Modeling Mating Patterns Given Mutual Mate Choice: The Importance Of Individual Mating Preferences And Mating System[1]

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0   ABSTRACT

When we consider structured populations with sexual reproduction, the distribution of characters among mating pairs may influence the population biology, namely its dynamics and genetics. In the present paper, we propose a general framework to estimate the population mating patterns taking into account individual mating preferences and mating system, thus taking into account for the inter- and intra-sexual interactions such as mate competition and mate choice. According to our results, mating patterns are not a direct reflection of mating preferences, but also depend upon the average sex ratio between individuals that are ready to mate at any given time (*i.e.* the Operational Sex Ratio, OSR). Therefore, mating patterns should be assessed not only in function of preferences, but also of OSR. It is then possible to distinguish 3 OSR regions: (1) the equilibrium OSR, where there is a predominance of assortative mating patterns due to differential access to mates (inter-sexual interactions); (2) the slightly biased OSR, where there is a high diversity of mating patterns and no clear predominance of inter- or intra-sexual interactions; and (3) the highly biased OSR where there is a predominance of mating patterns corresponding to single-sex uniform preferences and an increased influence of intra-sexual interactions. We hope that this approach may allow to further explore the interaction between OSR and mate choice, namely how such interaction may affect sexual selection and mate choice tactics.

Keywords: mating preferences, mating process, mating rates, mutual mate choice, operational sex ratio, pair formation, passive mate choice

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1   INTRODUCTION

When we consider structured populations with two sexes, the pair formation process is likely to originate mating patterns other than the random or proportionate mixing of individuals of both sexes [16]. Consequently, the bias in the distribution of characters among mating pairs may influence the population demography and genetics, because if the characters in question are heritable, their transmission from one generation to another depends largely on the mating patterns [17]. Hence, for human populations, it may be useful to have models that are structured at least by gender, age and economic status because many health care and education issues, for example, depend of such variables. More generally, mating patterns correlate with the variance in mating success [1, 2], and they may modulate parental investment and reproductive success [7, 13, 31], lead to local adaptations and promote speciation [35], thereby deeply influencing population genetics and dynamics.

Mating patterns are the result of a mating process during which individuals attempt to achieve their mating preferences. This achievement is constrained by the availability of the prospective partners and their own mating strategies, as well as by the presence and strategy of congeners. Thus, although mating preferences are an important determinant of mating patterns, these patterns may not be a direct reflection of mating preferences [17], as they also depend on inter-sexual and intra-sexual interactions such as sexual conflict, competition and cooperation.

Even though the distinction between mating preferences and patterns has previously been discussed for particular cases [17], the disentangling of these two levels has proved difficult, and is absent from much theoretical work [19-21, 28, 29, 34, 36]. The frequent confusion between mating preferences and mating patterns partially results from the fact that mate choice models have focused on the evolution of mating preferences given polygynous mating systems where males have unlimited mating opportunities [27]. Given this scenario, the average sex - ratio among individuals that are ready to mate at any given time is likely to be extremely male biased, as males are relatively more available

to mate than females, and females should be able exert choice without being constrained by competition with other females for preferred males. The population sex ratio corrected to account for the relative availability to mate is usually denominated as the operational sex ratio [11, 14]. Consequently, when the operational sex ratio is biased, the mating patterns should be compatible with the preferences of the rarest sex, which were the females in the polygyny example. Nevertheless, other mating systems should be explicitly taken into account, as they may greatly affect mating patterns.

Here, we propose a general framework to estimate mating patterns taking into account both the individual mating strategies and the conspecifics. In particular, we have centered our model in two aspects of individual mating strategies, the individual mating preferences and the maximum number of partners individuals may acquire, which will influence the population operational sex ratio. This framework was then used to explore the distinction between mating preferences and mating patterns, and the effect of the operational sex ratio on mating patterns.

2   *MATERIAL AND METHODS*

2.1 The modeling framework

The framework to estimate mating patterns here proposed combines some major factors affecting the mating process, namely the population structure, the mating system and the mating preferences. The present framework relies on the assumption that individuals have equal access to all prospective partners, not including the mate search strategy (i.e. no mobility or time costs). Hence, the modeling framework is centered on the level of the encounter between prospective mates within a single mating bout, and the breeding population at encounter may vary from a single pair to a mating swarm.

