



Non-random mating and information theory

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ABSTRACT

In this work, mate choice is modeled by means of the abstract concept of mutual mating propensity. This only assumes that different types of couples can have different mating success. The model is adequate for any population where mating occurs among distinct types. There is no extra assumption about particular mating scheme or preference model. The concept of mutual mating propensity permits to express the observed change in the mating phenotypes as the gain in information with respect to random mating. The obtained expression is a form of the Price equation in which the mapping between ancestral and descendant population is substituted by a mapping between random mating and non random mating population.

At the same time, this framework provides the connection between mate choice and the exact mathematical partition of the choice effects, namely sexual isolation, sexual selection and a mixed effect. The sexual selection component is the sum of the intra-sexual male and female selection.

The proposed framework helps to unveil previously hidden invariants. For example, if the mutual preference between partner types is multiplicative there is no sexual isolation (inter-sexual selection) effect on the frequencies, i.e. the only possible effect of mate choice is intra-sexual selection. On the contrary, whatever the contribution of each partner to the mutual preference, if it comes as a non-multiplicative factor, there is at least an inter-sexual selection detectable effect.

This new view over the mate choice problem, permits to develop general mating propensity models and to make predictions of the mate choice effects that may emerge from such models. This possibility opens up the way for setting a general theory of model fitting and multimodel inference for mate choice.

Thus, it is suggested that the proposed framework, by describing mate choice as the flow of information due to non-random mating, provides a new important setting for exploring different mating models and their consequences.

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1. Introduction

Mate choice is arguably one of the most active areas of evolutionary research. There has been a lot controversy regarding the concept of mate choice. The debate around mate choice was due in part to its importance for fields so diverse as population genetics, evolutionary-ecology, animal behavior, sociology, or psychology. In addition, there has been an excess of verbal models and imprecise terminology regarding different aspects of mate choice (Edward, 2015). Mate choice can be broadly described as the effect of some expressed traits leading to non-random mating. Under this broad definition there are various aspects that can be considered. Yet Darwin (1871) distinguishes between intrasexual selection and intersexual selection. The first arises directly from competition among individuals of the same sex while the second arises from choice of mates by the other sex (Kuijper et al., 2012). Alternatively, from a population genetics point of view, mate choice is defined as

the observed mating frequency deviation with respect to random mating, considering population gene or phenotype frequencies. So defined, mate choice can be partitioned into (intra)sexual selection, defined as the observed change in gene or phenotype frequencies in mated individuals with respect to population frequencies, and sexual isolation (behavioral isolation or intersexual selection), defined as the deviation from random mating in mated individuals (Rolán-Alvarez and Caballero, 2000). In this work I followed these definitions of mate choice, intrasexual and intersexual selection.

For an alternative description of these concepts and a discussion about some of the most widely used descriptions of evolutionary change within the context of sexual selection, I refer the reader to Kuijper et al. (2012) and Rosenthal (2017).

The many aspects and complexity of mate choice justify the extensive research that has been made in the last decades producing several theoretical models and empirical tests. Related to modeling and detection of mate choice, there is the question about the correct null hypothesis for testing the evolution of mate choice. The Lande–Kirkpatrick (L–K) model has been proposed as

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a null model (Kirkpatrick, 1982; Lande, 1981; Prum, 2010; Roff and Fairbairn, 2014). This model assumes neutral genetic variation for the mating preference trait while the target trait can be under natural selection. However, the L–K role as a null model is not clear when the preference is set by similarity (preference and target trait coincide) and the trait is under divergent selection (Servedio et al., 2011), i.e. the trait is “magic” sensu Gavrillets (2004), because in this case the preference trait is already under selection (Hughes, 2015).

Therefore, there is still a need for both, null models and a general framework, where the key essential facts of the mate choice can be adequately described. Here, I argue that the formalism provided by the information theory in the form of the Jeffreys’ divergence is the right tool to do so.

The information theory has already been elegantly applied for describing evolutionary change (Frank, 2009, 2012b, 2013). The present work takes advantage of that mathematical structure and applies it for modeling the change in mating frequencies due to mate choice. As far as I know there is no previous attempt of describing mate choice from the viewpoint of the information theory. Nevertheless, the potential of the informational view for evolutionary ecology has been already suggested (Dall et al., 2005).

