

The evolution of mutual mate choice under direct benefits

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Additional material

Supplementary Information

Abstract

2 In nature, the intensity of mate choice (*i.e.*, choosiness) is highly variable within and between
sexes. Despite growing empirical evidence showing male and/or mutual mate choice, theoretical
4 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
6 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
8 this trade-off can generate a diversity of stable combinations of choosiness. Mutual mate choice
can only evolve if both females and males exhibit long latency after mating. Further, we show
10 that an increase in choosiness in one sex does not necessarily prevent the evolution of mutual
mate choice: the outcome depends on details of the life history, the decision rule for mate choice,
12 and how the fecundity of a pair is shaped by the quality of both individuals. Lastly, we discuss
the power of the sensitivity of the relative searching time (*i.e.*, of the proportion of lifetime spent
14 searching for mates) as a predictor of the joint evolution of choosiness.

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42 Introduction

Mate choice corresponds to any behavior that increases (or decreases) the probability of mating
44 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
46 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
48 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).
50 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, including amphibians (Verrell, 1995),
52 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
54 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
56 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
58 primates (Gomez et al., 2012; Courtiol et al., 2010). Despite the ever-growing empirical literature
showing that choosiness is highly variable in both sexes, theoretical investigations of the joint
60 evolution of female and male choosiness are few compared to the large number of studies dealing
with unilateral mate choice (Bergstrom and Real, 2000).

62 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
64 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,
66 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
68 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).

70 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.

72 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;
74 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.
76 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
78 only mate once in their lives (because rejecting mates increases the probability of dying before
having reproduced). Mate choice is thus intrinsically associated with a trade-off between the
80 benefits per mating and the mating rate that, respectively, increase and decreases with choosiness
(Owens and Thompson, 1994; Kokko and Mappes, 2005; Härdling et al., 2008). We call this *the*
82 *fundamental trade-off of mate choice*. Etienne et al. (2014) evaluated the importance of this trade-off
under the assumption that mate choice can only evolve in one sex (the other being considered in-
84 discriminate). They showed that, depending on the biological and ecological context, the strength
of the trade-off varies and influences the evolution of choosiness.

86 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
88 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, choosi-
90 ness in each sex impacts on the competition for mates in the other sex, which influences in turn
the benefits and costs associated with choosiness in both sexes. Or as Johnstone (1997) put it: “the
92 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
94 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 pro-
96 portion of a lifetime devoted to searching for mates or RST for short (*i.e.*, the Relative Searching
Time). More specifically, the sensitivity of RST (*i.e.*, ∂RST) – the change in RST caused only by a

98 variation in any biological or ecological parameter affecting the mating rate of individuals, while
choosiness is fixed – gives the effect of such variation on selection on choosiness. When ∂RST is
100 positive, lower choosiness is selected, and *vice versa*. Here, we investigate the predictive power of
 ∂RST on the joint evolution of female and male choosiness.

102 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
104 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
106 et al., 2014). Second, these 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
108 selection of choosiness should help to disentangle the impacts of the various different selection
pressures that shape the evolution of mate choice. In particular, we consider the evolution of
110 choosiness given a previously established pattern of parental investment in each sex and do not
study the joint evolution that could occur between choosiness and parental care (Kokko and
112 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.

114 Our work complements existing theoretical studies on the evolution of mutual mate choice.
Specifically, we consider a continuous strategy set for choosiness and thereby extend previous
116 studies which considered two discrete categories of choosiness (Crowley et al., 1991; Härdling
et al., 2008). Moreover, our formalism relies on a game-theoretic approach allowing a full con-
118 sideration of the influence of other-sex and same-sex individuals' behaviors on the evolution of
choosiness, contrary to some earlier models (Owens and Thompson, 1994; Kokko and Monaghan,
120 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) that focused on the diversity of mat-
122 ing patterns emerging from mutual mate choice, and the one by Kokko and Johnstone (2002) that
focused on the joint evolution between choosiness, signaling and care. Finally, we allow for any
124 number of mating events throughout a lifetime, generalizing models that assume that individ-
uals mate only once (Parker, 1983; McNamara and Collins, 1990; Johnstone, 1997; Alpern and

126 Reyniers, 1999; Alpern and Reyniers, 2005; Alpern and Katrantzi, 2009; Ramsey, 2011).

The model

128

Individual traits

130 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 a quality $q_{x,i}$ and a choosiness $\phi_{x,i}$, both real numbers between 0 and 1 (see Table 1 for a summary of our notations). We assume $q_{x,i}$ to be directly proportional to the contribution of a mate to the fecundity of a given 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. This assumption 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 this trait 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.

148 The 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.). Then, at each time step, the latent individual, if it survives, remains in latency with rate l_x . 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):

$$\mathbf{L}_x = \begin{array}{cc} & \begin{array}{cc} \dots & \text{to available} & \dots & \text{to unavailable} \end{array} \\ \begin{array}{c} \text{from available...} \\ \text{from unavailable...} \end{array} & \left(\begin{array}{cc} s_x(1 - \gamma\mu_{x,i}l_x) & s_x\gamma\mu_{x,i}l_x \\ s_x(1 - l_x) & s_xl_x \end{array} \right), \end{array} \quad (1)$$

where $\mu_{x,i}$ is the probability that an individual i of the 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 mating probability $\mu_{x,i}$ of an individual i of sex x depends on the probability that it finds the potential mate encountered acceptable, thus on its choosiness (*i.e.*, $\phi_{x,i}$). In addition, $\mu_{x,i}$ depends on the availability of individuals of sex y , that is on the probability that a given individual of sex y is not in latency. This availability is in turn related to the choosiness of other individuals of sex x . The reason is that an individual that is encountered may be in latency after having previously mated – and is thus unavailable for a new mating. To take this competition for mates into account, we consider a mutant individual m with choosiness $\phi_{x,m}$ in a population where all other individuals of sex x have choosiness $\phi_{x,p}$ (with p for population). We also assume that all

individuals of sex y show the same choosiness, denoted $\phi_{y,p}$. Together, $\phi_{x,p}$ and $\phi_{y,p}$ define the
 176 residents in the population.

We now characterize the relationship between the mating probability $\mu_{x,m}$ of a mutant of the
 178 focal sex and the other parameters. First, $\mu_{x,m}$ depends on the quality of the mutant (*i.e.* $q_{x,m}$).
 Indeed, if the latter is not of sufficient quality to mate with (*i.e.*, with quality $q_{x,m} < q_x(\phi_{y,p})$),
 180 it is never chosen by other-sex individuals and thus its mating probability is null. If so, it does
 not transmit its choosiness alleles and thus does not influence the evolution of choosiness in the
 182 population. Therefore, only mutants who can obtain mates need to be taken into account. Two
 situations need to be distinguished for such a mutant. First, if it is choosier than other same-sex
 184 individuals ($\phi_{x,m} \geq \phi_{x,p}$), 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
 186 the probability that any individual i of sex y , with quality $q_{y,i} \geq q_y(\phi_{x,p})$, is in the available state
 in eq. 1, is denoted $a_{y,p}$. Second, if the mutant is less choosy than residents ($\phi_{x,m} < \phi_{x,p}$), it is
 188 willing to mate with two types of individuals: those who are also chosen by resident individuals
 of sex x , whose availability equals $a_{y,p}$, and those whose quality ranges from $q_y(\phi_{x,m})$ to $q_y(\phi_{x,p})$
 190 and who are thus always available for mating with this mutant. Therefore, we have:

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

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

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

194 **Calculating mating availabilities**

To obtain the expressions for the mating availability $a_{y,p}$, we need to compute, in each sex, the
 196 expected time spent by resident individuals in latency and to divide it by the expected lifes-
 pan. Because the states of the life cycle considered here forms a Markov chain where death is

