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The Evolution of Mutual Mate Choice under Direct Benefits

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abstract: In nature, the intensity of mate choice (i.e., choosiness) is highly variable within and between sexes. Despite growing empirical evidence of male and/or mutual mate choice, theoretical investigations of the joint evolution of female and male choosiness are few. In addition, previous approaches have often assumed an absence of trade-off between the direct benefits per mating and the lower mating rate that results from being choosy. Here we model the joint evolution of female and male choosiness when it is solely ruled by this fundamental trade-off. We show that this trade-off can generate a diversity of stable combinations of choosiness. Mutual mate choice can evolve only if both females and males exhibit long latency after mating. Furthermore, we show that an increase in choosiness in one sex does not necessarily prevent the evolution of mutual mate choice; the outcome depends on details shaping the trade-off: the life history, the decision rule for mate choice, and how the fecundity of a pair is shaped by the quality of both individuals. Last, we discuss the power of the sensitivity of the relative searching time (i.e., of the proportion of a lifetime spent searching for mates) as a predictor of the joint evolution of choosiness.

Keywords: choosiness, direct benefits, mutual mate choice, relative searching time (RST), sex roles, sexual selection.

Introduction

Mate choice corresponds to any behavior that increases (or decreases) the probability of mating with certain individuals (Halliday 1983). Darwin (1871) proposed mate choice as the mechanism responsible for the evolution of extravagant ornaments. Because males generally display these ornaments, the first empirical investigations of mate choice were highly focused on females. However, recent research has shown that the intensity of choice (i.e., choosiness) varies widely across taxa both within and between sexes. In particular, empirical evidence for male mate choice keeps accumulating (for reviews, see Clutton-Brock 2009; Edward and Chapman 2011). Besides, mutual mate choice—the situation in which both females and males are choosy—has also been documented in a wide variety of taxonomic groups, such as amphibians (Verrell 1995), arachnids (Rypstra et al. 2003; Cross et al. 2007; Luo et al. 2014), birds (Jones and Hunter 1993; Monaghan et al. 1996; Hansen et al. 1999; Faivre et al. 2001; Sæther et al. 2001; Romero-Pujante et al. 2002; Daunt et al. 2003; Pryke and Griffith 2007; Nolan et al. 2010), crustaceans (Aquiloni and Gherardi 2008), fishes (Rowland 1982; Hua Wen 1993; Kraak and Bakker 1998; Sandvik et al. 2000; Werner and Lotem 2003; Wong et al. 2004; Bahr et al. 2012; Myhre et al. 2012), insects (for a review, see Bonduriansky 2001), and mammals (Drickamer et al. 2003), including primates (Courtiol et al. 2010; Gomez et al. 2012). Despite the ever-growing empirical literature showing that choosiness is highly variable in both sexes, theoretical investigations of the joint evolution of female and male choosiness are few compared with the large number of studies dealing with unilateral mate choice (Bergstrom and Real 2000).

Why does choosiness vary so much both within and between sexes and species? One potential explanation is that its evolution is influenced by benefits and costs that vary due to differences in life-history traits and/or environmental conditions (Jennions and Petrie 1997). Mate choice is indeed often associated with direct fitness benefits (e.g., nuptial gifts, territory, food, protection, increased fertility, or parental care; Andersson 1994) and costs (e.g., increased predation risk or injuries caused by conspecifics; Andersson 1994) for the chooser, regardless of its sex. The presence of these direct benefits and costs in a wide variety of organisms suggests that direct selection plays an important role in the evolution of mate choice (Jones and Ratterman 2009). However, predicting variation in the direct selection of choosiness is difficult because the nature of benefits and costs involved often depends on the organism being studied.

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One general cost that has been ignored by most theoretical studies in sexual selection is that choosy individuals necessarily suffer a decrease in their mating rate (Etienne et al. 2014; Dechaume-Moncharmont et al. 2016). This is because choosy individuals spend time searching for particular mates instead of reproducing with the first member of the other sex they encounter. When mating events are sequential, the total number of matings for choosy individuals is thus reduced and this cost—sometimes qualified as an opportunity cost—occurs even if individuals mate only once. This is because rejecting mates increases the probability of dying before having reproduced. Furthermore, choosy individuals are also less likely to find a partner before the end of the reproductive season (see, e.g., Priklopil et al. 2015). Mate choice is thus intrinsically associated with a trade-off between the benefits per mating, which increases with choosiness, and the mating rate, which decreases with choosiness (Owens and Thompson 1994; Kokko and Mappes 2005; Härdling et al. 2008). We call this the fundamental trade-off of mate choice. Etienne et al. (2014) evaluated the importance of this trade-off under the assumption that mate choice can evolve in only one sex (the other being considered indiscriminate). They showed that, depending on the biological and ecological context, the strength of the trade-off varies and influences the evolution of choosiness.

Here we extend the model of Etienne et al. (2014) to study the influence of this fundamental trade-off of mate choice when choosiness is allowed to evolve in both sexes. Such a generalization is not trivial because the evolution of choosiness in one sex influences the evolution of choosiness in the other (Johnstone et al. 1996; Johnstone 1997; Kokko and Johnstone 2002). Indeed, choosiness in each sex has an effect on the competition for mates in the other sex, which in turn influences the benefits and costs associated with choosiness in both sexes. Or as Johnstone (1997) put it, “the best strategy for males depends on the behaviour of females, and vice versa.” We also attempt to obtain a simple metric that allows for general predictions about the evolution of choosiness when the trade-off is the sole evolutionary force shaping mate choice. Etienne et al. (2014) showed that, within this scope, the evolution of choosiness in one sex can be predicted in terms of the proportion of a lifetime devoted to searching for mates, or the relative searching time (RST). More specifically, the sensitivity of RST (i.e., ∂RST)—the change in RST caused only by a variation in any biological or ecological parameter affecting the mating rate of individuals, while choosiness is fixed—gives the effect of such variation in selection on choosiness. When ∂RST is positive, lower choosiness is selected, and vice versa. Here we investigate the predictive power of ∂RST for the joint evolution of female and male choosiness.

Factors other than the fundamental trade-off of mate choice certainly influence the evolution of choosiness (e.g., indirect benefits, sexual conflicts). Yet we chose to study the influence of this trade-off in isolation for two main reasons. First, the evolutionary consequences of this trade-off have been shown to be complex even when choosiness is free to evolve in only one sex (Etienne et al. 2014). Second, other sources of selection are likely to act in addition to, and not instead of, the trade-off we consider. Hence, computing how this trade-off influences the direct selection of choosiness should help disentangle the effects of the various selection pressures that shape the evolution of mate choice. In particular, we consider the evolution of choosiness given a certain amount of parental investment in each sex and do not study the joint evolution that could occur between choosiness and parental care (Kokko and Jennions 2008). This assumption allows us to study the fundamental trade-off of mate choice independently from the one between mating rate and parental care.

Our work complements existing theoretical studies of the evolution of mutual mate choice. Specifically, we consider a continuous strategy set for choosiness and thereby extend previous studies that considered two discrete categories of choosiness (Crowley et al. 1991; Härdling et al. 2008). We give game-theoretical solutions for such a continuous strategy set, taking into account the influence of other-sex and same-sex individuals’ behavior on the evolution of choosiness, contrary to some earlier models (Owens and Thompson 1994; Kokko and Monaghan 2001; Simao and Todd 2002; Kokko and Mappes 2005; Gowaty and Hubbell 2009). As such, our approach complements the study by Johnstone et al. (1996), which focused on the diversity of mating patterns emerging from mutual mate choice, and the one by Kokko and Johnstone (2002), which focused on joint evolution among choosiness, signaling, and care. Finally, we allow for any number of mating events throughout a lifetime, in contrast to models that assume that individuals mate only once (Parker 1983; McNamara and Collins 1990; Johnstone 1997; Alpern and Reyniers 1999, 2005; Alpern and Katrantzi 2009; Ramsey 2011).

Model

Individual Traits

We consider an infinite population at demographic equilibrium with two sexes in equal proportion (sex ratio $= 1:1$). One sex, denoted x, is treated as the focal sex. The other is denoted y. Each individual i of sex x is characterized by an environmentally determined quality $q_{x,i}$ and a genetically determined choosiness $\phi_{x,i}$, both real numbers between 0 and 1 (for a summary of our notations, see table 1). We assume $q_{x,i}$ to be directly proportional to the contribution of a mate to the fecundity of one mating (i.e., it directly translates into offspring quantity), which is why we call it “quality.” Quality is strictly environmentally determined and follows a beta distribution (with its two parameters denoted α_x and β_x), which we assume to be constant across generations. Assuming that quality has no genetic basis prevents the emergence of linkage disequilibrium between choosiness and quality. Thus, there is no indirect selection of choosiness (and thereby no so-called good genes) in this model. Choosiness sets the proportion of other-sex individuals whose quality is too low to be accepted as mates. For instance, an individual i of sex x with $\phi_{x,i} = 0.4$ rejects all individuals of sex y in the lower 40% of the quality distribution and accepts all those whose quality is higher. We denote $q_y(\phi_{x,i})$ the minimal value of quality in sex y that is accepted by the individual i of sex x. Thus, q_x and q_y correspond to quantile functions in each sex. We assume that individuals make no error in assessing the quality of their potential mates and that choosiness is strictly genetically determined by one sex-specific locus and is expressed as a fixed threshold. Choosiness is therefore considered to be independent from individual qualities.

Table 1: Summary of notation

Variable	Description
Individual level:	
q	Quality
Class level:	
m, p	Class (mutant, resident)
ϕ	Choosiness
$q(\phi)$	Minimal quality for being accepted by an individual of choosiness ϕ
μ	Mating probability
a	Availability
F	Lifetime fecundity
r	Mating rate
b	Benefits per mating
Sex level:	
x, y	Sex (focal, other)
α, β	Parameters of the beta distribution of quality
s	Survival rate
l	Latency rate
$f(q)$	Probability density of quality
ϕ^*	Choosiness at equilibrium
RST*	Relative searching time at equilibrium
R^*	Relative increase in mating rate at equilibrium
B^*	Relative increase in benefits per mating at equilibrium
Population level:	
γ	Encounter rate
z_r	A given biological or ecological variable affecting the mating rate
z_b	A given biological or ecological variable affecting benefits per mating

Life Cycle

Time is discrete, and at each time step, each individual of sex x survives with rate s_x. We consider that s_x is independent from all other individual traits (i.e., $q_{x,i}$ and $\phi_{x,i}$ have no effect on survival). The expected lifetime of individuals of sex x is thus $1/(1-s_x)$ (the time step during which an individual dies is included in its lifetime). At any time step for which an individual of sex x survives, it randomly encounters an individual of sex y with rate γ. (Due to the balanced sex ratio, individuals of sex y also encounter individuals of sex x at the same rate γ.) If both individuals are available and accept each other, mating occurs. In this case, mated individuals of sex x enter a latency period with rate l_x, during which they become unavailable for mating.