2.1.1 The mating function
In the absence of mating preferences, the number of mating pairs, c, formed in a given breeding season is a function of potentially reproducing females and males, f and m [9,

30], and of the maximum number of mates an individual may obtain, *i.e.* their potential mating rates. For the monogamous mating system, the potential mating rate of both sexes is equal to one, so that females and males mate in a one-to-one way. Therefore, the number of mating pairs, *c*, is determined by the less abundant sex,

$$c = \min(f, m). \tag{2.1}$$

When the potential mating rate exceeds one, the maximum number of pair bonds males and females may establish can be denoted *h* and *l*, respectively, and the number of mating pairs can be computed as being

$$c = \min(lf, hm). \tag{2.2}$$

The potential mating rates and breeding population sex ratio determine the relative availability of prospective partners. When *lf = hm*, all individuals in the breeding population are mated. But if *lf > hm*, there aren't enough males, and not all females will be able to reach their potential mating rate (and some may even remain unmated). Likewise, if *lf < hm*, females will constitute a scarce resource, and some males will remain unmated or not fully fulfill their potential mating rate. Hence, in this context the potential mating rate is parallel to the potential reproductive rate definition of Clutton-Brock and colleagues [12] and [11], and its going to determine the Operational Sex Ratio (hereafter OSR), together with the population structure. Hence, the OSR may be computed has being

$$OSR = \frac{lf}{lf + hm}. \tag{2.3}$$

Under equal potential mating rates, the tertiary sex ratio, i.e. the sex-ratio of the breeding population, corresponds to the OSR. However, when the potential mating rate of both sexes differ, the relation between the tertiary sex ratio and the OSR changes reflecting the difference in mating opportunities between the two sexes. Therefore, when the tertiary sex ratio is at equilibrium, the OSR is biased towards the sex that has the higher potential mating rate [32].

If the individuals are classified in different breeding classes, *e.g.* age, stage or attractiveness classes, the distribution of mating pairs should account for the joint distribution of male and female classes. Following Gimelfarb [17], if we assume a 1:1 sex-ratio ($f = m$), and a monogamous mating system, in the absence of mate choice the number of mating pairs c_{ij} can be computed as a function of the total number of females and the relative abundance of females in class i, f_i, and of males in class j, m_j,

$$c_{ij} = \frac{m_j}{\sum\limits_q m_q} \frac{f_i}{\sum\limits_q f_q} \sum_q f_q = \frac{m_j}{\sum\limits_q m_q} f_i \tag{2.4}$$

The above formulation can be generalized to other mating systems and to variable sex – ratios via the mating function previously presented (equation 2.2). Thus, in the absence of mate choice, the number of mating pairs c_{ij} are a function of the relative abundance of females in class i, f_i, and of males in class j, m_j, as well as of their respective mating rates, l_i and h_j,

$$c_{ij} = \min\left(\frac{h_j m_j}{\sum\limits_q h_q m_q} l_i f_i, \frac{l_i f_i}{\sum\limits_q l_q f_q} h_j m_j \right) \tag{2.5}$$

2.1.2 Mating preferences

The equation 2.5 assumes that individuals mate randomly. However, often this is not the case, and the outcome of the mating process is likely to be biased by the individual mating preferences.

In an evolutionary context, a preference is any trait that changes the probability that an individual mates with a given individual of the opposite sex [27]. Most operational definitions take preferences as being either the individual mating probability (rendering impossible the distinction between individual and population levels), or as being the probability of acceptance the potential partners [22, 32]. Hence, mating preferences may be represented by the probability of a female in class i accepting a male in class j, α_{ij}, and the probability of a male in class j accepting a female in class i, β_{ij}.