198 an absorbing state, the expected time spent in each state can be deduced from the transition
probabilities between the non-absorbing states of the life cycle (using $\mathbf{D}_x = (\mathbf{I} - \mathbf{L}_x)^{-1}$ with \mathbf{I} the
200 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
202 time steps d (first element of the matrix \mathbf{D}_x) that a focal-sex resident spends available for mating
throughout lifetime:

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

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

$$\begin{cases} a_{y,p} = (1 - s_y l_y) / (1 - s_y l_y + s_y \gamma (1 - \phi_{y,p}) a_{x,p} l_y) \\ a_{x,p} = (1 - s_x l_x) / (1 - s_x l_x + s_x \gamma (1 - \phi_{x,p}) a_{y,p} l_x) \end{cases} \quad (5)$$

210 which solution yields:

$$a_{y,p} = \frac{1}{2s_x \gamma \phi_{x,p} l_x (1 - s_y l_y)} \left(s_x \gamma l_x (s_y l_y (\phi_{x,p} - \phi_{y,p}) - \phi_{x,p}) + (1 - l_x)(1 - l_y) - 1 \right. \\ \left. - \sqrt{(s_x \gamma l_x (s_y l_y (\phi_{x,p} - \phi_{y,p}) - \phi_{x,p}) + (1 - l_x)(1 - l_y) - 1)^2 + 4s_x \gamma \phi_{x,p} l_x (1 - s_x l_x)(1 - s_y l_y)^2} \right). \quad (6)$$

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

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

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

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

Computing the expected lifetime fecundity of a mutant

216

Let us define the lifetime fecundity of an individual i as the number of offspring it produces as
218 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
220 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
222 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.*,
224 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
226 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
228 we call $b(q_{x,i})$, and its expected lifetime ($1/(1 - s_x)$):

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

To compute the expected benefits per mating $b(q_{x,i})$, we assume the reproductive success of a
230 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:

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

232 The fact 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
234 of $q_{x,i}$, and individuals of lower quality never mate. Further, $\bar{q}_y(i)$ differs among individuals
with different choosiness but is identical among individuals with the same choosiness. Thus the
236 expected lifetime fecundity $F_{x,m}$ among all mutants representing a mutant lineage can be written
as the product of expected values of the different terms of $F_x(q_{x,i})$:

$$F_{x,m} = r_{x,m} b_{x,m} \frac{1}{1 - s_x}, \quad (10)$$

238 in terms of expected mating rate $r_{x,m}$, and expected benefits per mating $b_{x,m}$, of mutants. We will now detail expressions for these expectations.

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

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

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

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

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

$$q_{x,m} = \frac{\int_{q_x(\phi_{y,p})}^1 q f_x(q) dq}{\int_{q_x(\phi_{y,p})}^1 f_x(q) dq} = \frac{\int_{q_x(\phi_{y,p})}^1 q f_x(q) dq}{1 - \phi_{y,p}}. \quad (13)$$

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

252 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 ($\phi_{x,m} \geq \phi_{x,p}$), it accepts any
254 individual of sex y whose quality is higher than $q_y(\phi_{x,m})$. 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 $q_y(\phi_{x,m})$
256 and 1. Second, if the mutant is less choosy than resident individuals of its sex ($\phi_{x,m} < \phi_{x,p}$), it

can mate with two types of individuals who differ in their availabilities: those whose quality
 258 ranges from $q_y(\phi_{x,m})$ to $q_y(\phi_{x,p})$ (who are always available) and those whose quality is higher
 than $q_y(\phi_{x,p})$ (who are also courted by focal-sex resident individuals and thus are available with
 260 probability $a_{y,p}$). In this case, the expected quality of the mates of the mutant is thus the mean of
 the quality distribution in the sex y restricted to the range between $q_y(\phi_{x,m})$ and 1, weighted by
 262 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:

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

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

$$b_{x,m} = \begin{cases} \frac{1}{2} \left(\frac{\int_{q_x(\phi_{y,p})}^1 q f_x(q) dq}{1 - \phi_{y,p}} + \frac{\int_{q_y(\phi_{x,m})}^1 q f_y(q) dq}{1 - \phi_{x,m}} \right) & \text{if } \phi_{x,m} \geq \phi_{x,p}, \\ \frac{1}{2} \left(\frac{\int_{q_x(\phi_{y,p})}^1 q f_x(q) dq}{1 - \phi_{y,p}} + \frac{\int_{q_y(\phi_{x,m})}^{q_y(\phi_{x,p})} q f_y(q) dq + a_{y,p} \int_{q_y(\phi_{x,p})}^1 q f_y(q) dq}{\phi_{x,p} - \phi_{x,m} + a_{y,p}(1 - \phi_{x,p})} \right) & \text{if } \phi_{x,m} < \phi_{x,p}. \end{cases} \quad (15)$$

266 In some particular cases, the expected benefits per mating of a mutant ($b_{x,m}$) take a simple
 form. For example, if the mutant is choosier than the resident (*i.e.*, $\phi_{x,m} \geq \phi_{x,p}$) and if quality
 268 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
 270 respectively $(1 + \phi_{y,p})/2$ and $(1 + \phi_{x,m})/2$ (as $q(\phi) = \phi$ under the uniform distribution). In this
 case, the expected benefits per mating of the mutant is simply given by:

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

272

Analytical study of the model

274 The full analytical methods are described in Supplementary Information, but all key steps will
 be presented here. We first assessed the existence of a joint equilibrium for choosiness (*i.e.*, a

276 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
 278 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:

$$\begin{cases} \frac{\partial F_{x,m}}{\partial \phi_{x,m}} \Big|_{\phi_{x,m}=\phi_{x,p}=\phi_x^*} = 0 \\ \frac{\partial F_{y,m}}{\partial \phi_{y,m}} \Big|_{\phi_{y,m}=\phi_{y,p}=\phi_y^*} = 0 \end{cases} \quad (17)$$

280 We identified such a solution and studied the convergence stability in each sex before investi-
 gating the joint convergence stability. The study of the joint convergence stability required the
 282 additional assumption of independent mutational effects between females and males. We also
 assessed the evolutionary stability in cases for which $\phi_y^* = 0$. We could not verify this property
 284 when non-zero choosiness is selected in both sexes, as we are not aware of the existence of any
 general method allowing for the assessment of the joint evolutionary stability of several evolving
 286 traits.

Second, we analyzed the effect of a change z in a given biological or ecological variable on the
 288 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.*, $\phi_{y,p} = \phi_y^*$). This implies the study
 290 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
 292 equilibrium we can rewrite eq. 10 as:

$$0 = \frac{\partial_+ \ln(F_{x,m})}{\partial \phi_{x,m}} \Big|_{\phi_{x,m}=\phi_x^*} = \overbrace{\frac{\partial_+ \ln(r_{x,m})}{\partial \phi_{x,m}} \Big|_{\phi_{x,m}=\phi_x^*}}^{R_x^*} + \overbrace{\frac{\partial_+ \ln(b_{x,m})}{\partial \phi_{x,m}} \Big|_{\phi_{x,m}=\phi_x^*}}^{B_x^*}, \quad (18)$$

where ∂_+ represents the right derivative (*i.e.*, we consider the case $\phi_{x,m} \geq \phi_{x,p}$ in eqs. 12 & 15,
 294 but considering the other case leads to same results as shown in Supplementary Information), R_x^*
 represents the relative change in mating rate in sex x at equilibrium and B_x^* the relative change
 296 in expected benefits per mating at equilibrium. Biologically, the value of $-R_x^*$ quantifies the
 decrease in mating rate when choosiness increases, *i.e.*, the cost of being choosy. The value of B_x^*
 298 quantifies the increase in expected benefits per mating when choosiness increases, *i.e.*, the benefit

of being choosy. When z influences the mating rate only (hereafter called z_r), we demonstrate
 300 in Supplementary Information that (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
 302 from the effect of z_r on the Relative Searching Time (*i.e.*, RST: the proportion of lifetime which is
 devoted to searching for mates):

$$\text{sgn} \left(\frac{\partial \phi_x^*}{\partial z_r} \right) = \text{sgn} \left(\frac{\partial R_x^*}{\partial z_r} \right) = -\text{sgn} \left(\frac{\partial \text{RST}^*}{\partial z_r} \right). \quad (19)$$