Biologically, latency can result from any process that prevents individuals from remating instantly (gamete depletion, mate guarding, parental care, etc.). Latency is not necessarily all-or-nothing in real living organisms, as assumed in our model. For example, an individual providing parental care may exhibit an intermediate level of latency since remating is possible, albeit limited, during this period. Nonetheless, latency is not all-or-nothing for a group of individuals in our model. This is true in particular for all individuals sharing an allele for choosiness because these individuals will each leave latency at different random times. Hence, selection will be similar at the level of choosiness alleles regardless of whether latency is, at a given time, all-or-nothing for each individual.

The latent individual, if it survives, then remains in latency with rate l_x at each following time step. We therefore assume that the duration of latency is independent between the male and the female of a given mating pair. Once latency is finished, the individual becomes available for mating again. The transition rates between “available” and “unavailable” states are thus given by the following matrix (see also Etienne et al. 2014):

$$\mathbf{L}_x = \begin{array}{rcc} & \text{... to available} & \text{... to unavailable} \\ \text{from available ...} & s_x(1-\gamma\mu_{x,i}l_x) & s_x\gamma\mu_{x,i}l_x \\ \text{from unavailable ...} & s_x(1-l_x) & s_x l_x \end{array}, \tag{1}$$

where $\mu_{x,i}$ is the probability that an individual i of sex x mates, given that it is available for mating and has encountered an individual of sex y. Similarly, the transition rates for individuals of sex y are obtained by substituting x for y in the previous matrix.

Calculating Mating Probabilities

The probability $\mu_{x,i}$ that a focal individual i of sex x mates with an individual j of sex y depends on the probability that j accepts i and on the probability that i accepts j. Let us first consider the probability that j accepts i. If i is not of sufficient quality to mate with, it is never chosen by other-sex individuals, and thus $\mu_{x,i} = 0$. If so, it does not transmit its choosiness alleles and thus does not influence the evolution of choosiness in the population. Therefore, only individuals that can obtain mates need to be taken into account in our evolutionary analysis. In this case, the probability that j accepts i equals 1.

Second, following our definition of choosiness, the probability that i accepts j directly depends on the choosiness of i (i.e., $\phi_{x,i}$) and, because individuals try to mate only with available partners, this probability also depends on the probability that j is in the available state in equation (1), which we now call the availability of j. The availability of j is in turn related to the choosiness of other individuals of sex x. The reason is that a given individual j may be in latency after having previously mated—and can thus be unavailable for a new mating. To take this competition for mates into account in a game-theoretical analysis, it is sufficient to analyze the case where the variation in choosiness among individuals reduces to the case where the focal individual i is a mutant in a population adopting some resident strategy. We therefore relabel the individual i as "m" and consider that this individual has choosiness $\phi_{x,\mathrm{m}}$ and a quality sufficient to mate ($q_{x,\mathrm{m}} \geq q_x(\phi_{y,\mathrm{p}})$). The mutant belongs to a population where all other individuals of sex x have choosiness $\phi_{x,\mathrm{p}}$ (with "p" for population). We also assume that all individuals of sex y show the same choosiness, denoted $\phi_{y,\mathrm{p}}$. Together, $\phi_{x,\mathrm{p}}$ and $\phi_{y,\mathrm{p}}$ define the residents in the population.

Two situations need to be distinguished to compute the probability that the mutant accepts j. First, if the mutant is choosier than other same-sex individuals ($\phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}$), the potential partners it is willing to mate with are also courted by residents and are thus not necessarily available. The availability of such potential partners—that is, the probability that any individual j of sex y with quality $q_{y,j} \geq q_y(\phi_{x,\mathrm{p}})$ is in the available state in equation (1)—is denoted $a_{y,\mathrm{p}}$. Second, if the mutant is less choosy than residents ($\phi_{x,\mathrm{m}} < \phi_{x,\mathrm{p}}$), it is willing to mate with two types of individuals: those that are also chosen by resident individuals of sex x, whose availability equals $a_{y,\mathrm{p}}$, and those whose quality ranges from $q_y(\phi_{x,\mathrm{m}})$ to $q_y(\phi_{x,\mathrm{p}})$ and are thus always available for mating with this mutant. Therefore, the mating probability $\mu_{x,\mathrm{m}}$ that a focal mutant individual i of sex x mates with an individual j of sex y is given by

$$\mu_{x,\mathrm{m}} = \begin{cases} (1 - \phi_{x,\mathrm{m}})a_{y,\mathrm{p}} & \text{if } \phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}, \\ (1 - \phi_{x,\mathrm{p}})a_{y,\mathrm{p}} + \phi_{x,\mathrm{p}} - \phi_{x,\mathrm{m}} & \text{if } \phi_{x,\mathrm{m}} < \phi_{x,\mathrm{p}}. \end{cases} \tag{2}$$

To characterize the mating probability $\mu_{x,\mathrm{p}}$ of a focal-sex resident whose quality is sufficient to mate with (i.e., with quality $q_{x,i} \geq q_x(\phi_{y,\mathrm{p}})$), we set $\phi_{x,\mathrm{m}} = \phi_{x,\mathrm{p}}$ in the previous equation. We obtain

$$\mu_{x,\mathrm{p}} = (1 - \phi_{x,\mathrm{p}})a_{y,\mathrm{p}}. \tag{3}$$

Calculating Mating Availabilities

To obtain the expressions for the mating availability $a_{y,\mathrm{p}}$, we need to compute, in each sex, the expected time spent by resident individuals in latency and to divide it by the expected lifespan. Because the states of the life cycle considered here forms a Markov chain where death is an absorbing state, the expected time spent in each state can be deduced from the transition probabilities between the nonabsorbing states of the life cycle (using $\mathbf{D}_x = (\mathbf{I} - \mathbf{L}_x)^{-1}$, with $\mathbf{I}$ the identity matrix and $\mathbf{L}_x$ from eq. [1]; see, e.g., Caswell 2001, p. 112). Assuming that individuals start their reproductive life available for mating, we can therefore deduce the average number of time steps d (first element of the matrix $\mathbf{D}_x$) that a focal-sex resident spends available for mating throughout its lifetime:

$$d = \frac{1}{(1 - s_x)(1 + (s_x\gamma\mu_{x,\mathrm{p}}l_x)/(1 - s_xl_x))}. \tag{4}$$

By dividing d by the expected lifespan $(1/(1 - s_x))$ and substituting $\mu_{x,\mathrm{p}}$ for the value obtained from equation (3), we obtain the probability $a_{x,\mathrm{p}}$, which represents the availability of residents of sex x whose quality is sufficient to mate (i.e., with quality $q_{x,i} \geq q_x(\phi_{y,\mathrm{p}})$). Substituting x for y, we similarly obtain the availability $a_{y,\mathrm{p}}$ for a resident of sex y whose quality is sufficient to mate (i.e., with quality $q_{y,i} \geq q_y(\phi_{x,\mathrm{p}})$) at a given time step. This leads to the following system of two equations with two unknowns:

$$\begin{cases} a_{y,\mathrm{p}} = \dfrac{1 - s_yl_y}{1 - s_yl_y + s_y\gamma(1 - \phi_{y,\mathrm{p}})a_{x,\mathrm{p}}l_y}, \\ a_{x,\mathrm{p}} = \dfrac{1 - s_xl_x}{1 - s_xl_x + s_x\gamma(1 - \phi_{x,\mathrm{p}})a_{y,\mathrm{p}}l_x}, \end{cases} \tag{5}$$

the solution of which yields

$$\begin{aligned} a_{y,\mathrm{p}} = \frac{1}{2s_x\gamma\phi_{x,\mathrm{p}}l_x(1 - s_yl_y)}\Big(& s_x\gamma l_x(s_yl_y(\phi_{x,\mathrm{p}} - \phi_{y,\mathrm{p}}) - \phi_{x,\mathrm{p}}) + (1 - l_x)(1 - l_y) - 1 \\ & - \big((s_x\gamma l_x(s_yl_y(\phi_{x,\mathrm{p}} - \phi_{y,\mathrm{p}}) - \phi_{x,\mathrm{p}}) + (1 - l_x)(1 - l_y) - 1)^2 \\ & + 4s_x\gamma\phi_{x,\mathrm{p}}l_x(1 - s_xl_x)(1 - s_yl_y)^2\big)^{1/2}\Big). \end{aligned} \tag{6}$$

Exchanging x and y in this expression gives $a_{x,\mathrm{p}}$.

As further computations require the expression of the availability of a mutant of sex x, we used the same approach to compute $a_{x,\mathrm{m}}$ and obtained

$$a_{x,\mathrm{m}} = \frac{1}{1 + s_x\gamma\mu_{x,\mathrm{m}}l_x/(1 - s_xl_x)}, \tag{7}$$

where $\mu_{x,\mathrm{m}}$ (a function of $a_{y,\mathrm{p}}$) is given by equation (2).