Although the probability of acceptance is undoubtedly an appealing idea, mate choice may often be based on a simpler relative "attractiveness" ranking [15, 23-26, 33]. In fact, several experimental observations indicate that individuals may be ranked according to their "attractiveness" to the opposite sex in the absence of refusal [6, 8, 37]. If the mating preferences are defined by the relative attractiveness ranking of prospective partners, in addition to the probability of acceptance, the notation can be reviewed in order to include this ranking. Hence, we may denote the female and male mating preference by $\alpha_{ij}(r)$ and $\beta_{ij}(r)$, where r stands for the relative attractiveness rank, and when $\alpha_{ij}(r)$ or $\beta_{ij}(r)$ equal 1, there is no refusal of potential partners. Such a scenario corresponds to passive mate choice, when, although individuals have a relative ranking of potential partners, they do not refuse less preferred potential partners. If any acceptance probability is smaller than one, we will have an active (and potentially more costly) mate choice apart from the relative ranking of potential partners.

This representation can be generalized for any finite number of distinct classes and ranks. Furthermore, it does not make any assumptions on the relative attractiveness ranking, being extremely flexible. For example, if the relative attractiveness of individuals of a given sex is the same for all members of the opposite sex, the preference shape will be uniform (e.g. good genes, sensory exploitation). If the attractiveness level of an individual varies for different members of the opposite sex, the preference shape will be conditional (e.g. assortative preferences, selection for MHC polymorphism).

The mating process should reflect the relative attractiveness hierarchy, so that individuals should mate in priority with the relatively more attractive partners, thus acquiring the most attractive mate possible. Therefore, as long as potential partners of the upper ranks are available, the individuals in lower ranks will be unacceptable.

In the present approach, we assume that the mating preferences of both sexes equally influence the output of the mating process. Mutual mate choice implies that the availability of partners depends not only of their relative abundance, but also of their

own preferences. Hence, the relative attractiveness ranking of both sexes must be taken into account. The mating preferences of both sexes can be summarized in a set of parameters that we designate as inter-sexual interaction elements π_{ij}. These elements are ranked relative to each other so that no individual will be available for mating with a prospective partner in rank r while more attractive prospective partners are still available. Therefore, the relative rank k of the inter-sexual interaction elements, $\pi_{ij}(k)$, is a function of both sexes preference ranks, r and r' ($k = f(r, r')$ where $r \leq r'$), so that given two inter-sexual interaction ranks indexes, k_1 and k_2, where $k_1 = f(r_1, r_1')$ and $k_2 = f(r_2, r_2')$, k_1 is larger than k_2 ($k_1 > k_2$) if and only if $r_1' > r_2'$ or $r_1' = r_2'$ and $r_1 > r_2$. The inter-sexual interaction rank index k can be computed as being

$$k = \begin{cases} \dfrac{r'(r'-1)}{2} + r, & r' \leq z \\ r + zr' - \dfrac{z(z+1)}{2}, & r' > z \end{cases} , \qquad (2.6)$$

where $z = \min(r_f, r_m)$, and r_m and r_f are the total number of ranks of male and female preference hierarchies, respectively.

Whenever two distinct preference ranks are integrated ($r < r'$), this integration is mutual in order to insure mutual mate choice, so that the probability π_{ij} that a male j accept the female i and in turn is himself accepted, can be computed as being

$$\pi_{ij}(k) = \begin{cases} \alpha_{ij}(r)\beta_{ij}(r') & \text{if} \quad r = r' \\ \alpha_{ij}(r)\beta_{ij}(r') + \alpha_{ij}(r')\beta_{ij}(r) - \alpha_{ij}(r)\beta_{ij}(r')\alpha_{ij}(r')\beta_{ij}(r) & \text{if} \quad r < r' \end{cases} . \qquad (2.7)$$

This hierarchical view of both sexes mating preferences and resulting inter-sexual interaction, can be modeled through an iterative algorithm whose iterations correspond to the inter-sexual interaction ranks. Let $f_i(k)$ be the number of females from mating class i, and $m_j(k)$ be the number of males from mating class j at iteration k. The equation 2.4 can be re-written for each iteration k, so that the number $c_{ij}(k)$ of ij pairs formed at iteration k depends on the inter-sexual interaction,

$$c_{ij}(k) = \min\left(\frac{\pi_{ij}(k)h_j m_j(k)}{\sum_q \pi_{iq}(k)h_q m_q(k)} \pi_{ij}(k)l_i f_i(k), \frac{\pi_{ij}(k)l_i f_i(k)}{\sum_q \pi_{qj}(k)l_q f_q(k)} \pi_{ij}(k)h_j m_j(k) \right) \qquad (2.8)$$