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

When z influences the expected benefits per mating only (hereafter called z_b), we also demon-
 strate in Supplementary Information that 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^* :

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

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

Third, we analyzed the effect of a change in z on the joint equilibrium for choosiness. Indeed,
 310 in the analyzes used to obtain eqs. 19 and 20 we only considered 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,
 312 the total variation of the choosiness in both sexes following a change in z is described by the
 system:

$$\begin{cases} \frac{d\phi_x^*}{dz} = \frac{\partial \phi_x^*}{\partial z} + \frac{\partial \phi_x^*}{\partial \phi_y^*} \frac{d\phi_y^*}{dz} \\ \frac{d\phi_y^*}{dz} = \frac{\partial \phi_y^*}{\partial z} + \frac{\partial \phi_y^*}{\partial \phi_x^*} \frac{d\phi_x^*}{dz} \end{cases}, \quad (21)$$

314 where $d\phi_x^*/dz$ ($d\phi_y^*/dz$) represents the total variation of the choosiness in the sex x (y) that
 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 of
 316 ϕ_x^* (ϕ_y^*) caused by a change in ϕ_y^* (ϕ_x^*) while z remains fixed.

We have already described the analysis of $d\phi_x^*/dz$ in terms of R_x^* and B_x^* , so the same goes for
318 $d\phi_y^*/dz$ (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 $\phi_{y,p}$. However, no more definite analytical result could be obtained
320 for $\partial\phi_x^*/\partial\phi_y^*$ and thus for the overall effect of z on the joint equilibrium for choosiness.

Numerical analysis

322 Despite the simplicity of the life cycle we consider, some mathematical complexity emerges be-
cause of the joint evolution between sexes. As a consequence, some specific results cannot be
324 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
326 R (R Core Team, 2015). To minimize the risk of missing exceptions to our main conclusions, we
investigated a large number of parameter sets.

328 To study equilibrium conditions for each choosiness, we considered the 16 possible combi-
nations between 4 different quality distributions for females and males: uniform ($\alpha = \beta = 1$),
330 bell-curve ($\alpha = \beta = 4$), left-skewed ($\alpha = 4$ and $\beta = 10$) and right-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 ,
332 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 (that we call the “continuous tables”), and the other for which all
334 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, 0.999 (that we call the “discrete tables”). In total we therefore analyzed 3.2×10^6
336 ($= 16 \times 10^5 \times 2$) different parameter sets.

We also used the continuous tables to study the joint evolution of choosiness between sexes.
338 The procedure is described in figure 4.

Finally, we studied the predictive power of ∂RST numerically. To do so, we first randomly
340 drew 10^6 pairs of parameters 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 of
342 choosiness, the total variation of choosiness and ∂RST . Second, we then randomly drew 10^6 pairs
of parameters sets (which could here potentially differ in γ , s_x , s_y , l_x and l_y) from the same discrete

344 tables. We computed again the partial variation of choosiness, the total variation of choosiness
and ∂RST for all these pairs. We were therefore able to determine the predictive power of ∂RST
346 when only one parameter changes, as well as when all parameters are free to change at the same
time, using 1.6×10^7 ($= 16 \times 10^6$) different parameter sets in each case. The numerical analysis
348 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
350 choice and unilateral choice situations have already been analyzed in Etienne et al. (2014).

Results

352 Scope

We will indicate below whether a given result has been analytically obtained (hereafter labeled
354 as *analytical result*), if it has been obtained for the complete numerical exploration (*numerical
result*), or if it has been obtained numerically and correspond to an effect found in only part of
356 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
358 the scope of the assumptions made in this model. Yet, because this statement cannot be proven
without being able to apply a pure analytical approach, we chose to make the distinction between
360 *numerical* and *analytical* results explicit.

The evolution of mutual mate choice

362 **Result 1.** There is always one and only one convergence stable (joint) equilibrium for choosiness
both in situation of unilateral and mutual mate choice (*numerical result*).

364 We numerically solved equilibrium eq. 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 (*numeri-
366 cal 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
368 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 non-focal sex was constrained to
370 be null. In this case, the equilibrium is always convergence and evolutionarily stable (*numerical
result*). Second, we found parameter settings under which choosiness is non-null at equilibrium
372 in both sexes ($\phi_x^* \neq 0$ and $\phi_y^* \neq 0$), and such equilibria are always jointly convergence stable (*nu-
merical result*). No conclusion could be derived for the evolutionary stability but individual-based
374 simulations for numerous parameters settings suggest that the equilibrium is also evolutionary
stable in this case (not shown).

376 **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*).

378 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.*, $\phi^* = 0.7$)
380 choosiness in both sexes, with all possible intermediates (*e.g.*, see figure 1).

Result 3. Within our numerical exploration, mutual mate choice occurs at equilibrium only when
382 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 (figure 1 & S4),
384 (ii) higher survival (figure 2 & S5) or (iii) lower variance in quality (figures S4-S6). The evolution
of non-null choosiness in a sex requires latency rate in this sex, survival rate in this sex and
386 variance in other-sex quality to be non-null (*numerical result*). However, fulfilling these conditions
in both sexes is not sufficient to observe mutual mate choice at equilibrium. Indeed, the latter
388 outcome is obtained only when both latency and survival rates approach 1 in the two sexes (see
figures 1-2 & S4-S5). Once this criterion is satisfied, the level of mutual choosiness at equilibrium
390 is influenced by other parameters. In particular, high choosiness in both sexes is favored when
encounter rate and/or variance in quality of both sexes is high, and/or mean quality of both
392 sexes is low (figures S4-S6).

The joint evolution of choosiness

394 **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*).

396 From the definition of R_x^* (see eq. 18) and the expression for $r_{x,m}$ (see eq. 12), the effect of a change in other sex choosiness (*i.e.*, $\phi_{y,p}$) upon the cost R_x^* of being choosy is:

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

398 When $\phi_{y,p}$ increases, fewer individuals of the focal sex mate, which increases the availability $a_{y,p}$ of other-sex individuals whose quality is sufficient to mate. Thus the partial derivative of R_x^* with respect to $\phi_{y,p}$ is also positive (*analytical result*). Therefore, an increase in $\phi_{y,p}$ 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 the sex y , as a consequence of the higher choosiness in this sex, reduces the competition among individuals of sex x for the access to other-sex individuals. Thereby the cost of being choosy in sex x reduces, which is why $\phi_{y,p}$ has, here, 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.*, $\phi_{y,p}$) upon the benefit B_x^* of being choosy can generally be written

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

The mixed derivative of $b_{x,m}$ vanishes (from eq. 15), so that this reduces to

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

408 When $\phi_{y,p}$ 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 $b_{x,m}$ increases as well (see eq. 15). Then, $b_{x,m}$ also increases with $\phi_{x,m}$ (see eq. 15). Both derivatives in the right-hand term of the previous equation are thus positive. This implies that the derivative of B_x^* with respect to $\phi_{y,p}$ is negative (*analytical result*), and that an increase in $\phi_{y,p}$ selects for lower focal-sex choosiness via its effect on the relative change in expected benefits per mating (see eq. 20). To sum up, 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 $\phi_{y,p}$ would thus have a negative effect on ϕ_x^* .

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

$$\frac{\partial B_x^*}{\partial \phi_{y,p}} = \frac{\partial_+ \left(\frac{1}{q_{x,m}\bar{q}_y} \frac{\partial_+(q_{x,m}\bar{q}_y)}{\partial \phi_{x,m}} \right) \Big|_{\phi_{x,m}=\phi_x^*}}{\partial \phi_{y,p}} = \frac{\partial_+ \left(\frac{1}{\bar{q}_y} \frac{\partial_+\bar{q}_y}{\partial \phi_{x,m}} \right) \Big|_{\phi_{x,m}=\phi_x^*}}{\partial \phi_{y,p}} = 0, \quad (25)$$

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

426 **Result 5.** An increase in choosiness in one sex does not necessarily prevent the evolution of
 choosiness in the other (*restricted result*).