Computing the Expected Lifetime Fecundity of a Mutant

Let us define the lifetime fecundity of an individual i as the number of offspring it produces as a result of all mating events. We define the expected lifetime fecundity as the lifetime fecundity computed in a lineage of individuals. That is, the expected lifetime fecundity is computed over the distribution of contexts in which an individual of this lineage could be. To obtain this expected lifetime fecundity, we first compute the expected fecundity $F_x(q_{x,i})$ of an individual i of sex x given its quality $q_{x,i}$. Then we will compute its expectation over the distribution of quality of $q_{x,i}$. For these computations, we assume that the number of offspring obtained from any mating (i.e., the benefits per mating) depends neither on the number of previous matings nor on the number of offspring obtained from these previous matings. Therefore, by Wald's formula for optional stopping (e.g., Durrett 2010, p. 185), $F_x(q_{x,i})$ is the product of the individual's mating rate ($r_{x,i}$); its expected benefits per mating (integrated over the distribution of each partner's quality), which we call $b(q_{x,i})$; and its expected lifetime ($1/(1-s_x)$):

$$F_x(q_{x,i}) = r_{x,i}\ b(q_{x,i})\ \frac{1}{1-s_x}. \tag{8}$$

To compute the expected benefits per mating $b(q_{x,i})$, we assume the reproductive success of a mating pair to be equal to the mean of qualities of the two members of the pair, which makes it linear in the individual quality $q_{x,i}$ and in the expected quality $\bar{q}_y(i)$ of its mates:

$$b(q_{x,i}) = \frac{q_{x,i} + \bar{q}_y(i)}{2}. \tag{9}$$

That all individuals of sex y are assumed to have the same choosiness (see above) implies that among individuals with different $q_{x,i}$ above the threshold of sex y, $r_{x,i}$ is independent of $q_{x,i}$, and individuals of quality lower than the threshold never mate. Furthermore, $\bar{q}_y(i)$ differs among individuals with different choosiness but is identical among individuals with the same choosiness. Thus, the expected lifetime fecundity $F_{x,\mathrm{m}}$ among all mutants representing a mutant lineage can be written as the product of expected values of the different terms of $F_x(q_{x,i})$:

$$F_{x,\mathrm{m}} = r_{x,\mathrm{m}} b_{x,\mathrm{m}}\ \frac{1}{1-s_x}. \tag{10}$$

We will now detail expressions for these expectations.

The expected mating rate $r_{x,\mathrm{m}}$ of a focal-sex mutant equals its availability ($a_{x,\mathrm{m}}$) multiplied by the probability that it finds an individual of the other sex and mates with it at this time step ($s_x\gamma\mu_{x,\mathrm{m}}$). From equation (7), this is

$$r_{x,\mathrm{m}} = a_{x,\mathrm{m}} s_x \gamma \mu_{x,\mathrm{m}} = \frac{s_x\gamma\mu_{x,\mathrm{m}}}{1 + s_x\gamma\mu_{x,\mathrm{m}} l_x/(1-s_x l_x)}. \tag{11}$$

From the expression for $\mu_{x,\mathrm{m}}$ (eq. [2]), this becomes

$$r_{x,\mathrm{m}} = \begin{cases} \dfrac{s_x\gamma(1-\phi_{x,\mathrm{m}})a_{y,\mathrm{p}}}{1 + (s_x\gamma(1-\phi_{x,\mathrm{m}})a_{y,\mathrm{p}} l_x)/(1-s_x l_x)} & \text{if } \phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}, \\ \dfrac{s_x\gamma((1-\phi_{x,\mathrm{p}})a_{y,\mathrm{p}} + \phi_{x,\mathrm{p}} - \phi_{x,\mathrm{m}})}{1 + (s_x\gamma((1-\phi_{x,\mathrm{p}})a_{y,\mathrm{p}} + \phi_{x,\mathrm{p}} - \phi_{x,\mathrm{m}}) l_x)/(1-s_x l_x)} & \text{if } \phi_{x,\mathrm{m}} < \phi_{x,\mathrm{p}}. \end{cases} \tag{12}$$

The expected benefits per mating $b_{x,\mathrm{m}}$ of a mutant equals the mean of the respective terms in equation (9), which we rewrite $(q_{x,\mathrm{m}} + \bar{q}_y)/2$. Because other-sex resident individuals accept any focal-sex individual whose quality is higher than $q_x(\phi_{y,\mathrm{p}})$, the expected quality of the mutant $q_{x,\mathrm{m}}$ is the mean of the quality distribution in sex x restricted to the range between $q_x(\phi_{y,\mathrm{p}})$ and 1. This can be written

$$q_{x,\mathrm{m}} = \frac{\displaystyle\int_{q_x(\phi_{y,\mathrm{p}})}^{1} q f_x(q)\,\mathrm{d}q}{\displaystyle\int_{q_x(\phi_{y,\mathrm{p}})}^{1} f_x(q)\,\mathrm{d}q} = \frac{\displaystyle\int_{q_x(\phi_{y,\mathrm{p}})}^{1} q f_x(q)\,\mathrm{d}q}{1-\phi_{y,\mathrm{p}}}, \tag{13}$$

where $f_x(q)$ denotes the probability density of quality in sex x and where the denominator of the right-hand side results from the definition of $\phi_{y,\mathrm{p}}$ as the proportion of other-sex individuals whose quality is too low to be accepted as mates.

We need to distinguish two cases when computing the expected quality of the mutant's mate ($\bar{q}_y$). First, if the mutant is choosier than resident individuals of its sex ($\phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}$), it accepts any individual of sex y whose quality is higher than $q_y(\phi_{x,\mathrm{m}})$. In this case, the expected quality of its mates is thus the mean of the quality distribution in sex y restricted to the range between $q_y(\phi_{x,\mathrm{m}})$ and 1. Second, if the mutant is less choosy than resident individuals of its sex ($\phi_{x,\mathrm{m}} < \phi_{x,\mathrm{p}}$), it can mate with two types of individuals that differ in their availabilities: those whose quality ranges from $q_y(\phi_{x,\mathrm{m}})$ to $q_y(\phi_{x,\mathrm{p}})$ (which are always available) and those whose quality is higher than $q_y(\phi_{x,\mathrm{p}})$ (which are also courted by focal-sex resident individuals and thus are available with probability $a_{y,\mathrm{p}}$). In this case, the expected quality of the mates of the mutant is thus the mean of the quality distribution in sex y restricted to the range between $q_y(\phi_{x,\mathrm{m}})$ and 1, weighted by the respective availabilities of the two kinds of potential mates. By denoting $f_y(q)$ the density of the distribution of quality in sex y, we therefore have

$$\bar{q}_y = \begin{cases} \dfrac{\displaystyle\int_{q_y(\phi_{x,\mathrm{m}})}^{1} q f_y(q)\,\mathrm{d}q}{1-\phi_{x,\mathrm{m}}} & \text{if } \phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}, \\ \dfrac{\displaystyle\int_{q_y(\phi_{x,\mathrm{m}})}^{q_y(\phi_{x,\mathrm{p}})} q f_y(q)\,\mathrm{d}q + a_{y,\mathrm{p}}\int_{q_y(\phi_{x,\mathrm{p}})}^{1} q f_y(q)\,\mathrm{d}q}{(1-\phi_{x,\mathrm{p}})a_{y,\mathrm{p}} + \phi_{x,\mathrm{p}} - \phi_{x,\mathrm{m}}} & \text{if } \phi_{x,\mathrm{m}} < \phi_{x,\mathrm{p}}. \end{cases} \tag{14}$$

The general expression for the expected benefits per mating of the mutant is the average of the expressions for $q_{x,\mathrm{m}}$ and $\bar{q}_y$:

$$b_{x,\mathrm{m}} = \begin{cases} \dfrac{1}{2}\left(\dfrac{\int_{q_x(\phi_{y,\mathrm{p}})}^{1} qf_x(q)\,\mathrm{d}q}{1-\phi_{y,\mathrm{p}}} + \dfrac{\int_{q_y(\phi_{x,\mathrm{m}})}^{1} qf_y(q)\,\mathrm{d}q}{1-\phi_{x,\mathrm{m}}}\right) & \text{if } \phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}, \\ \dfrac{1}{2}\left(\dfrac{\int_{q_x(\phi_{y,\mathrm{p}})}^{1} qf_x(q)\,\mathrm{d}q}{1-\phi_{y,\mathrm{p}}} + \dfrac{\int_{q_y(\phi_{x,\mathrm{m}})}^{q_y(\phi_{x,\mathrm{p}})} qf_y(q)\,\mathrm{d}q + a_{y,\mathrm{p}}\int_{q_y(\phi_{x,\mathrm{p}})}^{1} qf_y(q)\,\mathrm{d}q}{(1-\phi_{x,\mathrm{p}})a_{y,\mathrm{p}} + \phi_{x,\mathrm{p}} - \phi_{x,\mathrm{m}}}\right) & \text{if } \phi_{x,\mathrm{m}} < \phi_{x,\mathrm{p}}. \end{cases} \tag{15}$$

In some particular cases, $b_{x,\mathrm{m}}$ take a simple form. For example, if the mutant is choosier than the resident (i.e., $\phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}$) and if quality is uniformly distributed in both sexes (i.e., $f_x(q)$ and $f_y(q)$ are the beta distribution with $\alpha_x = \beta_x = \alpha_y = \beta_y = 1$), then the expected quality of the focal-sex mutant lineage and of mates are, respectively, $(1+\phi_{y,\mathrm{p}})/2$ and $(1+\phi_{x,\mathrm{m}})/2$ (as $q(\phi) = \phi$ under the uniform distribution). In this case, the expected benefits per mating of the mutant is simply given by

$$b_{x,\mathrm{m}} = \frac{1}{2}\left(\frac{1+\phi_{y,\mathrm{p}}}{2} + \frac{1+\phi_{x,\mathrm{m}}}{2}\right). \tag{16}$$

Analytical Study of the Model

The full analytical methods are described in appendix A (apps. A, B are available online), but all key steps will be presented here. We first assessed the existence of a joint equilibrium for choosiness (i.e., a situation in which both sexes are simultaneously at an equilibrium for choosiness) and studied its convergence and evolutionary stability (sensu Eshel 1996) using standard methods from adaptive dynamics (Metz et al. 1996; Rousset 2004). A joint equilibrium, if it exists, corresponds to the joint solution (ϕ_x^*, ϕ_y^*) of the following system:

$$\begin{cases} \left.\dfrac{\partial F_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}}}\right|_{\phi_{x,\mathrm{m}} = \phi_{x,\mathrm{p}} = \phi_x^*} = 0, \\ \left.\dfrac{\partial F_{y,\mathrm{m}}}{\partial \phi_{y,\mathrm{m}}}\right|_{\phi_{y,\mathrm{m}} = \phi_{y,\mathrm{p}} = \phi_y^*} = 0. \end{cases} \tag{17}$$

We identified such a solution and studied the convergence stability in each sex before investigating the joint convergence stability. The study of the joint convergence stability required the additional assumption of independent mutational effects between females and males. We also assessed the joint evolutionary stability.

