., 2012. Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. Ecol. Lett. 15, 1340–1351. https://doi.org/10.1111/j.1461-0248.2012.01859.x
Kullback, S., 1997. Information Theory and Statistics, New edition. ed. Dover Publications, Mineola, N.Y.
Lau, S.L.Y., Williams, G.A., Carvajal-Rodríguez, A., Rolán-Alvarez, E., 2021. An integrated approach to infer the mechanisms of mate choice for size. Anim. Behav. 175, 33–43. https://doi.org/10.1016/j.anbehav.2021.02.020
Lehtonen, J., 2022. Bateman gradients from first principles. Nat. Commun. 13, 3591. https://doi.org/10.1038/s41467-022-30534-x
Lewontin, R., Kirk, D., Crow, J., 1968. Selective mating, assortative mating, and inbreeding: definitions and implications. Eugen Q 15, 141–3.
Lindsay, W.R., Andersson, S., Bererhi, B., Höglund, J., Johnsen, A., Kvarnemo, C., Leder, E.H., Lifjeld, J.T., Ninnes, C.E., Olsson, M., Parker, G.A., Pizzari, T., Qvarnström, A., Safran, R.J., Svensson, O., Edwards, S.V., 2019. Endless forms of sexual selection. PeerJ 7, e7988. https://doi.org/10.7717/peerj.7988
López-Cortegano, E., Carpena-Catoira, C., Carvajal-Rodríguez, A., Rolán-Alvarez, E., 2020. Mate choice based on body size similarity in sexually dimorphic populations causes strong sexual selection. Anim. Behav. 160, 69–78. https://doi.org/10.1016/j.anbehav.2019.12.005
Merrell, D.J., 1950. Measurement of sexual isolation and selective mating. Evolution 326–331.
Ng, T.P.T., Rolán-Alvarez, E., Dahlén, S.S., Davies, M.S., Estévez, D., Stafford, R., Williams, G.A., 2019. The causal relationship between sexual selection and sexual size dimorphism in marine gastropods. Anim. Behav. 148, 53–62. https://doi.org/10.1016/j.anbehav.2018.12.005
Pardo, L., 2018. Statistical Inference Based on Divergence Measures. Chapman and Hall/CRC. https://doi.org/10.1201/9781420034813
Parker, G.A., 2014. The sexual cascade and the rise of pre-ejaculatory (Darwinian) sexual selection, sex roles, and sexual conflict. Cold Spring Harb. Perspect. Biol. 6, a017509–a017509. https://doi.org/10.1101/cshperspect.a017509
Parker, G.A., Pizzari, T., 2015. Sexual Selection: The Logical Imperative, in: Hoquet, T. (Ed.), Current Perspectives on Sexual Selection: What's Left after Darwin? Springer Netherlands, Dordrecht, pp. 119–163. https://doi.org/10.1007/978-94-017-9585-2_7
Price, G.R., 1970. Selection and covariance. Nature 227, 520–521.

Prum, R.O., 2012. Aesthetic evolution by mate choice: Darwin's really dangerous idea. Philos. Trans. R. Soc. Lond. B Biol. Sci. 367, 2253–2265. https://doi.org/10.1098/rstb.2011.0285

Reid, D.G., 2007. The genus Echinolittorina Habe, 1956 (Gastropoda: Littorinidae) in the Indo-West Pacific Ocean. Zootaxa 1420, 1–161. https://doi.org/10.11646/zootaxa.1420.1.1

Rettelbach, A., Kopp, M., Dieckmann, U., Hermisson, J., 2013. Three Modes of Adaptive Speciation in Spatially Structured Populations. Am. Nat. 182, E215–E234.

Rolán-Alvarez, E., Caballero, A., 2000. Estimating sexual selection and sexual isolation effects from mating frequencies. Evolution 54, 30–6.

Rolán-Alvarez, E., Carvajal-Rodriguez, A., de Coo, A., Cortes, B., Estevez, D., Ferreira, M., Gonzalez, R., Briscoe, A.D., 2015. The scale-of-choice effect and how estimates of assortative mating in the wild can be biased due to heterogeneous samples. Evolution 69, 1845–57.

Rolán-Alvarez, E., Williams, G., Ng, T., Estévez-Barcia, D., Davies, M., Saltin, S., Stafford, R., 2021. Data for: The causal relationship between sexual selection and sexual size dimorphism in marine gastropods 1. https://doi.org/10.17632/n27kg4cvdx.1

Rosenthal, G.G., 2017. Mate choice: the evolution of sexual decision making from microbes to humans. Princeton University Press.

Roughgarden, J., Adkins-Regan, E., Akçay, E., Crawford, JC., Gadagkar, R., Griffith, SC., Hinde, CA., Hoquet, T., O'Connor, C., Prokop, ZM., Prum, RO., Shafir, S., Snow, SS., Taylo, r D., Van Cleve, J., Weisberg, M., 2015. Sexual selection studies: a NESCent catalyst meeting. PeerJ Prepr. 3e680v3.

Roughgarden, J., Oishi, M., Akçay, E., 2006. Reproductive social behavior: cooperative games to replace sexual selection. Science 311, 965–969.

Sachdeva, H., Barton, N.H., 2017. Divergence and evolution of assortative mating in a polygenic trait model of speciation with gene flow. Evolution 71, 1478–1493. https://doi.org/10.1111/evo.13252

Sherwin, W.B., 2018. Entropy, or Information, Unifies Ecology and Evolution and Beyond. Entropy 20, 727. https://doi.org/10.3390/e20100727

Sherwin, W.B., Chao, A., Jost, L., Smouse, P.E., 2017. Information Theory Broadens the Spectrum of Molecular Ecology and Evolution. Trends Ecol. Evol. 32, 948–963. https://doi.org/10.1016/j.tree.2017.09.012

Sherwin, W.B., Prat i Fornells, N., 2019. The Introduction of Entropy and Information Methods to Ecology by Ramon Margalef. Entropy 21, 794. https://doi.org/10.3390/e21080794

Shuker, D.M., 2010. Sexual selection: endless forms or tangled bank? Anim. Behav. 79, e11–e17.

Shuker, D.M., Kvarnemo, C., 2021. The definition of sexual selection. Behav. Ecol. 32, 781–794. https://doi.org/10.1093/beheco/arab055

Spieth, H.T., Ringo, J.M., 1983. Mating behavior and sexual isolation in Drosophila. Genet. Biol. Drosoph.

Taylor, P.D., 1996. The Selection Differential in Quantitative Genetics and Ess Models. Evolution 50, 2106–2110. https://doi.org/10.2307/2410769

Vries, C. de, Lehtonen, J., 2023. Sex-specific assumptions and their importance in models of sexual selection. Trends Ecol. Evol. 0. https://doi.org/10.1016/j.tree.2023.04.013

Wacker, S., Amundsen, T., 2014. Mate competition and resource competition are inter related in sexual selection. J. Evol. Biol. 27, 466–477.
Wade, M.J., Arnold, S.J., 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. Anim. Behav. 28, 446–461. https://doi.org/10.1016/S0003-3472(80)80052-2
Xie, Y., Cheng, S., Zhou, X., 2015. Assortative mating without assortative preference. Proc. Natl. Acad. Sci. 112, 5974–5978. https://doi.org/10.1073/pnas.1504811112
Yukilevich, R., 2023. Female preferences between incipient species of Drosophila athabasca reveal divergent closed functions, epistasis, and segregation of veiled preference alleles. Evolution 77, 496–508. https://doi.org/10.1093/evolut/qpac055