At each iteration, the number of individuals available for mating depends on the previous iterations and on the respective mating rates, so that

$$f_i(k+1) = f_i(k) - \frac{1}{l_i}\sum_j c_{ij}(k)$$

$$m_j(k+1) = m_j(k) - \frac{1}{h_j}\sum_i c_{ij}(k) \qquad (2.11)$$

The sum of the $c_{ij}(k)$ over all k, $c_{ij}(\ )$, is the mating pattern.

2.2 The relation of mating patterns with mating preferences and operational sex ratio

In the present paper, we analyzed the relation between mating preferences and mating patterns, and the effect of the OSR on mating patterns. We have chosen not to select any attractiveness hierarchy in particular and, instead, use a combinatorial approach in order to generate a wide set of male and female preferences. Therefore, for each population structure, we explore all possible distinct sets of male and female passive mating preferences where no more than one type can be preferred per rank, by generating all possible combinations of individual preferences under two conditions: (1) no more than one class of the opposite sex could be preferred at a given rank, and (2) the choice was passive (*i.e.* all preference elements $\alpha_{ij}(r)$ and $\beta_{ij}(r)$ are either 0 or 1).

Mating patterns were evaluated given each distinct set of mutual mating preferences and considering a population of 100 sexually mature individuals, uniformly distributed on d mating classes (d = 2, 3, 4), and assuming that the numbers of female and male mating classes were equal. We consider variation in the OSR in the interval [0.025, 0.975].

For each population structure, OSR, and combinatorial set of mating preference spaces, we assessed the number of distinct mating patterns and their relative frequency. For

simplicity, whenever the overall patterns are not influenced by the number of classes, we present results only for $d = 3$.

2.2.1 Characterization of the mating patterns

In order to characterize the mating patterns, we also analyzed the relative frequency of the different type of pairs within each mating pattern. For each OSR, the mating patterns issued from the different mating preferences were compared with the mating pattern resulting from the model without mate choice (equation 2.4). This mating pattern, denoted $c^*_{ij(\ )}$, can be referred to as the random mating pattern because mating probabilities reflect the relative proportions of individuals in the population.

For each mating pattern we estimated the overall difference θ from the random mating patterns, *i.e.* the number of pairs that differed from the random mating pattern. This difference was normalized by the maximum number of pairs by which they could differ in order to assure its independence from the total number of pairs formed (which depends on population size and OSR). Hence, θ ranges between 0 and 1, and is computed as

$$\theta = \frac{\sum\limits_{i,j}^{d} \left| c_{ij(\ )} - c^*_{ij(\ )} \right|}{2\sum\limits_{i,j}^{d} c_{ij(\ )}} \tag{2.12}$$

Besides this criterion, we have also considered the proportion of pairs that differed from the expected mating pattern if these patterns were solely determined by the mating preferences, namely by assortative, male uniform, or female uniform mating preferences. By assortative mating pattern we considered not only the strictly assortative patterns, but also all other mating patterns that were consistent with a conditional mating preference. In order to do so, we computed the sum over the diagonal elements for all possible permutations of the mating pattern. We then selected the permuted matrix with the highest sum and we applied the same permutation to the random mating pattern. The difference between the observed number of assortative pairs and the expected given the

random mating pattern was normalized by the number of non-assortative pairs in the random mating pattern. Therefore, this criterion ranges between -1 and 1.

$$\theta_{dA} = \frac{\displaystyle\sum_{i=1}^{c}\sum_{j=i}^{i}\left(c_{ij(\ )} - c_{ij(\ )}^{*}\right)}{\displaystyle\sum_{i=1}^{c}\sum_{j=1}^{c}c_{ij(\ )} - \sum_{i=1}^{c}\sum_{j=i}^{i}c_{ij(\ )}} \qquad (2.13)$$

The difference between the number of pairs in the observed mating patterns reflecting single-sex (male or female) uniform preferences and the random mating pattern was computed in a similar way. However, instead of considering the sum over the diagonals, we focused on the sum over all columns (for female uniform preferences) or rows (for male uniform preferences), and we selected the one with the highest sum of preferred pairs. This difference was normalized by the number of non-preferred pairs in the random mating pattern, and consequently it may range between -1 and 1.