Second, we analyzed the effect of a change in a given biological or ecological variable z on the equilibrium for choosiness in sex x while assuming that other-sex choosiness remains fixed at the equilibrium value reached before the change happens (i.e., $\phi_{y,\mathrm{p}} = \phi_y^*$). This implies the study of the effect of a change in z on the mating rate and/or the expected benefits per mating near ϕ_x^* (but not on the expected lifetime because this latter is not related to choosiness). Indeed, at equilibrium we can rewrite equation (10) as

$$\begin{aligned} 0 &= \left.\frac{\partial_+ \ln(F_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{m}}}\right|_{\phi_{x,\mathrm{m}} = \phi_x^*} \\ &= \overbrace{\left.\frac{\partial_+ \ln(r_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{m}}}\right|_{\phi_{x,\mathrm{m}} = \phi_x^*}}^{R_x^*} + \overbrace{\left.\frac{\partial_+ \ln(b_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{m}}}\right|_{\phi_{x,\mathrm{m}} = \phi_x^*}}^{B_x^*}, \end{aligned} \tag{18}$$

where ∂_+ represents the right derivative (i.e., we consider the case $\phi_{x,\mathrm{m}} \geq \phi_{x,\mathrm{p}}$ in eqq. [12] and [15], but considering the other case leads to the same results as shown in app. A), R_x^* represents the relative change in mating rate in sex x at equilibrium, and B_x^* represents the relative change in expected benefits per mating at equilibrium. Biologically, the value of $-R_x^*$ quantifies the decrease in mating rate when choosiness increases, that is, the cost of being choosy. The value of B_x^* quantifies the increase in expected benefits per mating when choosiness increases, that is, the benefit of being choosy. We demonstrate in appendix A that when z influences the mating rate only (hereafter called z_r), (i) the effect of a change in z_r on the evolution of focal-sex choosiness can be deduced from the effect of z_r on R_x^* and (ii) this effect can also be deduced from the effect of z_r on the RST (i.e., the proportion of a lifetime that is devoted to searching for mates):

$$\operatorname{sgn}\left(\frac{\partial \phi_x^*}{\partial z_r}\right) = \operatorname{sgn}\left(\frac{\partial R_x^*}{\partial z_r}\right) = -\operatorname{sgn}\left(\frac{\partial \mathrm{RST}_x^*}{\partial z_r}\right). \tag{19}$$

The term $\partial\mathrm{RST}_x^*/\partial z_r$ (which is more compactly denoted ∂RST) corresponds to the sensitivity of the RST of sex x with respect to z_r, that is, the variation in the RST caused by the change in z_r while choosiness remains fixed in both sexes.

We also demonstrate in appendix A that when z influences the expected benefits per mating only (hereafter called z_b), the effect of a change in z_b on the evolution of focal-sex choosiness can be deduced from the effect of z_b on B_x^*:

$$\operatorname{sgn}\left(\frac{\partial \phi_x^*}{\partial z_b}\right) = \operatorname{sgn}\left(\frac{\partial B_x^*}{\partial z_b}\right). \tag{20}$$

In this situation, we did not find a simple metric such as ∂RST to summarize the effect of a change in z_b.

Third, we analyzed the effect of a change in z on the joint equilibrium for choosiness. Indeed, in the analysis used to obtain equations (19) and (20) we considered only the direct effect of z on ϕ_x^* while ϕ_y^* remains fixed, but z can also influence ϕ_y^*, and ϕ_y^* could in turn also influence ϕ_x^*. Formally, the total variation in the choosiness in both sexes following a change in z is described by the system

$$\begin{cases} \dfrac{\mathrm{d}\phi_x^*}{\mathrm{d}z} = \dfrac{\partial\phi_x^*}{\partial z} + \dfrac{\partial\phi_x^*}{\partial\phi_y^*}\dfrac{\mathrm{d}\phi_y^*}{\mathrm{d}z}, \\ \dfrac{\mathrm{d}\phi_y^*}{\mathrm{d}z} = \dfrac{\partial\phi_y^*}{\partial z} + \dfrac{\partial\phi_y^*}{\partial\phi_x^*}\dfrac{\mathrm{d}\phi_x^*}{\mathrm{d}z}, \end{cases} \tag{21}$$

where $\mathrm{d}\phi_x^*/\mathrm{d}z$ ($\mathrm{d}\phi_y^*/\mathrm{d}z$) represents the total variation in choosiness in sex x (y), which includes the effect of z on the choosiness of both sexes, and $\partial\phi_x^*/\partial\phi_y^*$ ($\partial\phi_y^*/\partial\phi_x^*$) is the variation in ϕ_x^* (ϕ_y^*) caused by a change in ϕ_y^* (ϕ_x^*) while z remains fixed.

We have already described the analysis of $\partial\phi_x^*/\partial z$ in terms of R_x^* and B_x^*, so the same goes for $\partial\phi_y^*/\partial z$ (swapping x and y). To study $\partial\phi_x^*/\partial\phi_y^*$, we would similarly consider the changes in R_x^* and B_x^* caused by a change in $\phi_{y,\mathrm{p}}$. However, no more definite analytical result could be obtained for $\partial\phi_x^*/\partial\phi_y^*$ and thus for the overall effect of z on the joint equilibrium for choosiness.

Numerical Analysis

Despite the simplicity of the life cycle we consider, some mathematical complexity emerges because of the joint evolution between sexes. As a consequence, some specific results cannot be analytically derived from the equations presented above. We thus complemented the analysis of our model by computing the numerical solution of our analytical equations using the software R (R Core Team 2015). To minimize the risk of missing exceptions to our main conclusions, we investigated a large number of parameter sets.

To study equilibrium conditions for choosiness in each sex, we considered the 16 possible combinations between four different quality distributions for females and males: uniform ($\alpha = \beta = 1$), bell curve ($\alpha = \beta = 10$), right skewed ($\alpha = 4$ and $\beta = 10$), and left skewed ($\alpha = 10$ and $\beta = 4$). For each of these 16 cases, we generated two tables of 10^5 combinations of the other parameters (γ, s_x, s_y, l_x, and l_y), one for which values for each parameter were randomly drawn from a uniform distribution between 0 and 1 (which we call the continuous tables) and the other for which all combinations of values among the following range were considered: 0.001, 0.1, 0.5, 0.6, 0.7, 0.8, 0.9, 0.95, 0.99, and 0.999 (which we call the discrete tables). In total, we therefore analyzed 3.2×10^6 (i.e., $16 \times 10^5 \times 2$) different parameter sets. We also used the continuous tables to study the joint evolution of choosiness between sexes.[1]

Finally, we studied the predictive power of ∂RST numerically. To do so, we first randomly drew 10^6 pairs of parameter sets differing in the value of only one parameter from each of the 16 discrete tables. For each pair of parameter sets we computed the partial variation in choosiness, the total variation in choosiness, and ∂RST. Second, we then randomly drew 10^6 pairs of parameter sets (which could here potentially differ in γ, s_x, s_y, l_x, and l_y) from the same discrete tables. We computed again the partial variation in choosiness, the total variation in choosiness, and ∂RST for all these pairs. We were therefore able to determine the predictive power of ∂RST when only one parameter changes as well as when all parameters are free to change at the same time, using 1.6×10^7 (i.e., 16×10^6) different parameter sets in each case. The numerical analysis of the predictive power of ∂RST was not replicated using the continuous table, as most of the parameter space sampled in the continuous tables does not lead to situations of mutual mate choice and unilateral choice situations have already been analyzed in Etienne et al. (2014).

Results

Scope

We will indicate below whether a given result has been obtained analytically (hereafter labeled as an analytical result), whether it has been obtained for the complete numerical exploration (numerical result), or whether it has been obtained numerically and corresponds to an effect found in only part of the parameter space (restricted result). Numerical results are consistent across the entire numerical exploration and are likely to be as general as our analytical derivations, that is, true within the scope of the assumptions made in this model.

Evolution of Mutual Mate Choice

Result 1: There is always one and only one convergence stable and evolutionary stable (joint) equilibrium for choosiness in both unilateral choice and mutual mate choice (numerical result). We numerically solved equilibrium conditions (17) for the 3.2×10^6 parameter sets and found that there is always one single combination of choosiness that satisfies the equilibrium condition (numerical result). For these 3.2×10^6 equilibria we found only two outcomes for both convergence and evolutionary stability. First, when the equilibrium is characterized by a null choosiness in at least one sex ($\phi_x^* = 0$ and/or $\phi_y^* = 0$), the values of choosiness at equilibrium are the same as in the model of Etienne et al. (2014), in which the choosiness of the nonfocal sex was constrained to be null. In this case, the equilibrium is always convergence and evolutionarily stable (numerical result). Second,

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[1] The procedure is described in the legend of figure 3.

we found parameter settings under which choosiness is nonnull at equilibrium in both sexes ($\phi_x^* \neq 0$ and $\phi_y^* \neq 0$), and such equilibria are always jointly convergence stable and joint evolutionary stable (numerical result). Individual-based simulations for numerous parameter settings confirm this result (not shown).

Result 2: The fundamental trade-off of mate choice generates a high diversity of combinations of focal-sex and other-sex choosiness at equilibrium (restricted result). Cases of mutual mate choice at equilibrium ($\phi_x^* > 0$ and $\phi_y^* > 0$) are highly diverse within our numerical exploration, ranging from very low (e.g., $\phi^* = 0.01$) to very high (e.g., $\phi^* = 0.7$) choosiness in both sexes, with all possible intermediates (e.g., see fig. 1).

Result 3: Within our numerical exploration, mutual mate choice occurs at equilibrium only when both latency and survival rates are high in the two sexes (numerical result). Everything else being equal, the choosier sex is the sex with the (i) higher latency (figs. 1, B1; figs. A1–A3, B1–B3 are available online), (ii) higher survival (figs. 2, B2), or (iii) lower variance in quality (figs. B1–B3). The evolution of nonnull choosiness in a sex requires the latency rate in this sex, the survival rate in this sex, and the variance in other-sex quality to be nonnull (numerical result). However, fulfilling these conditions in both sexes is not sufficient to observe mutual mate choice at equilibrium. Indeed, the latter outcome is obtained only when both latency and survival rates approach 1 in the two sexes (see figs. 1, 2, B1, B2). Once this criterion is satisfied, the level of mutual choosiness at equilibrium is also influenced by other parameters. In particular, high choosiness in both sexes is favored when the encounter rate and/or variance in the quality of both sexes is high and/or the mean quality of both sexes is low (figs. B1–B3).