428 We have numerically found that when 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*, figure 4). However, this result
 430 is *restricted* when latency is high in both sexes, which corresponds to cases of mutual mate choice
 at equilibrium (see figure 1). In this latter situation, parameter values determine which of the two
 432 antagonistic effects of ϕ_y^* on ϕ_x^* can outweigh the other (figure 4).

∂ RST and the effect of a change in mating rate on the evolution of choosiness

434 **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*).

436 If a change z_r in a given biological or ecological variable is a function of only one of the parameters
 which 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
 438 variations of choosiness were always of the same sign for all of the 1.6×10^7 combinations of
 parameters performed (*numerical result* obtained using the discrete tables). This is because in
 440 such cases, the partial variation of focal choosiness triggered by z_r outweighs the variation of

focal choosiness caused by a change in other-sex choosiness. In these circumstances, computing
442 ∂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
444 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
446 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
448 for the other one (because available mates are rarer), leading to higher and lower choosiness
respectively (figure 1). The effect of survival is identical to the effect of latency (figure 2). Indeed,
450 the proportion of the lifetime spent in latency increases with the survival rate in both sexes. This
is because when an individual dies, it is always replaced by an available individual, whether the
452 deceased was in latency or not. Finally, when encounter rate increases, ∂RST of both sexes is
negative, which selects for higher choosiness in both sexes (figure 3).

454 **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
456 variation of choosiness. Indeed, when several parameters affecting the mating rate vary simul-
taneously, we have numerically found that the variation in choosiness caused by the change in
458 other sex choosiness can outweigh the partial variation of focal choosiness. Cases where ∂RST
loses its predictive power are rare within the parameter space investigated ($\sim 0.09\%$, or 14847 out
460 of the 1.6×10^7 combinations of parameters sampled in the discrete tables, see section *Numerical*
analysis; figure 5). The cases for which ∂RST fails to predict the evolutionary change in choosiness
462 are not associated with particular values of the parameters. We found however that ∂RST can
fail when its value is very low (*i.e.*, < 0.01) in one sex (this is the case for 8890 out of the 14847
464 erroneous predictions). It can also fail when both ∂RST are large. The only structure that we have
detected in this latter case is that 84% of erroneous predictions happen when the absolute value
466 of ∂RST in the focal sex is lower than in the other sex (figure 5).

Discussion

468 In this article, we have modeled the direct selection of choosiness when mate choice is allowed
to evolve in both sexes by considering that mate choice is solely associated with direct benefits
470 in terms of increased mate quality and 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
472 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
474 and obtained most of our results based on the numerical evaluation of our analytical expressions.
Opting for a numerical analysis was necessary due to the complexity of our analytical results.
476 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 (*e.g.*, compare our analysis
478 to that of Kokko and Johnstone, 2002). However, a numerical analysis is necessarily less complete
than a full analytical study because one cannot *a priori* exclude the possibility that any identified
480 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
482 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
484 within our set of assumptions, true in our complete numerical exploration, or true for part of the
parameter space, respectively.

486 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
488 of mate choice) is sufficient to generate the evolution of a high diversity of convergence stable
combinations of choosiness between sexes at equilibrium (*Results 1 & 2* in section *Results*). Within
490 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 choosi-
492 ness in a sex can either be promoted or limited by the evolution of choosiness in the other sex
(*Results 4 & 5*). Third, ∂RST (*i.e.*, the change in the proportion of lifetime devoted to searching for
494 mates caused only by a variation in any biological or ecological parameter affecting the mating

rate of individuals, while choosiness is fixed) correctly predicts the evolution of choosiness in
496 response to a change in mating rate in many but not all cases of mutual mate choice (*Results 6 &*
7). We now discuss these results in more detail before examining some key assumptions of our
498 model.

Life history, through its effect on the fundamental trade-off of mate choice, can select 500 for various convergence stable combinations of choosiness between sexes

Each equilibrium identified during our numerical exploration always corresponds to a single
502 combination of female and male convergence stable choosiness (*Result 1: numerical*). Depending
on the values of the parameters (encounter rate, sex-specific latency rates, sex-specific survival
504 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 the following combinations can be
506 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)
508 to very high values (*e.g.*, 70% of other-sex individuals are always rejected) in both sexes. This
result leaves open the possibility that direct selection may be sufficient to explain the evolution of
510 mutual mate choice in situations that other studies have interpreted as the result of more complex
mechanisms (*e.g.*, see Hooper and Miller, 2008; Ihara and Aoki, 1999; Servedio and Lande, 2006;
512 South et al., 2012). In our case direct selection is expressed purely in terms of differential fecundity
emerging from differences in the number or in the identity of mates, *i.e.*, sexual selection (*sensu*
514 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
516 or females (Kokko and Johnstone, 2002). Taken together, our model and those of others suggest
that there are many paths to mutual mate choice (pre- or post-mating) in nature. In the case of
518 sequential mate choice however, other mechanisms should operate in addition to, and not instead
of, the direct sexual selection generated by the fundamental trade-off of mate choice.

520 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

522 the fraction of the lifetime spent in latency is positively related to both latency and survival rates
(see *Result 6*). The latency state in our model can result from any process that prevents individ-
524 uals 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
526 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
528 promotes the evolution of mutual choosiness (Crowley et al., 1991; Johnstone et al., 1996; Kokko
and Johnstone, 2002; Owens and Thompson, 1994; Parker, 1983). Nonetheless, our definition of
530 latency also encompasses biological situations other than parental investment. Consequently, we
also predict mutual mate choice to emerge in organisms that express high latencies for reasons
532 other than high parental investment in both sexes. We therefore predict mutual mate choice to
evolve in species in which males suffer high spermatic depletion (because of sperm competition
534 that leads them to produce a high amount of sperm per copulation) and females invest a lot in
offspring. This situation may for example explain why in some lekking species such as the great
536 snipe *Gallinago media* (Sæther et al., 2001), or the cichlid fish *Astatotilapia flavijosephi* (Werner and
Lotem, 2003), choice is mutual despite the lack of paternal care. This prediction contrasts with
538 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
540 assumptions about the mating decision-rule makes the evolution of mutual mate choice more
difficult in their case.

542 The importance of the duration of latency does not preclude other parameters from influenc-
ing the level of mutual choosiness (*Result 3: numerical*). Indeed, provided that latency and survival
544 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;
546 Kokko and Johnstone, 2002), by a high variance in the quality of both sexes (Hårdling et al., 2008;
Johnstone et al., 1996; Kokko and Johnstone, 2002; Owens and Thompson, 1994 and Parker, 1983)
548 or by low mean quality of both sexes (Gowaty and Hubbell, 2009).

An increase in choosiness in one sex does not necessarily prevent the evolution of mutual mate choice

550

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 upon selection for choosiness in the other (*Result 4: analytical*). 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 or not is therefore related to the relative extent to which low-quality and high-quality individuals contribute to the gene pool.

562 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. 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 who 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. Empirical knowledge of mating

decision rules (e.g., Kirkpatrick et al., 2006; Courtiol et al., 2010; Castellano et al., 2012; Reinhold
578 and Schielzeth, 2015) appears therefore crucial for the implementation of realistic models of the
evolution of choosiness.

580 An increase in choosiness in the other sex does not only decrease the cost of being choosy for
the focal sex. It also decreases its benefit of being choosy. Indeed, we found that an increase in
582 other-sex choosiness has a positive impact 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
584 increase in benefits per mating with choosiness) in this focal sex (*analytical result*). In most of the
numerical cases that we have explored, this negative effect on the benefit of being choosy is larger
586 than the cost (*Result 5: restricted*), which leads choosiness to decrease in one sex when it increases
in the other sex.