3   RESULTS

3.1 The distinction between mating preferences and mating patterns

In order to analyze the relationship between mating preferences and mating patterns we compared the number of mating preferences associated with distinct mating patterns.

Even with preference restrained to a single mating class being preferred *per* rank and acceptance being always equal to one, we have an enormous set of distinct mutual mating preferences that increases more than exponentially with the number d of classes considered (the number of mating preferences is equal to d^{2d}). Nevertheless, when we consider the resulting mating patterns, we observe a dramatic reduction in the number of distinct patterns, meaning that many mating preferences resulted in the same mating pattern (Figure 1). This reduction becomes more pronounced as the number of attractiveness classes increases. For a population with four classes, and under an equilibrium operational sex ratio (i.e. OSR = 0.5), the number of distinct mating pattern

is almost a thousand fold smaller. If the operational sex ratio is biased (OSR = 0.45), the maximum number of distinct mating patterns is one fifth of the mating preferences. Thus, although the disparity between mating preferences and mating patterns is reduced for biased OSR, the number of patterns observed is always small compared to the number of mating preferences considered, supporting the importance of distinguishing mating patterns from preferences.
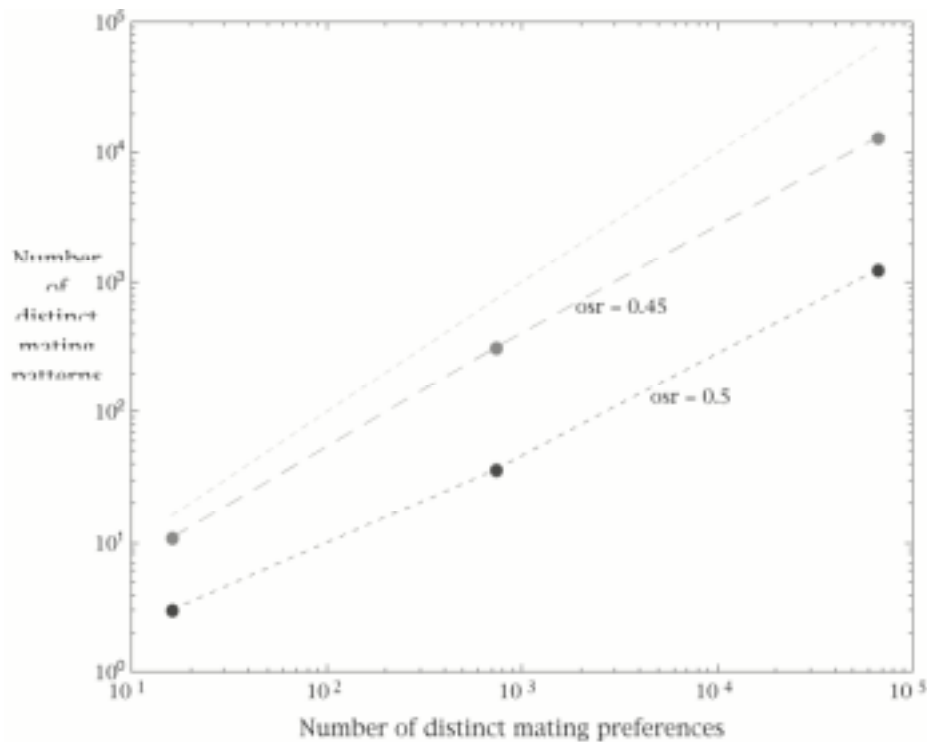

Figure 1. Log number of distinct passive mutual mating preferences versus log number of distinct mating patterns, assuming equal number of female and male mating types (d = 2, 3, 4), and that no more than one type can be preferred per rank. In light gray is the line $y = x$.