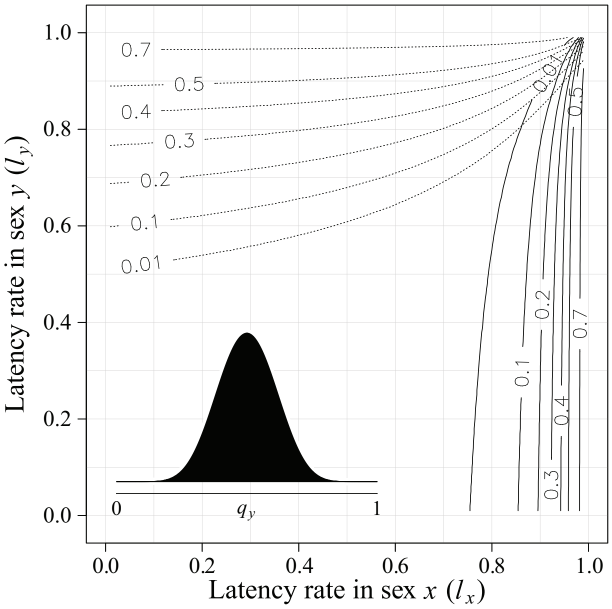

Figure 1: Choosiness at equilibrium in both sexes as a function of latency rates. Contour lines depict the value of choosiness at equilibrium in sex x (solid lines) and sex y (dotted lines). In this plot, the distribution of quality in sex y ($\alpha_y = \beta_y = 10$) is represented in the bottom-left corner of the plot, whereas it is uniform in sex x ($\alpha_x = \beta_x = 1$). This explains why there is an asymmetry between sexes. Other distributions are shown in figure B1. The encounter and survival rates were chosen to favor the evolution of mutual mate choice ($\gamma = s_x = s_y = 0.999$).

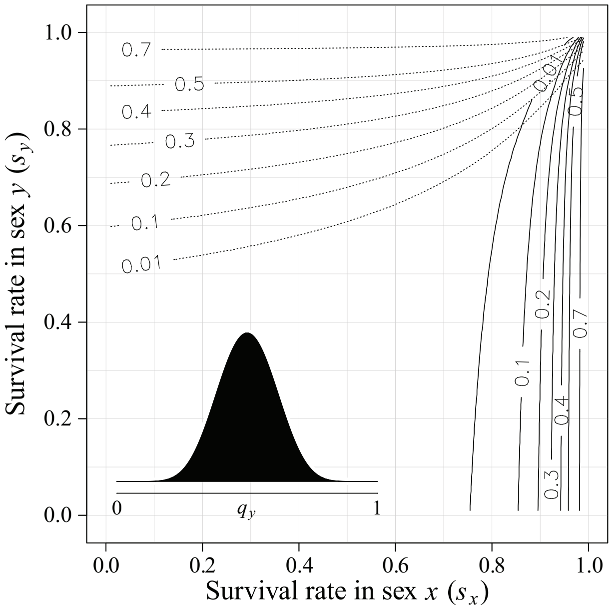

Figure 2: Choosiness at equilibrium in both sexes as a function of survival rates. See the legend of figure 1 for details. The encounter and latency rates were chosen to favor the evolution of mutual mate choice ($\gamma = l_x = l_y = 0.999$).

Joint Evolution of Choosiness

Result 4: An increase in choosiness in one sex decreases both the cost and the benefit of being choosy in the other sex (analytical result). From the definition of R_x^* (see eq. [18]) and the expression for $r_{x,\mathrm{m}}$ (see eq. [12]), the effect of a change in other-sex choosiness (i.e., $\phi_{y,\mathrm{p}}$) on the cost R_x^* of being choosy is

$$\frac{\partial R_x^*}{\partial \phi_{y,\mathrm{p}}} = \frac{\partial_+\left(-\left(1+s_x\gamma(1-\phi_{x,\mathrm{m}})a_{y,\mathrm{p}}l_x/(1-s_xl_x)\right)(1-\phi_{x,\mathrm{m}})\right)^{-1}}{\partial \phi_{y,\mathrm{p}}}\Bigg|_{\phi_{x,\mathrm{m}}=\phi_x^*}. \tag{22}$$

When $\phi_{y,\mathrm{p}}$ increases, fewer individuals of the focal sex mate, which increases the availability $a_{y,\mathrm{p}}$ of other-sex individuals whose quality is sufficient to mate. Thus, the partial derivative of R_x^* with respect to $\phi_{y,\mathrm{p}}$ is also positive (analytical result). Therefore, an increase in $\phi_{y,\mathrm{p}}$ selects for higher focal-sex choosiness via its effect on the relative change in mating rate (see eq. [19]). Simply put, the increasing availability in sex y, as a consequence of the higher choosiness in this sex, reduces the competition among individuals of sex x for access to other-sex individuals. Thereby the cost of being choosy in sex x reduces, which is why $\phi_{y,\mathrm{p}}$ here has a positive effect on ϕ_x^*.

From the definition of B_x^* (see eq. [18]), the effect of a change in other-sex choosiness (i.e., $\phi_{y,\mathrm{p}}$) on the benefit B_x^* of being choosy can generally be written as

$$\frac{\partial B_x^*}{\partial \phi_{y,\mathrm{p}}} = \frac{1}{b_{x,\mathrm{m}}^2}\left(b_{x,\mathrm{m}} \frac{\partial_+^2 b_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}} \partial \phi_{y,\mathrm{p}}} - \frac{\partial_+ b_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}}} \frac{\partial_+ b_{x,\mathrm{m}}}{\partial \phi_{y,\mathrm{p}}} \right)\Bigg|_{\phi_{x,\mathrm{m}} = \phi_x^*} . \tag{23}$$

The mixed derivative of $b_{x,\mathrm{m}}$ vanishes (from eq. [15]), so this equation reduces to

$$\frac{\partial B_x^*}{\partial \phi_{y,\mathrm{p}}} = -\frac{1}{b_{x,\mathrm{m}}^2}\left(\frac{\partial_+ b_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}}} \frac{\partial_+ b_{x,\mathrm{m}}}{\partial \phi_{y,\mathrm{p}}} \right)\Bigg|_{\phi_{x,\mathrm{m}} = \phi_x^*} . \tag{24}$$

When $\phi_{y,\mathrm{p}}$ increases, the mean quality of focal-sex individuals whose quality is sufficient to mate increases (see eq. [13]), and thus the expected benefits per mating $b_{x,\mathrm{m}}$ increases as well (see eq. [15]). Moreover, $b_{x,\mathrm{m}}$ also increases with $\phi_{x,\mathrm{m}}$ (see eq. [15]). Both derivatives in the right-hand term of equation (24) are thus positive. This implies that the derivative of B_x^* with respect to $\phi_{y,\mathrm{p}}$ is negative (analytical result) and that an increase in $\phi_{y,\mathrm{p}}$ selects for lower focal-sex choosiness via its effect on the relative change in expected benefits per mating (see eq. [20]). Simply put, when choosiness increases in sex y, the expected quality of individuals that can qualify as mates increases in sex x. This reduces the benefit of being choosy in sex x, which implies that $\phi_{y,\mathrm{p}}$ would have a negative effect on ϕ_x^*.

Result 5: An increase in choosiness in one sex does not necessarily prevent the evolution of choosiness in the other (restricted result + analytical result). We have found numerically that when the latency rate is low (<0.7) in both sexes, the negative effect of ϕ_y^* on ϕ_x^* is always larger than its positive effect (numerical result; fig. 3). However, the reverse can happen when latency is high in both sexes (restricted result), which corresponds to cases of mutual mate choice at equilibrium (see fig. 1). In this latter situation, parameter values determine which of the two antagonistic effects of ϕ_y^* on ϕ_x^* can outweigh the other (fig. 3).

Furthermore, had we assumed the reproductive success of a mating pair to be equal to the product of qualities of the two members of the pair ($b_{x,\mathrm{m}} = q_{x,\mathrm{m}}\bar{q}_y$) instead of its average (eq. [9]), then an increase in other-sex choosiness would have always selected for a higher choosiness in the focal sex (analytical result). Indeed, instead of equation (24), equation (23) would then lead to

$$\begin{aligned} \frac{\partial B_x^*}{\partial \phi_{y,\mathrm{p}}} &= -\frac{1}{(q_{x,\mathrm{m}}\bar{q}_y)^2}\left(\frac{\partial_+(q_{x,\mathrm{m}}\bar{q}_y)}{\partial \phi_{x,\mathrm{m}}} \frac{\partial_+(q_{x,\mathrm{m}}\bar{q}_y)}{\partial \phi_{y,\mathrm{p}}} \right)\Bigg|_{\phi_{x,\mathrm{m}} = \phi_x^*} \\ &= -\frac{1}{\bar{q}_y{}^2}\left(\frac{\partial_+ \bar{q}_y}{\partial \phi_{x,\mathrm{m}}} \frac{\partial_+ \bar{q}_y}{\partial \phi_{y,\mathrm{p}}} \right)\Bigg|_{\phi_{x,\mathrm{m}} = \phi_x^*} \\ &= 0, \end{aligned} \tag{25}$$

because $q_{x,\mathrm{m}}$ is not a function of $\phi_{x,\mathrm{m}}$ (see eq. [13]) and $\bar{q}_y$ is not a function of $\phi_{y,\mathrm{p}}$ (see eq. [14]). Therefore, the negative effect caused by the influences of $\phi_{y,\mathrm{p}}$ on the benefit of being choosy vanishes, and other-sex choosiness would thus no longer exert a negative effect on focal-sex choosiness. Under this alternative assumption, an increase in $\phi_{y,\mathrm{p}}$ would thus always lead to an increase in ϕ_x^* (analytical result).