588 Nevertheless, the opposite result can be observed, in particular when latency is high in both
sexes, i.e., when both sexes are expected to be choosy (*Result 5: restricted*). This negative effect
590 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
592 (see eq. 16). Kokko and Johnstone (2002) showed that certain forms of non additive parental
care could facilitate the evolution of mate choice. Here, we have shown that this effect is not
594 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
596 for reproductive success instead of an additive one, other-sex choosiness no longer reduces the
benefit of being choosy in the focal sex (*Result 4: analytical*). Under such an assumption, other-sex
598 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
600 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
602 the pair, and of 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
604 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*).

606 **The power of ∂ RST as a predictor for the evolution of choosiness must be assessed empirically**

608 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 found that the sign of this change was opposed to the sign of ∂ RST (*i.e.*, the variation in the proportion of the 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 case of joint evolution of choosiness (*Result 6: numerical*). However, when z_r impacts simultaneously on 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 (*restricted result*). Importantly, whether the few numerical cases in which ∂ RST fails (on average 9.3 cases per 10,000 trials) represent widespread biological situations or not, is an empirical question – the answer to which shall determine how useful ∂ RST really is.

626 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; (iii) z_r does not affect the distribution of mate quality, regardless of the form of the latter.

630 Despite these limitations, we believe that ∂ RST remains superior to all alternative metrics proposed thus far. In particular, Kokko and Monaghan (2001) have clearly demonstrated the

632 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). While they did
634 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
636 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
638 where *C* produces an erroneous prediction). This weakness emerges from the fact that *C*, as with
the *OSR* in many models, is considered as fixed (*i.e.*, it depends only on the parameter setting)
640 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
642 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
644 may allow for deriving the expression of ∂RST or a related metric while relaxing assumptions
(i) and (ii), a big challenge stems in relaxing the third assumption: as for alternative metrics,
646 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
648 identify a predictor that would simultaneously include variations of mating rate and benefits per
mating.

650 In the absence of further developments, we therefore believe that ∂RST , albeit imperfect, re-
mains the best available predictor of the evolution of choosiness because (i) it holds across a wide
652 range of mating systems, (ii) it encompasses many alternative variables proposed thus far to ex-
plain the evolution of choosiness by direct selection (*i.e.*, the time invested in breeding, the adult
654 sex-ratio, the operational sex-ratio, and the cost of breeding; see Etienne et al., 2014) and (iii) it
can be used empirically to infer qualitative differences in choosiness. We therefore encourage the
656 use of ∂RST to study the evolution of choosiness in nature both in unilateral and mutual mate
choice situations. The guidelines proposed in Etienne et al. (2014) still apply when mate choice is
658 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

660 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 empiri-
662 cal 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 before choosiness
664 changes (because of selection or phenotypic plasticity).

Such an experimental protocol aims at predicting the evolution of choosiness in the face of
666 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
668 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
670 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
672 experiments using the framework of Bateman's gradients (*e.g.*, Anthes et al., 2010; Jones, 2009)
should indeed allow the inference of the amount of sexual selection acting on choice in such
674 cases.

Our work should also stimulate empirical perspectives that do not involve ∂ RST. In particular,
676 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
678 of this trade-off. We are well aware that the empirical assessment of any trade-off is notoriously
difficult, however as it has been shown with respect to other questions it is generally worth
680 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 impacting on other
682 parameters influencing the trade-off.

A critical evaluation of the assumptions of the model

684 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
686 of how robust these predictions are when extended to more realistic and/or specific situations.

Due to the complexity of the model, making verbal predictions of the effect of relaxing the key
688 assumptions is highly speculative. Therefore, we encourage theoreticians to build on our formal-
ism to study the effect of some key assumptions that we made for the sake of simplicity. For
690 example, we neglected condition dependence at all levels: choosiness, survival, latency and en-
counter rate are not influenced by individual quality in our model. This is obviously not realistic
692 (see *e.g.*, Cotton et al., 2006) and many other models of the evolution of mutual mate choice have
relaxed this hypothesis at some levels (*e.g.*, Crowley et al., 1991; Johnstone et al., 1996; Johnstone,
694 1997; Alpern and Reyniers, 1999; Kokko and Johnstone, 2002). It would be therefore extremely
insightful to do the same in our model. We predict that including condition dependence may
696 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 re-
698 ducing 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,
700 which would produce an effect similar to the one triggered by the mating decision-rule used by
Kokko and Johnstone (2002).

702 A second assumption in our model is that we only consider the evolution of choosiness.
However, other traits can evolve jointly with choosiness. Many models focusing on the evolution
704 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,
706 see Kokko et al. 2006 and Kuijper et al. 2012). While introducing heritable variation in genetic
quality in our model would introduce indirect benefits and therefore have a profound impact
708 on the complexity the analyses, ornaments and parental care have been successfully modeled in
other work considering only direct selection, even in case of joint evolution between sexes (*e.g.*,
710 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
712 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
714 mate choice. Examples are the evolution of morphological adaptations such as spermathecae

that allow female invertebrates to store sperm (Simmons, 2001), or of behaviors such as mate
716 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
718 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.

720 In our model, we have assumed no indirect benefits. This assumption was necessary to study
precisely the direct cost that increased choosiness may exert upon the mating rate. Indirect
722 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 of indirect benefits
724 in mate choice evolution within the framework introduced here may therefore help to study the
influence of ecological traits upon the evolution of traits that co-vary genetically with choosiness.
726 It would also help to tackle the controversial topic of the relative role of direct and indirect benefits
for mate choice evolution (Kotiaho and Puurtinen, 2007). Moreover, such a model could help to
728 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
730 for which they are not (*e.g.*, in the case of female choice for attractiveness in house crickets, Head
et al., 2005).

732 Finally, we shall discuss one assumption we made that may *a priori* appear limiting but that
may not be necessary so: in the real world, latency is not necessarily all-or-nothing in living
734 organisms as assumed in our model, but more likely to vary continuously (one can be more or
less available). For example, an individual providing parental care may exhibit an intermediate
736 level of latency since remating is possible, albeit limited, during this period. This seems to
contrast with our assumption. However, in our model latency is not all-or-nothing for a group of
738 individuals. 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
740 similar at the level of choosiness alleles whether or not latency is, at a given time, all-or-nothing
for each individual.

742 Conclusion

In this paper, we studied how the choosiness of males and females jointly evolve when selection pressures acting on this trait are only shaped 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. 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), the decision rule they use for mate choice, and on how the fecundity of a pair is shaped by the quality of both individuals. We have finally demonstrated that ∂RST , a metric recently proposed in the context of unilateral choice, might also be used to generate global predictions on the evolutionary change in choosiness when mate choice is free to evolve in both sexes.

Our approach reinforces the view that one does not need to enforce any intrinsic difference between the sexes in a model to study “sex roles” (*i.e.*, the partition of choosiness and care between females and males). Indeed, 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 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, as others have done (*e.g.*, Johnstone et al., 1996).

Our model also highlights the benefits of considering choosiness as a quantitative trait. In particular, our results show that mutual mate choice can be associated with high choosiness in one or both sexes but also with weak choosiness in one or both sexes. The relatively few empirical studies adopting such a quantitative view of mate choice simultaneously in both sexes have al-

770 ready 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
772 Lotem, 2003; Aquiloni and Gherardi, 2008). Pursuing this quantitative approach both theoret-
ically and empirically may lead to greater insights into the frequency of mutual mate choice in
774 nature.