3.2 OSR and the number of distinct mating patterns

The relation between the OSR and the number of distinct mating patterns is not linear (Figure 2). Attending to the number of distinct mating patterns observed, we identify three main OSR regions, namely the equilibrium OSR (OSR = 0.5), the slightly biased OSR (0.3 < OSR < 0.5 and 0.5 < OSR < 0.7), and the highly biased OSR (OSR ≤ 0.3 and OSR ≥ 0.7). The equilibrium and highly biased OSR correspond to regions of low number of distinct mating patterns, where preferences lead to a reduced set of possible patterns, achieving

its minimum at equilibrium OSR. In contrast, the slightly biased OSR corresponds to diversification regions, where we can find many more distinct mating patterns.
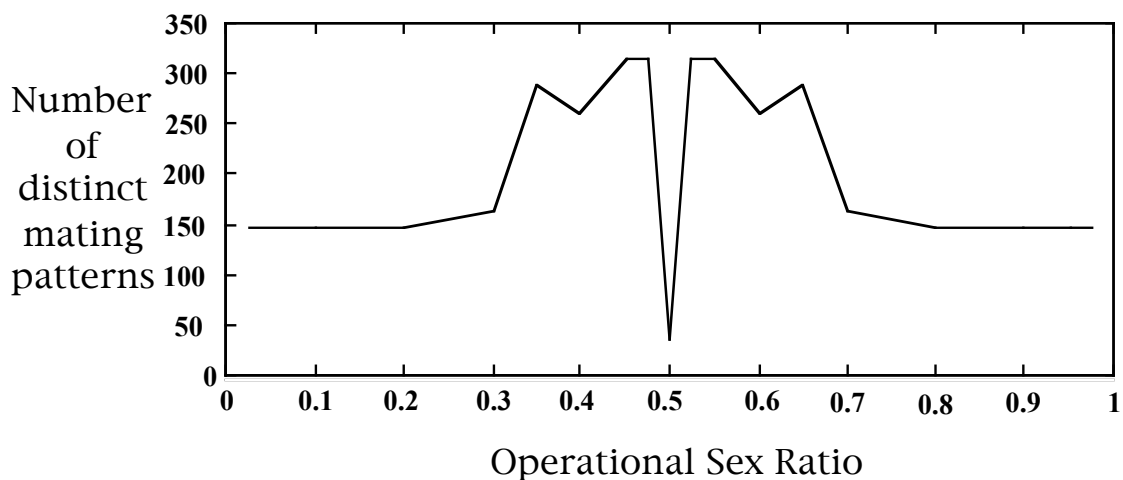

Figure 2. Variation of the number of distinct mating patterns with operational sex ratio ($d = 3$).

3.3 OSR and the type of mating patterns

The OSR influences not only the number and frequency of distinct mating patterns but also the mating patterns themselves. In fact, the majority of the observed mating patterns differed from the null model, i.e. the random mating pattern (Figure 3). When we considered a population structured into two classes, the proportion of random mating patterns was only 12.5%, independently of the OSR. Furthermore, when the population was structured in 3 or 4 classes, we found virtually no random mating pattern.

The relationship between the median difference from the random mating pattern and the OSR was also not linear (Figure 3), and the same three OSR regions found previously were still identifiable. When the OSR is at equilibrium or is highly biased, the median difference from the random mating pattern is maximal, but when the OSR is slightly biased, the median decreases. This means that, in the low mating pattern diversity regions, the mating preferences result in a low number of distinct mating patterns that are very different from a random mating pattern. In the diversification regions, although we had a higher number of distinct mating patterns, we had a higher proportion of mating patterns that are closer to a random mating pattern.
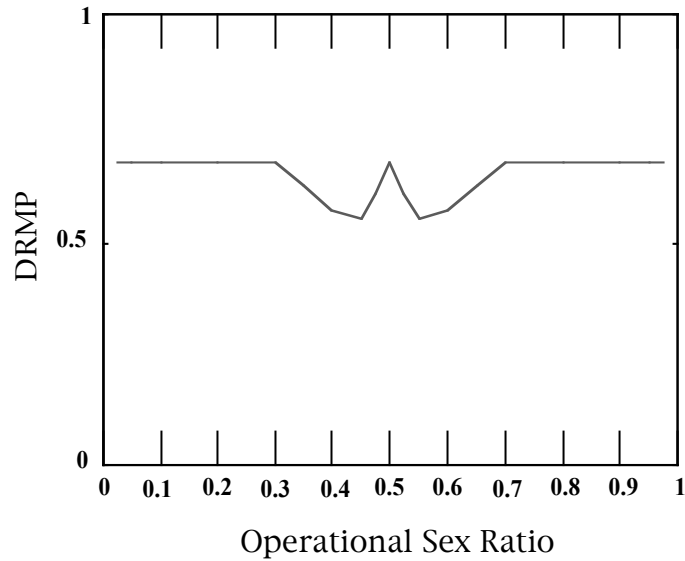
Figure 3. Variation of the median difference from the random mating pattern (DRMP) with operational sex ratio.