∂RST and the Effect of a Change in Mating Rate on the Evolution of Choosiness

Result 6: ∂RST in one sex predicts the evolutionary change in choosiness in this sex so long as the change in mating rate is triggered by variation in a single parameter (numerical result). If a change z_r in a given biological or ecological variable is a function of only one of the parameters that affect the mating rate (i.e., l_x, l_y, s_x, s_y, or γ), then we have found that the partial and total variations in choosiness were always of the same sign for all 1.6×10^7 combinations of parameters investigated (numerical result). This is because in such cases, the partial variation in focal choosiness triggered by z_r outweighs the variation in focal choosiness caused by a change in other-sex choosiness. In these circumstances, computing ∂RST in a sex is thus sufficient to predict the independent effect of any of these parameters on the evolution of choosiness in this sex even if this parameter also influences the evolution of choosiness in the other sex. As a consequence, the effects of latency, survival, and encounter rates are qualitatively similar between our mutual mate choice model and the one of Etienne et al. (2014), which neglected the effect of a change in other-sex choosiness. Specifically, when latency increases in a sex, ∂RST is negative for this sex (because lifetime is constant) and positive for the other one (because available mates are rarer), leading to higher choosiness in the sex for which latency increases and lower choosiness in the other (fig. 1). The effect of survival is identical to the effect of latency (fig. 2). Indeed, the proportion of a lifetime spent in latency increases with survival rate in both sexes. This is because when an individual dies, it is always replaced by an available individual, regardless of whether the deceased was in latency. Finally,

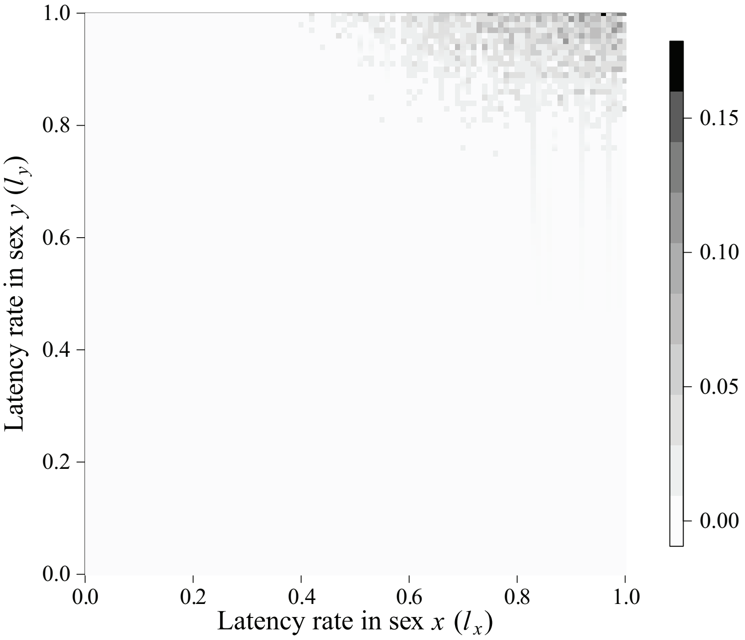

Figure 3: Effect of other-sex choosiness. For each combination of latency rates in sexes x and y, the grayscale indicates the frequency of cases for which an increase in choosiness in sex y has a resulting positive effect on choosiness in sex x. This has been obtained by computing the derivative of choosiness in sex x at equilibrium (ϕ_x^*) with respect to choosiness in sex y at equilibrium (ϕ_y^*) in 1.6×10^6 cases exploring the whole range of possible parameter values (using the continuous table; see "Numerical Analysis"). To measure frequencies, the continuous variation in latency was discretized into 101 bins for each axis. The lack of smoothness is explained by the fact that numerical computations are performed for parameters randomly drawn from a uniform distribution. The frequency in each cell of the figure is therefore measured on the variable number of numerical computations (mean ± SD = 156.8 ± 49.5) falling within the corresponding bin for latencies.

when the encounter rate increases, the ∂RST of both sexes is negative, which selects for higher choosiness in both sexes (fig. 4).

Result 7: When several parameters vary, the predictive power of ∂RST is reduced (restricted result). If z_r is a function of more than one parameter, then ∂RST does not always predict the total variation in choosiness. Indeed, when several parameters affecting the mating rate vary simultaneously, we have numerically found that the variation in choosiness caused by the change in other-sex choosiness can outweigh the partial variation in focal choosiness. Cases where ∂RST loses its predictive power are rare within the parameter space investigated (~0.09%, or 14,847 of the 1.6×10^7 combinations of parameters sampled in the discrete tables; see "Numerical Analysis"; fig. 5). The cases for which ∂RST fails to predict the evolutionary change in choosiness are not associated with particular values of the parameters. We found, however, that ∂RST can fail when its value is very low (i.e., ≤ 0.095) in one sex (this is the case for 11,720 of the 14,847 erroneous predictions). It can also fail when both ∂RSTs are large (i.e., >0.095). The only structure we have detected in this latter case is that 95% of erroneous predictions happen when the absolute value of ∂RST in the focal sex is lower that that in the other sex.

Discussion

In this article, we have modeled the direct selection of choosiness when mate choice is allowed to evolve in both sexes. We did so by considering that mate choice is solely associated with direct benefits in terms of increased mate quality and with costs in terms of reduced mating rate. We have neglected all other selection pressures (e.g., indirect benefits, energy and predation costs induced by mate search, sexual conflicts) and all other evolutionary forces (e.g., drift, migration, recombination). Under these conditions, we derived the complete analytical expression of individual fecundities and obtained most of our results from numerical evaluation of our analytical expressions. Opting for a numerical analysis was necessary due to the complexity of our analytical results. This procedure allows for the investigation of the properties of a model under a much larger number of parameter values than when analytical results are lacking. However, a numerical analysis is necessarily less complete than a full analytical study because one cannot

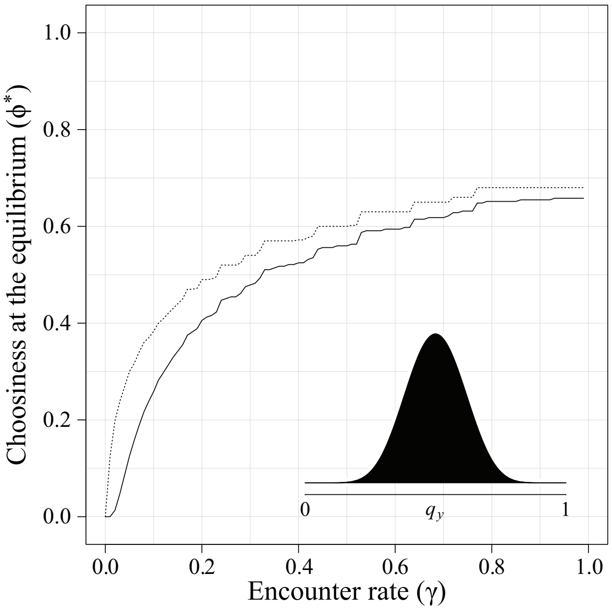

Figure 4: Choosiness at equilibrium in both sexes as a function of encounter rate. See the legend of figure 1 for details. The latency and survival rates were chosen to favor the evolution of mutual mate choice ($l_x = l_y = s_x = s_y = 0.999$). Numerical evaluation of the selection gradient was often affected by numerical singularities, in which case the gradient was computed only for a coarse grid of choosiness values, which leads to the stepwise aspect of the lines.

a priori exclude the possibility that any identified pattern may fail if other parameter values were used. While there is no escape from this general limitation of numerical studies, our analysis explored the entire range of possible values for the life-history parameters at a fine scale. For clarity, we will therefore label each specific result, as in the previous section, as analytical, numerical, or restricted depending on whether it is always true within our set of assumptions, true in our complete numerical exploration, or true for part of the parameter space, respectively.

With these caveats in mind, we have obtained three main results. First, the trade-off between the decrease in mating rate and the increase in benefits per mating (i.e., the fundamental trade-off of mate choice) is sufficient to generate the evolution of a high diversity of stable combinations of choosiness between sexes at equilibrium (results 1 and 2 in "Results"). Within this diversity, mutual mate choice is always characterized by high survival and latency in both sexes but is also influenced by other life-history traits (result 3). Second, the evolution of choosiness in a sex can either be promoted or be limited by the evolution of choosiness in the other sex (results 4 and 5). Third, ∂RST (i.e., the change in the proportion of a lifetime devoted to searching for mates caused only by variation in any biological or ecological parameter affecting the mating rate of individuals while choosiness is fixed) correctly predicts the evolution of choosiness in response to a change in mating rate in many but not all cases of mutual mate choice (results 6 and 7). We now discuss these results in more detail before examining some key assumptions of our model.

Life History, through Its Effect on the Fundamental Trade-Off of Mate Choice, Can Select for Various Stable Combinations of Choosiness between Sexes

Each equilibrium identified during our numerical exploration always corresponds to a single combination of female and male convergence stable and evolutionary stable choosiness (result 1: numerical). Depending on the values of the parameters (encounter rate, sex-specific latency rates, sex-specific survival rates, and sex-specific distributions of quality), it is possible to observe a high diversity of values of choosiness at equilibrium in each sex. In particular, all of the following combinations can be attained: neither, one, or both sexes are choosy. Cases of mutual mate choice are very diverse, with choosiness ranging from very low (e.g., 1% of other-sex individuals are always rejected) to very high (e.g., 70% of other-sex individuals are always rejected) values in each sex. The relatively few empirical studies adopting such a quantitative view of mate choice simultaneously in both sexes have accordingly revealed several cases of asymmetric mutual mate choice that were previously documented as unilateral choice (e.g., Rowland 1982; Kraak and Bakker 1998; Sæther et al. 2001; Werner and Lotem 2003; Aquiloni and Gherardi 2008).

That a great variety of mutual mate choice situations emerges during the analysis of our model leaves open the possibility that direct selection may be sufficient to explain the evolution of mutual mate choice in situations that other studies have interpreted as the result of more complex mechanisms (see, e.g., Ihara and Aoki 1999; Servedio and Lande 2006; Hooper and Miller 2008; South et al. 2012). In our case, direct selection is expressed purely in terms of differential fecundity emerging from differences in the number or identity of mates, that is, sexual selection (sensu Andersson 1994, p. 7). Therefore, our model challenges the prediction that for mutual choice to evolve, one necessary condition is that breeding imposes a large mortality cost on either males or females (Kokko and Johnstone 2002). Taken together, our model and those of others suggest that there are several evolutionary pathways that can lead to mutual mate choice (pre- or postmating) in nature.