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782 **References**

- Alpern, S., and I. Katrantzi. 2009. Equilibria of two-sided matching games with common prefer-
784 ences. *European Journal of Operational Research* 163:1214–1222.
- Alpern, S., and D. Reyniers. 1999. Strategic mating with homotypic preferences. *Journal of*
786 *Theoretical Biology* 198:71–88.
- . 2005. Strategic mating with common preferences. *Journal of Theoretical Biology* 237:337–
788 354.
- Amundsen, T. 2000. Why are female birds ornamented? *Trends in Ecology and Evolution* 15:149–
790 155.
- Andersson, M. B. 1994. *Sexual selection*. Princeton University Press, Princeton.
- 792 Anthes, N., P. David, J. R. Auld, J. N. Hoffer, P. Jarne, J. M. Koene, H. Kokko, M. C. Lorenzi,
B. Péliissié, D. Sprenger, et al. 2010. Bateman gradients in hermaphrodites: an extended ap-
794 proach to quantify sexual selection. *The American Naturalist* 176:249–263.
- Aquiloni, L., and F. Gherardi. 2008. Mutual mate choice in crayfish: large body size is selected by
796 both sexes, virginity by males only. *Journal of Zoology* 274:171–179.
- Bahr, A., S. Sommer, B. Mattle, and A. B. Wilson. 2012. Mutual mate choice in the potbellied
798 seahorse (*Hippocampus abdominalis*). *Behavioral Ecology* 23:869–878.
- Bergstrom, C. T., and L. A. Real. 2000. Towards a theory of mutual mate choice: lessons from
800 two-sided matching. *Evolutionary Ecology Research* 2:493–508.
- Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and
802 evidence. *Biological Reviews* 76:305–339.
- Castellano, S., G. Cadeddu, and P. Cermelli. 2012. Computational mate choice: theory and em-
804 pirical evidence. *Behavioural processes* 90:261–277.
- Caswell, H. 2001. *Matrix population models*. Sinauer Associates, Inc.

- 806 Clutton-Brock, T. 2009. Sexual selection in females. *Animal Behaviour* 77:3–11.
- Cotton, S., J. Small, and A. Pomiankowski. 2006. Sexual selection and condition-dependent mate
808 preferences. *Current Biology* 16:R755–R765.
- Courtiol, A., M. Raymond, B. Godelle, and J.-B. Ferdy. 2010. Mate choice and human stature:
810 homogamy as a unified framework for understanding mating preferences. *Evolution* 64:2189–
2203.
- 812 Cross, F. R., R. R. Jackson, and S. D. Pollard. 2007. Male and female mate-choice decisions by
Evarcha culicivora, an east african jumping spider. *Ethology* 113:901–908.
- 814 Crowley, P. H., S. E. Travers, M. C. Linton, S. L. Cohn, A. Sih, and R. C. Sargent. 1991. Mate
density, predation risk, and the seasonal sequence of mate choices: a dynamic game. *American*
816 *Naturalist* 137:567–596.
- Darwin, C. 1871. *The Descent of man, and selection in relation to sex*. Murray, London.
- 818 Daunt, F., P. Monaghan, S. Wanless, and M. P. Harris. 2003. Sexual ornament size and breeding
performance in female and male european shags *Phalacrocorax aristotelis*. *Ibis* 145:54–60.
- 820 Dechaume-Moncharmont, F.-X., T. Brom, and F. Cézilly. 2016. Opportunity costs resulting from
scramble competition within the choosy sex severely impair mate choosiness. *Animal Be-*
822 *haviour* 114:249–260.
- Drickamer, L. C., P. A. Gowaty, and D. M. Wagner. 2003. Free mutual mate preferences in house
824 mice affect reproductive success and offspring performance. *Animal Behaviour* 65:105–114.
- Durrett, R. 2010. *Probability: Theory and Examples*. 4th ed. Cambridge University Press, Cam-
826 bridge.
- Edward, D. A., and T. Chapman. 2011. The evolution and significance of male mate choice. *Trends*
828 *in Ecology and Evolution* 26:647–654.

- Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a
830 changing point of view in the quantitative theory of evolution. *Journal of Mathematical Biology*
34:485–510.
- 832 Etienne, L., F. Rousset, B. Godelle, and A. Courtiol. 2014. How choosy should I be? The relative
searching time predicts evolution of choosiness under direct benefits. *Proceedings of the Royal*
834 *Society B: Biological Sciences* 281:20140190.
- Faivre, B., M. Pr eault, M. Th ery, J. Secondi, B. Patris, and F. C ezilly. 2001. Breeding strategy
836 and morphological characters in an urban population of blackbirds *Turdus merula*. *Animal*
Behaviour 61:969–974.
- 838 Galipaud, M., L. Bollache, A. Oughadou, and F.-X. Dechaume-Moncharmont. 2015. Males do not
always switch females when presented with a better reproductive option. *Behavioral Ecology*
840 26:359–366.
- Gomez, D., E. Huchard, P.-Y. Henry, and M. Perret. 2012. Mutual mate choice in a female-
842 dominant and sexually monomorphic primate. *American journal of physical anthropology*
147:370–379.
- 844 Gowaty, P. A., and S. P. Hubbell. 2009. Reproductive decisions under ecological constraints: it’s
about time. *Proceedings of the National Academy of Sciences of the USA* 106 Suppl 1:10017–
846 10024.
- Halliday, T. 1983. The study of mate choice. Pages 3–32 in P. Bateson, ed. *Mate choice*. Cambridge
848 University Press, Cambridge.
- Hansen, L. T., T. Amundsen, and E. Forsgren. 1999. Symmetry: attractive not only to females.
850 *Proceedings of the Royal Society B: Biological Sciences* 266:1235–1240.
- H ardling, R., T. Gosden, and R. Aguil ee. 2008. Male mating constraints affect mutual mate choice:
852 prudent male courting and sperm-limited females. *American Naturalist* 172:259–271.
- Head, M. L., J. Hunt, M. D. Jennions, R. Brooks, et al. 2005. The indirect benefits of mating with
854 attractive males outweigh the direct costs. *PLoS Biol* 3:e33.

- 856 Hooper, P. L., and G. F. Miller. 2008. Mutual mate choice can drive costly signaling even under perfect monogamy. *Adaptive Behavior* 16:53–70.
- 858 Houston, A. I., and J. M. McNamara. 2005. John maynard smith and the importance of consistency in evolutionary game theory. *Biology and Philosophy* 20:933–950.
- 860 Hua Wen, Y. 1993. Sexual dimorphism and mate choice in *Hyalella azteca* (Amphipoda). *American Midland Naturalist* 129:153–160.
- 862 Huchard, E., A. Courtiol, J. A. Benavides, L. A. Knapp, M. Raymond, and G. Cowlshaw. 2009. Can fertility signals lead to quality signals? insights from the evolution of primate sexual swellings. *Proceedings of the Royal Society of London B: Biological Sciences* 276:1889–1897.
- 864 Ihara, Y., and K. Aoki. 1999. Sexual selection by male choice in monogamous and polygynous human populations. *Theoretical Population Biology* 55:77–93.
- 866 Jennions, M. D., and M. Petrie. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews* 72:283–327.
- 868 Johnstone, R. A. 1997. The tactics of mutual mate choice and competitive search. *Behavioral Ecology and Sociobiology* 40:51–59.
- 870 Johnstone, R. A., J. D. Reynolds, and J. C. Deutsch. 1996. Mutual mate choice and sex differences in choosiness. *Evolution* 50:1382–1391.
- 872 Jones, A. G. 2009. On the opportunity for sexual selection, the bateman gradient and the maximum intensity of sexual selection. *Evolution* 63:1673–1684.
- 874 Jones, A. G., and N. L. Ratterman. 2009. Mate choice and sexual selection: what have we learned since Darwin? *Proceedings of the National Academy of Sciences of the USA* 106 Suppl 1:10001–
876 10008.
- 878 Jones, I. L., and F. M. Hunter. 1993. Mutual sexual selection in a monogamous seabird. *Nature* 362:238–239.