3.4 Assortative and uniform preferences

Likewise, the proportion of pairs that were consistent with assortative or single-sex uniform preferences also depends on the three preceding OSR regions (Figure 4). If we consider the equilibrium OSR, the median proportion of assortative pairs is one, meaning that more that 50% of the observed mating patterns have 100% assortative couples (Figure 4: "assortative"). This result is due to the maximization of the achievement of both sexes. This maximization leads to differential access to mates and to the positive assortment of individuals by attractiveness, even in the absence of assortative preferences [6, 7]. As the OSR becomes slightly biased, the number of assortative pairs declines, but the number of mating patterns in conformity with single-sex uniform preferences increases (Figure 4: "female uniform" and "male uniform"). When the OSR is highly biased, the median distance between assortative or single sex uniform mating patterns is constant. In this case, the number of mating patterns compatible with single-sex uniform preferences is maximal. Which sex achieves its uniform preference depends on which sex is the rarest. More than 50% of the mating patterns correspond to the rarest sex uniform preference, whereas no mating pattern corresponds to the opposite sex uniform preference.
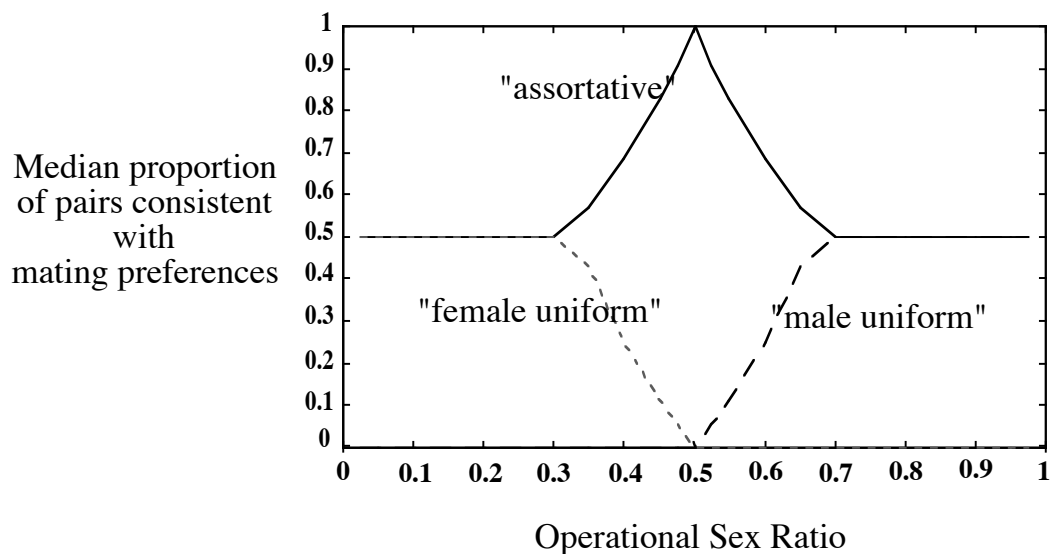
Figure 4. Variation of the median proportion of pairs in conformity with assortative and uniform female and male preferences with operational sex ratio, given passive mutual mate choice.