In our model, high latency and survival rates in both sexes are necessary for the evolution of mutual mate choice (result 3: numerical). Both parameters exert the same effect here because the fraction of a lifetime spent in latency is positively related to both latency and survival rates (see re-

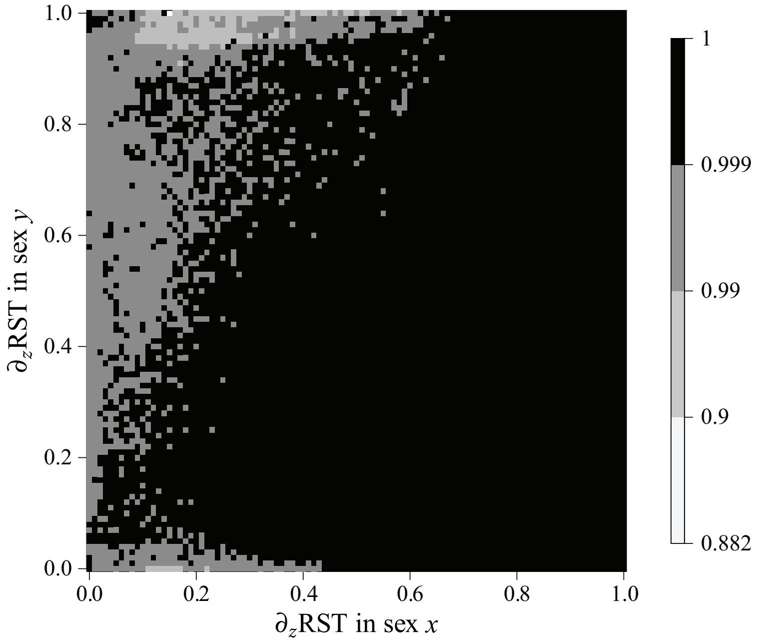

Figure 5: Predictive power of the sensitivity of the relative searching time (∂RST). For each combination of the absolute values of ∂RST in both sexes, the grayscale indicates the frequency of cases for which the sign of ∂RST in sex x correctly predicts the direction of selection of choosiness in this sex. This has been obtained by computing ∂RST and the total variation in choosiness in both sexes for 1.6×10^7 combinations of parameter settings exploring the whole range of possible parameter values (derived from the discrete tables; see "Numerical Analysis"). As for latency in figure 3, ∂RST was discretized into 101 bins for each axis. The minimal predictive power computed within a cell is 88.2%. A variable number of computations falls within each cell, which explains the lack of smoothness: the average number of numerical computations for ∂RST falling within a bin is 1,568 ± 3,055 (the SD exceeds the mean because the distribution is right skewed).

sult 6). When the time spent in latency increases in a sex, the relative proportion of a lifetime that individuals spend searching for mates decreases in this sex but increases in the other (fig. 1; see also Etienne et al. 2014). This outcome, in turn, selects for higher levels of choosiness in this sex and for lower levels of choosiness in the other sex (see eq. [19]). The joint evolution of choosiness between sexes may then intervene (see the next section), but our results suggest that—irrespective of this joint evolution—the negative feedback that choosiness in the other sex exerts on the focal choosiness is no longer sufficient to lead to an absence of choice in the other sex when latency and survival rates are sufficiently high in each sex.

The latency state in our model can result from any process that prevents individuals from remating instantly, which includes parental investment. Therefore, our findings are consistent with the many empirical studies showing evidence for mutual mate choice in species with biparental care (Amundsen 2000; Kraaijeveld et al. 2007). Our findings are also consistent with the theoretical studies that showed that a high level of parental investment in both sexes promotes the evolution of mutual choosiness (Parker 1983; Crowley et al. 1991; Owens and Thompson 1994; Johnstone et al. 1996; Kokko and Johnstone 2002). Nonetheless, our definition of latency also implies biological situations where latency is high in both sexes for reasons other than high parental investment in both sexes. For example, we predict mutual mate choice to evolve in species in which males suffer high spermatic depletion (because of sperm competition that leads them to produce a high amount of sperm per copulation) and females invest a lot in offspring. This situation may explain why in some lekking species, such as the great snipe *Gallinago media* (Sæther et al. 2001) and the cichlid fish *Astatotilapia flaviijosephi* (Werner and Lotem 2003), choice is mutual despite the lack of paternal care. This prediction contrasts with the one made by Kokko and Johnstone (2002), who argued that parental care per se and not just mating latency is needed for mutual mate choice to evolve. However, as we shall see later, their assumption about the mating decision rule makes the evolution of mutual mate choice more difficult in their case.

The importance of the duration of latency does not preclude other parameters from influencing the level of mutual choosiness (result 3: numerical). Indeed, provided that latency and survival rates are high in both sexes, we have obtained predictions similar to those emerging from other theoretical work: high mutual choosiness is favored by a high encounter rate (Crowley et al. 1991; Kokko and Johnstone 2002), by a high variance in the quality of both sexes (Parker

1983; Owens and Thompson 1994; Johnstone et al. 1996; Kokko and Johnstone 2002; Härdling et al. 2008), or by low mean quality of both sexes (Gowaty and Hubbell 2009).

Increase in Choosiness in One Sex Does Not Necessarily Prevent the Evolution of Mutual Mate Choice

In addition to the role played by the aforementioned parameters, we confirmed that the emergence of mutual mate choice can be promoted or constrained by the influence that selection for choosiness in one sex exerts on selection for choosiness in the other (results 4 and 5). Previous work has suggested that the apparent lack of mutual choice in many organisms occurs because an increase in other-sex choosiness may reduce mating opportunities for individuals of the focal sex and would thereby make them less choosy (Kokko and Johnstone 2002). It is indeed true that if other-sex choosiness does increase, mating opportunities are reduced for low-quality individuals of the focal sex. However, mating opportunities simultaneously increase for high-quality individuals of this sex. Whether this impedes the evolution of mutual mate choice is therefore related to the relative extent to which low-quality and high-quality individuals contribute to the gene pool.

In our model, choosiness is expressed as a fixed threshold that is identical for all individuals of a sex. Therefore, we assumed that individuals showing a quality lower than the threshold to be chosen by the other sex do not reproduce at all. As a consequence, only high-quality individuals contribute to the next generation, and as such they actually benefit from improved mating opportunities. Formally, when other-sex choosiness increases, the cost of being choosy (i.e., the relative decrease in mating rate with choosiness) decreases in the focal sex, which eases the evolution of mutual mate choice in our model (result 4: analytical). Kokko and Johnstone (2002) assumed a different mating decision rule. They considered choosiness to be condition dependent (i.e., related to the quality of the individual that chooses), which allows low-quality individuals to pass on their genes to the next generation. Then the authors observed that the selection pressure caused by the decrease in mating opportunities for low-quality individuals outweighs that caused by the increase in mating opportunities for high-quality individuals, thereby impeding the evolution of mutual mate choice. Therefore, differences between the outcomes of our model and that of Kokko and Johnstone (2002) suggest that the occurrence of mutual mate choice may be strongly influenced by the type of decision rule individuals use to choose their mates. Errors in the assessment of individual quality—which we neglected—can be considered equivalent to an alternative decision rule (e.g., if a Gaussian error is considered around the choosiness defining the threshold, the expected mating decisions will correspond to a sigmoid depicted by the cumulative density function of a normal distribution). Empirical knowledge of mating decision rules (e.g., Kirkpatrick et al. 2006; Courtiol et al. 2010; Castellano et al. 2012; Reinhold and Schielzeth 2015) therefore appears crucial for the implementation of realistic models of the evolution of choosiness.

An increase in choosiness in the other sex not only decreases the cost of being choosy for the focal sex, it also decreases its benefit of being choosy (result 4: analytical). Indeed, we found that an increase in other-sex choosiness has a positive effect on the mean quality of individuals qualifying as mates in the focal sex, which in turn leads to a reduction of the benefit of being choosy (i.e., the relative increase in benefits per mating with choosiness) in this focal sex. In most of the numerical cases we have explored, this negative effect on the benefit of being choosy is larger than the cost (result 5: restricted), which leads choosiness to decrease in one sex when it increases in the other sex.

Nevertheless, the opposite result can be observed, in particular when latency is high in both sexes, that is, when both sexes are expected to be choosy (result 5: restricted). This negative effect of other-sex choosiness on the benefit of being choosy also rests on the questionable assumption that the reproductive success of a mating pair is an additive function of female and male qualities (see eq. [16]). Kokko and Johnstone (2002) showed that certain forms of nonadditive parental care could facilitate the evolution of mate choice. Here we have shown that this effect is not necessarily limited to care per se but can generally emerge from how the fecundity of a pair is determined by the qualities of the two mates. For example, if we consider a multiplicative form for reproductive success instead of an additive one, other-sex choosiness no longer reduces the benefit of being choosy in the focal sex (result 5: analytical). Under such an assumption, other-sex choosiness would always promote the evolution of choosiness in the focal sex in our model.

In sum, in terms of joint evolution of choosiness between sexes, the balance between the mechanism selecting for an increase in choosiness and the mechanism selecting against it are strongly dependent on the decision rule, on how the qualities of mates shape the fecundity of the pair, and on parameter values. Therefore, the only reliable predictions we can propose at this stage are that (i) the evolution of choosiness in one sex can trigger selection pressures both for and against the evolution of choosiness in the other sex and (ii) the relative effects of these forces are strongly related to biological and ecological factors (result 4: analytical).

Power of ∂RST as a Predictor for the Evolution of Choosiness Must Be Assessed Empirically

We assessed whether one can qualitatively predict an evolutionary change in choosiness triggered by any factor z_r

influencing the mating rate of individuals. We found that this is indeed the case, but only under specific conditions. Etienne et al. (2014) showed that one can qualitatively predict an evolutionary change in choosiness triggered by any factor z_r that influences the mating rate of individuals when the other sex is constrained to be indiscriminate. They analytically found that the sign of this change was opposed to the sign of ∂RST (i.e., the variation in the proportion of a lifetime devoted to searching for mates at fixed choosiness). Here we have assessed the power of this prediction when mate choice is free to evolve in both sexes. When z_r corresponds to a modification of a single parameter in our model, we confirmed this full predictive power of ∂RST in the case of joint evolution of choosiness (result 6: numerical). However, when z_r simultaneously affects several parameters, this is no longer true, as computing ∂RST in a sex fails to predict the resulting evolutionary change in choosiness in this sex in a few cases of our numerical exploration (result 7: restricted). We did not identify any obvious relationship between the predictive power of ∂RST and the location in the parameter space, but failures occur either when ∂RST is very small in one sex or when the absolute value of ∂RST in the focal sex is much larger than that in the other sex. Importantly, whether the few numerical cases in which ∂RST fails (~1/1,000 trials) represent widespread biological situations is an empirical question—the answer to which shall determine how useful ∂RST really is.