- Kirkpatrick, M., A. S. Rand, and M. J. Ryan. 2006. Mate choice rules in animals. *Animal Behaviour* 71:1215–1225.
880
- Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* 21:919–948.
882
- Kokko, H., M. D. Jennions, and R. Brooks. 2006. Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics* 37:43–66.
884
- Kokko, H., and R. A. Johnstone. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical transactions of the Royal Society B: Biological Sciences* 357:319–330.
886
- Kokko, H., and J. Mappes. 2005. Sexual selection when fertilization is not guaranteed. *Evolution* 59:1876–1885.
888
- Kokko, H., and P. Monaghan. 2001. Predicting the direction of sexual selection. *Ecology Letters* 4:159–165.
890
- Kotiaho, J., and M. Puurtinen. 2007. Mate choice for indirect genetic benefits: scrutiny of the current paradigm. *Functional Ecology* 21:638–644.
892
- Kraaijeveld, K., F. J. Kraaijeveld-Smit, and J. Komdeur. 2007. The evolution of mutual ornamentation. *Animal Behaviour* 74:657–677.
894
- Kraak, S. B., and T. C. M. Bakker. 1998. Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Animal Behaviour* 56:859–866.
896
- Kuijper, B., I. Pen, and F. J. Weissing. 2012. A guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics* 43:287–311.
898
- Luo, Z., C. Li, H. Wang, M. Zhao, Q. Gu, Z. Gu, C. Liao, and H. Wu. 2014. Mutual mate choice in the Asiatic toad, *Bufo gargarizans*, exerts stabilizing selection on body size. *Chinese Science Bulletin* 59:38–45.
900
902

- McNamara, J. M., and E. J. Collins. 1990. The job search problem as an employer-candidate game.
904 *Journal of Applied Probabilities* 27:815–827.
- Mead, L. S., and S. J. Arnold. 2004. Quantitative genetic models of sexual selection. *Trends in*
906 *Ecology & Evolution* 19:264–271.
- Metz, J., S. Geritz, G. Meszena, F. Jacobs, and J. van Heerwaarden. 1996. Adaptive Dynamics, a
908 geometrical study of the consequences of nearly faithful reproduction. *In* *Stochastic and Spatial*
Structures of Dynamical Systems. S.J. van Strien and S.M. Verduyn Lunel, KNAW Verhandelin-
910 gen, North Holland, Amsterdam.
- Monaghan, P., N. B. Metcalfe, and D. C. Houston. 1996. Male finches selectively pair with fecund
912 females. *Proceedings of the Royal Society B: Biological Sciences* 263:1183–1186.
- Myhre, L. C., K. de Jong, E. Forsgren, and T. Amundsen. 2012. Sex roles and mutual mate choice
914 matter during mate sampling. *American Naturalist* 179:741–755.
- Nolan, P. M., F. S. Dobson, M. Nicolaus, T. J. Karels, K. J. McGraw, and P. Jouventin. 2010. Mutual
916 mate choice for colorful traits in king penguins. *Ethology* 116:635–644.
- Owens, I. P., and D. B. A. Thompson. 1994. Sex differences, sex ratios and sex roles. *Proceedings*
918 *of the Royal Society B: Biological Sciences* 258:93–99.
- Parker, G. 1983. Mate quality and mating decisions. *In* P. Bateson, ed., *Mate choice*. Cambridge
920 University Press, Cambridge.
- Pryke, S. R., and S. C. Griffith. 2007. The relative role of male vs. female mate choice in main-
922 taining assortative pairing among discrete colour morphs. *Journal of Evolutionary Biology*
20:1512–1521.
- 924 R Core Team. 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for
Statistical Computing, Vienna, Austria.
- 926 Ramsey, D. M. 2011. Mutual mate choice with multiple criteria. *Advances in Dynamic Games*
11:337–355.

928 Reinhold, K., and H. Schielzeth. 2015. Choosiness, a neglected aspect of preference functions: a
review of methods, challenges and statistical approaches. *Journal of Comparative Physiology*
930 *A* 201:171–182.

Romero-Pujante, M., H. Hoi, D. Blomqvist, and F. Valera. 2002. Tail length and mutual mate
932 choice in bearded tits (*Panurus biarmicus*). *Ethology* 108:885–895.

Rousset, F. 2004. *Genetic Structure and Selection in Subdivided Populations*. Princeton University
934 Press.

Rowland, W. J. 1982. Mate choice by male sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*
936 30:1093–1098.

Rypstra, A. L., C. Wieg, S. E. Walker, and M. H. Persons. 2003. Mutual mate assessment in wolf
938 spiders: differences in the cues used by males and females. *Ethology* 109:315–325.

Sæther, S. A., P. Fiske, and J. A. Kålås. 2001. Male mate choice, sexual conflict and strategic
940 allocation of copulations in a lekking bird. *Proceedings of the Royal Society B: Biological*
Sciences 268:2097–2102.

942 Sandvik, M., G. Rosenqvist, and A. Berglund. 2000. Male and female mate choice affects offspring
quality in a sex-role-reversed pipefish. *Proceedings of the Royal Society B: Biological Sciences*
944 267:2151–2155.

Servedio, M. R., and R. Lande. 2006. Population genetic models of male and mutual mate choice.
946 *Evolution* 60:674–685.

Simao, J., and P. M. Todd. 2002. Modeling mate choice in monogamous mating systems with
948 courtship. *Adaptive Behavior* 10:113–136.

Simmons, L. W. 2001. *Sperm Competition and its Evolutionary Consequences in the Insects*.
950 Princeton University Press.

South, S. H., G. Arnqvist, and M. R. Servedio. 2012. Female preference for male courtship effort
952 can drive the evolution of male mate choice. *Evolution* 66-12:3722–3735.

Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional ecology* 3:259–268.

954 Verrell, P. A. 1995. Males choose larger females as mates in the salamander *Desmognathus santeet-*
lah. *Ethology* 99:162–171.

956 Werner, N. Y., and A. Lotem. 2003. Choosy males in a haplochromine cichlid: first experimental
evidence for male mate choice in a lekking species. *Animal Behaviour* 66:293–298.

958 Wong, B. B., M. D. Jennions, and J. S. Keogh. 2004. Sequential male mate choice in a fish, the
Pacific blue-eye *Pseudomugil signifer*. *Behavioral Ecology and Sociobiology* 56:253–256.

960 **Tables and figures**

Table 1: Summary of notation.

962 **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 (full lines) and in sex y (dotted lines). In this plot the distribution of quality in sex y is represented by an insert ($\alpha_y = \beta_y = 4$), whereas it is uniform in sex x ($\alpha_x = \beta_x = 1$), but other distributions are shown in Figure S4. 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 legend of figure 1 for details. The encounter and latency rates were chosen to favor the evolution of mutual mate choice ($\gamma = l_x = l_y = 0.999$).

970 **Figure 3:** Choosiness at equilibrium in both sexes as a function of encounter rate. See legend of figure 1 for details. The latency and survival rates were chosen to favor the evolution of mutual mate choice ($l_x = l_y = s_x = s_y = 0.999$). The stepwise aspect of the lines is explained by the use of rounded values for choosiness.

974 **Figure 4:** The effect of other-sex choosiness. For each combination of latency rates in sexes x and y , the color 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 section *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 \pm sd = 156.8 ± 49.5) falling within the corresponding bin for latencies.

Figure 5: The predictive power of the sensitivity of the relative searching time (∂RST). For each

986 combination of the absolute values of ∂RST in both sexes, the color indicates the frequency of
cases for which the sign of ∂RST in sex x correctly predicts the direction of selection of choosiness
988 in this sex. This has been obtained by computing ∂RST and the total variation of choosiness in
both sexes for 1.6×10^7 combinations of parameter settings exploring the whole range of possible
990 parameter values (using the discrete tables, see section *Numerical analysis*). Using this approach,
the minimal predictive power computed is 88.2%. As in figure 5, ∂RST was discretized and a
992 variable number of computations falls within each cell, which explains the lack of smoothness
(here the number of numerical computations falling within the corresponding bin for ∂RST is:
994 1568 ± 3055).