4   *DISCUSSION*

4.1   The   distinction   between   mating   preferences   and   mating patterns

The analysis of the relation between mating preferences and mating patterns reinforces the importance of distinguishing both, due to the lack of bijectivity between them. Although the observation had already been done for some particular cases [17], the combinatorial approach used to generate the mating preferences allowed us to expand the previous observations for to a much broader context. Consequently, even though mating preferences influence the mating pattern, they are seldom accurately described by these patterns when the OSR is not highly biased in favor of the opposite sex. Thus, if mating patterns are taken to be the mating preferences, the intra- and inter-sexual interactions, such as mutual mate choice and competition for mates, are ignored. This raises the question of how to measure individual mating preferences. The answer is likely to depend on the context, but the distinction between different aspects of the individual preferences, as well as how they can be limited by intra- and inter-sexual interactions, is fundamental to understand the evolution of mating preferences.

4.2 The OSR effect on mating patterns

Mating patterns are strongly influenced by the interaction between individual mating preferences and the relative availability of males and females to mate. We were able to identify three distinct OSR regions. The first case is the equilibrium OSR, for instance when both sexes have identical potential mating rates and the tertiary sex ratio is at equilibrium. Under such conditions, which are commonly assumed to generate little sexual selection, mutual mate choice leads to mating patterns that differ from random. Under equilibrium OSR, we have observed a clear predominance of a few mating patterns where most pairs could be described as assortative. The main reason behind this result is that under equilibrium OSR, mating patterns are largely determined by inter-sexual interactions, the maximization of mating preference achievement of both sexes leading to differential access to mates [6, 7], even in the absence of assortative preferences. This result differs from the observation of Jonhstone and colaborators [22] because in the present work the differential access to mates does not result from individuals with different fitness values having different acceptance thresholds. Instead, it emerges even in the absence of any variability in acceptance probabilities or fitness considerations and for a wide range of mating preferences. The assortative mating pattern is, in fact, one of the most common mating patterns in natural populations [4, 13], and it has already been recognized that it could result from non-assortative mating preferences [3, 5, 10, 18].

The second case is when the OSR is slightly biased. In this region we observe a diversification of mating patterns, due to the fact that some mating preferences are able to "escape" from the dominant patterns. This phenomenon is likely to depend both on intra-sexual interactions such as competition, interference or facilitation, and inter-sexual interactions, like mutual mate choice, the interaction between mutual mating preferences and OSR being fundamental. In other words, in the slightly biased OSR region there is no clear predominance of either inter- or intra-sexual interactions in

determining the mating pattern, which results in mating patterns that are close to a random mating pattern.

The third case is the highly biased OSR region, where mating preferences converge to a small number of distinct mating patterns. These patterns are quite distinct from the random mating patterns, corresponding mainly to single-sex uniform mating preferences and, to a lesser extent than in the other regions, to assortative mating preferences. Not surprisingly, in these regions we observe that the rarer sex is generally more able to achieve its preferences. The interplay between inter-sexual interactions and OSR results in one single sex being able to have larger control over the pair formation process.

5   *CONCLUSION*

In this paper, we propose a modeling framework for mating patterns that combines some major factors affecting pair formation, as well as their interdependency. One fundamental point of this framework is that by explicitly taking into account the individual strategies and the interaction with conspecifics, it liberates us from many of the assumptions that have marked previous theoretical work on mate choice and OSR.

The present framework relies on discrete attractiveness classes, distinguishing between preference and acceptance probability. Their representation is, in itself, very general, and its flexible, differing from previous approaches that are often more specific, different shapes being given by different functions, which renders difficult their comparison [29]. Furthermore, by discriminating between preference and acceptance probabilities, the preference representation allows for the exploration of the relative attractiveness of prospective partners and decision rules independently.

The generality of the proposed framework opens new perspectives for the analysis of different aspects of breeding systems, such as the relation between preference shapes, OSR, choosy behavior, mate search and parental care. By explicitly taking into account individual potential mating rates and mating preferences, it will be possible to further explore the direction and intensity of sexual selection given the OSR, explicitly

considering fitness consequences, such as direct and indirect benefits associated with different mating patterns.

6   ACKNOWLEDGMENTS

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