In cases where ∂RST accurately predicts the joint evolutionary changes in choosiness, the use of this metric rests on the same three main assumptions as in the model of Etienne et al. (2014): (i) choosiness does not affect survival, (ii) choosiness does not affect the time spent in one latency period, and (iii) z_r does not affect the distribution of mate quality regardless of the form of the latter. Despite these limitations, we believe that ∂RST remains superior to all alternative metrics proposed to date. In particular, Kokko and Monaghan (2001) have clearly demonstrated the limitations of the widely used operational sex ratio (OSR). They have suggested using a metric that reflects the cost of breeding (C) instead (see also Kokko and Johnstone 2002). Although they did so while relaxing our first assumption (i.e., choosiness does not affect survival), the predictive power of their metric remains poor: an increase in C appears to be a necessary but insufficient condition for the evolution of choosiness in either sex (e.g., insufficient when C varies from 10^{-3} to 10^{-2} in figure 4 of Kokko and Johnstone [2002]; see also Etienne et al. [2014] for an example where C produces an erroneous prediction). This weakness emerges from the fact that C, as with the OSR in many models, is considered fixed (i.e., it depends only on the parameter setting) and does not covary with the evolution of choosiness. Our metric, ∂RST, does not suffer from this limitation (i.e., it is internally consistent sensu Houston and McNamara 2005). Therefore, ∂RST captures the complex influence of choosiness on the availability of individuals that qualify as potential partners, which shapes both the benefits and the costs of choice. While additional work may allow for deriving the expression of ∂RST or a related metric while relaxing the first and second assumptions, a big challenge stems from relaxing the third assumption: as for alternative metrics, the predictive power of ∂RST rests on the hypothesis that benefits per mating (and thus the distributions of quality) remain unchanged while z_r varies. It would therefore be relevant to identify a predictor that would simultaneously include variations in mating rate and benefits per mating.

In the absence of further developments, ∂RST, albeit imperfect, remains the best available predictor of the evolution of choosiness by direct selection. In particular, this metric combines three main benefits (for details, see Etienne et al. 2014): (i) it holds across a wide range of mating systems, (ii) it encompasses many alternative variables proposed to date to explain the evolution of choosiness (i.e., the time invested in breeding, the adult sex ratio, the OSR, and the cost of breeding), and (iii) it can be used empirically to infer qualitative differences in choosiness.

We therefore encourage the use of ∂RST to study the evolution of choosiness in nature in both unilateral and mutual mate choice situations. The guidelines proposed in Etienne et al. (2014) still apply when mate choice is potentially present in both sexes. That is, one should use any proxy that could give an estimation of RST (e.g., the time spent sampling mates or courting) and measure this proxy before and after the variable considered has changed (naturally or during the course of an experiment). Then the difference between the two estimations of RST provide the estimation of ∂RST. The main empirical constraint is that the first measurement has to be done in a situation in which choosiness is as close as possible to its evolutionary equilibrium in both sexes and the second has to be done before choosiness changes (because of selection or phenotypic plasticity). Such an experimental protocol aims at predicting the evolution of choosiness in the face of environmental change. If an increase in choice is predicted in one or both sexes, it could also be useful to determine whether the sexual selection predicted to act on mate choice will be strong enough to overcome the influence of other potentially conflicting selection pressures as well as that of other evolutionary forces. One possibility is to couple the experimental design outlined above with an empirical study in which the environment is maintained constant, the choosiness manipulated, and the mating and reproductive success recorded. Analyzing the outcome of these experiments using the framework of Bateman's gradients (e.g., Jones 2009; Anthes et al. 2010) should allow the inference of the amount of sexual selection acting on choice in such cases.

Our work should also stimulate empirical perspectives that do not involve ∂RST. In particular, a precise characterization of the fundamental trade-off of choice in different species would allow the quantification of the direct cost of being choosy and thereby the assessment of the importance of this trade-off. We are well aware that the empirical assessment of any trade-off is notoriously difficult; however, as has been shown with respect to other questions, it is generally worth pursuing (Stearns 1989). Here the main difficulty will be—as for the measurement of sexual selection discussed above—to modify the choosiness of individuals without affecting other parameters influencing the trade-off.

Our Formalism Could Be Extended to Encompass More Realistic Situations

In our model, we have made simplifying assumptions in order to conserve some analytical tractability and thus be able to make general predictions. This naturally raises the question of how robust these predictions are when extended to more realistic and/or specific situations. Given the complexity of the model, making verbal predictions about the effect of relaxing the key assumptions is highly speculative. Therefore, we encourage theoreticians to build on our formalism to study the effect of some key assumptions we made for the sake of simplicity. For example, we neglected condition dependence at all levels: choosiness, survival, latency, and encounter rate are not influenced by individual quality in our model. This is obviously not realistic (see, e.g., Cotton et al. 2006), and many other models of the evolution of mutual mate choice have relaxed this hypothesis at some level (e.g., Crowley et al. 1991; Johnstone et al. 1996; Johnstone 1997; Alpern and Reyniers 1999; Kokko and Johnstone 2002). It would therefore be insightful to do the same in our model. We predict that including condition dependence may reduce the predictive power of ∂RST because this metric does not capture the effect of variables influencing benefits per mating. It may also impede the evolution of mutual mate choice by reducing the decrease that we observed in the cost of being choosy in the other sex. Indeed, in such a case, if assortative mating evolves, low-quality individuals should qualify for reproduction, which would produce an effect similar to the one triggered by the mating decision rule used by Kokko and Johnstone (2002).

A second strong assumption in our model is that we consider only the evolution of choosiness. However, other traits can evolve jointly with choosiness. Many models focusing on the evolution of mate choice have also focused on how this trait evolves jointly with genetic quality, ornaments (traits indicating the quality of individuals but doing so at a cost), or parental care (for reviews, see Kokko et al. 2006; Kuijper et al. 2012). While introducing heritable variation in genetic quality in our model would introduce indirect benefits and therefore have a profound effect on the complexity of the analyses, ornaments and parental care have been successfully modeled in other work considering only direct selection, even in the case of joint evolution between sexes (e.g., Kokko and Johnstone 2002). A natural extension of the present work would therefore be to study how the fundamental trade-off of choice influences the joint evolution between choosiness and these other traits. In the context of this trade-off, it would also be interesting to study the joint evolution between choosiness and traits that may mitigate the fundamental trade-off of mate choice. Examples are the evolution of morphological adaptations, such as spermathecae, that allow female invertebrates to store sperm (Simmons 2001) or of such behaviors as mate switching during amplexus in male gammarids (Galipaud et al. 2015). A trivial prediction is that the evolution of such traits should facilitate the evolution of choosiness (in females and males, respectively), but the real question is under which circumstances these adaptations will evolve despite their costs once the benefits of choice are taken into account.

In our model, we have assumed no indirect benefits. This assumption was necessary to study precisely the direct cost that increased choosiness may exert on the mating rate. Indirect benefits may, however, occur in nature and strongly influence the joint evolution of mate choice, ornaments, and genetic quality (Mead and Arnold 2004). Studying the role played by indirect benefits in mate choice evolution within the framework introduced here may therefore help to assess the influence that ecological traits have on the evolution of traits that covary genetically with choosiness. It would also help tackle the controversial topic of the relative role played by direct and indirect benefits in mate choice evolution (Kotiaho and Puurtinen 2007). Moreover, such a model could help identify the natural conditions for which direct and indirect benefits are aligned (e.g., in the case of male choice for sexual swellings in chacma baboons; Huchard et al. 2009) or the conditions for which they are not (e.g., in the case of female choice for attractiveness in house crickets; Head et al. 2005).

Finally, we have not constrained life-history parameters to particular values according to the sex to which they refer. As such, our model allows the description of the full range of combinations of “sex roles” (i.e., the partition of choosiness and care between females and males) regardless of their distribution in nature. However, the same model could be used to tackle questions such as why females are often choosier than males. This could be done by imposing constraints on the parameter values (e.g., higher latency rate in females than in males), as others have done (e.g., Johnstone et al. 1996).

Conclusion

In this article, we studied how the choosiness of males and females jointly evolve when selection pressures acting on this trait are shaped only by the fundamental trade-off of mate choice: that is, the trade-off between the direct benefits individuals gain from choosing their mates and the decrease in mating rate that individuals suffer when they are choosy. We have found that this simple scenario is sufficient to derive several results previously associated with more complex biological assumptions. As the fundamental trade-off of mate choice will always emerge in populations in which individuals mate sequentially, we encourage theoreticians as well as empiricists to consider that other mechanisms influencing the evolution of choosiness should operate in addition to, and not instead of, the direct sexual selection generated by this trade-off. Contrary to previous claims, we have also revealed that an increase in choosiness in one sex does not necessarily prevent the evolution of mutual mate choice. Indeed, we showed that whether the feedback between the evolution of male and female choosiness promotes or impedes the occurrence of mutual mate choice depends on the life history of individuals (characterized in our model by a survival rate, a latency rate, and an encounter rate as well as a distribution of the quality of individuals), on the decision rule they use for mate choice, and on how the fecundity of a pair is shaped by the quality of both individuals. Finally, we have demonstrated that ∂RST, a metric recently proposed in the context of unilateral choice, might also be used to generate global predictions about the evolutionary change in choosiness when mate choice is free to evolve in both sexes.

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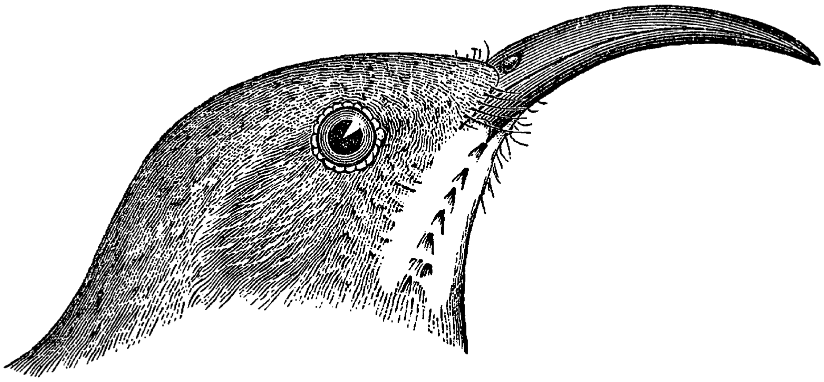

"Next comes the Red-vented, or Crissal Thrush (*H. crissalis*); also inhabiting the Colorado and Gila valleys. It is fully as large as *redivivus* or var. *Lecontei*, with the tail even longer, and the bill, if not larger, at least slenderer and more arcuate, as shown [above]." From "Some United States Birds, New to Science, and Other Things Ornithological" by Elliott Coues (*The American Naturalist*, 1873, 6:321–331).