First, I defined a general model that only requires an abstract functional relationship connecting the observed mating frequencies with the expected by random mating from the population gene or phenotype frequencies. This suffices for developing a general information equation for mate choice that can be adequately partitioned into intrasexual and intersexual information components, plus a mixed term provoked by the confounding effect of the marginal frequencies when the mating propensity effects are asymmetric. Interestingly, the three terms can be separately estimated from the observed frequencies and so, the researcher can study how different models and parameters translate into the different mate choice components. Also, it is proposed that this setting provides the baseline for solving the mate choice null hypothesis problem, since the null model emerges naturally from the idea of zero information. Thus, the correct null should not rely on neutral preference or trait genes but on zero information.

The utility of this framework is shown by analyzing a real data example. I will show how the view obtained from the unveiled relationships can be utilized to classify different general models from its consequences which facilitates the multimodel inference of the mate choice. However, a deeper study on the outcomes of different forms of the mating preference functions is out of the scope of the present article and is part of a different paper.

2. Model of mate choice

As mentioned above, the following model is as a particular specification of the information theory interpretation for evolutionary models, proposed in Frank (2012b, 2013). The general framework developed by this author fits perfectly for the purpose of describing the occurrence of non-random mating and the flow of information that it provokes. Remarkably, once the basic equation for the gain in information due to non-random mating is formalized, the relationship between mate choice and its different evolutionary outcomes emerges naturally, providing a clear and useful picture of the intrasexual and intersexual selection effects.

2.1. General model

Let us consider a population with a number of n_1 females and n_2 males. For a given female phenotype X (e.g. shell color) with K different classes having values $X_1, X_2 \dots X_k$, the frequency of the phenotype X_i in the female population is $p_{1i} = n_{1X_i}/n_1$, i.e. the number of females with that phenotypic value divided by the total

number of females. Similarly, for the male phenotype Y (could be the same as X) with K' classes, the frequency of Y_j in the male population is $p_{2j} = n_{2Y_j}/n_2$.

In this way, by using the frequency of the phenotype for each sex, the expected mating frequencies if mating is at random are

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

Now, given a female phenotype X_i and a male phenotype Y_j , let us define the mutual mating propensity $m_{ij}(x, y, e)$ as the number of matings of X_i with Y_j after their encounter in the environment e . The normalized mating propensity is

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

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

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

$$q'_{ij} = q_{ij} \frac{m_{ij}(x, y, e)}{M}. \tag{1}$$

Therefore, the observed mating frequencies are the result of the functions $m_{ij}(x, y, e)$ (hereafter noted as m_{ij}), that can be any kind of composition of the preference of female X_i for male Y_j , and vice versa, in the environment e .

Note that random mating is a particular case of the model in (1) when the propensities are equal for every mating pair. The mutual mating propensity functions can represent empirical or analytical functions, as for example the Gaussian-like preference functions (reviewed in Carvajal-Rodríguez and Rolán-Alvarez, 2014). Moreover, each m_{ij} can be composed of female and male preferences, so mutual mate choice models (Bergstrom and Real, 2000) are also available under this setting. The standardized m_{ij} values could also be estimated a posteriori from the data. In this case they coincide with the pair total index i.e. the ratio of the frequency of the observed types divided by the expected pair types calculated from the total frequencies ($PTI_{ij} = q'_{ij}/q_{ij}$, Rolán-Alvarez and Caballero, 2000) which becomes an observation of the mutual mating propensity from the mating phenotypes (see below).

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

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

The mean population change for a combined phenotype $Z = X * Y$ is

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

Because the relationship in (1) that is defined by ratios is more natural to express the quantities in the logarithmic scale and so we can express m_{ij} as

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

which in the logarithmic scale becomes

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

Thus, if we take the logarithm of the propensity as the combined phenotype Z and by noting that $\sum \Delta q_{ij} = 0$ and that $\log(M)$ is constant through the summation, then we can measure the mean population change ΔL in relative propensity as

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

which is the Kullback–Leibler symmetrized divergence (noted as Jeffreys in Frank, 2012b), that measures the gain in information

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