Table 1:

Individual-level variables	
q	quality
Class-level variables	
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 variables	
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 variables	
γ	encounter rate
z_r	a given biological or ecological variable affecting the mating rate
z_b	a given biological or ecological variable affecting the benefits per mating

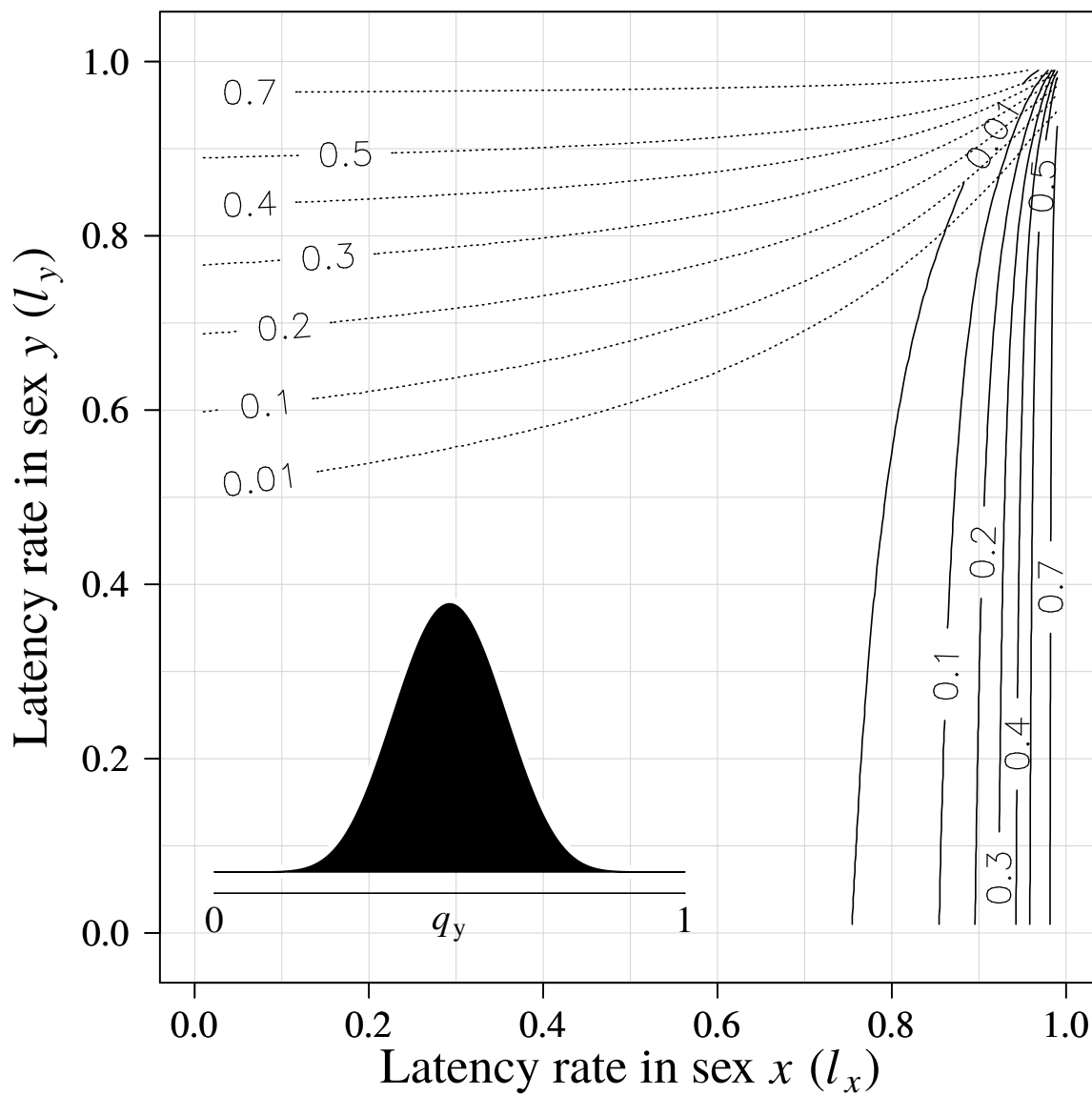


Figure 1:

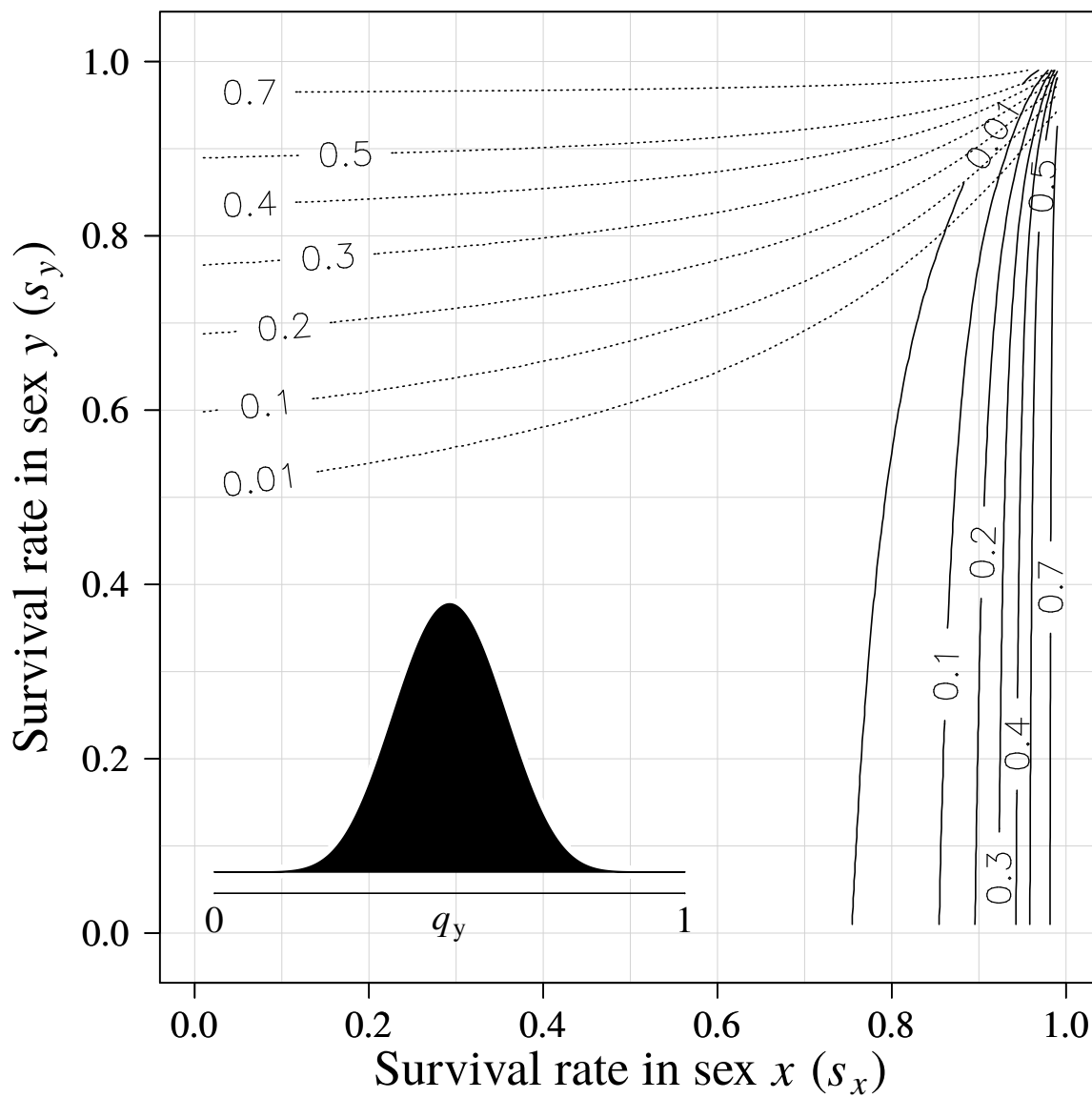


Figure 2:

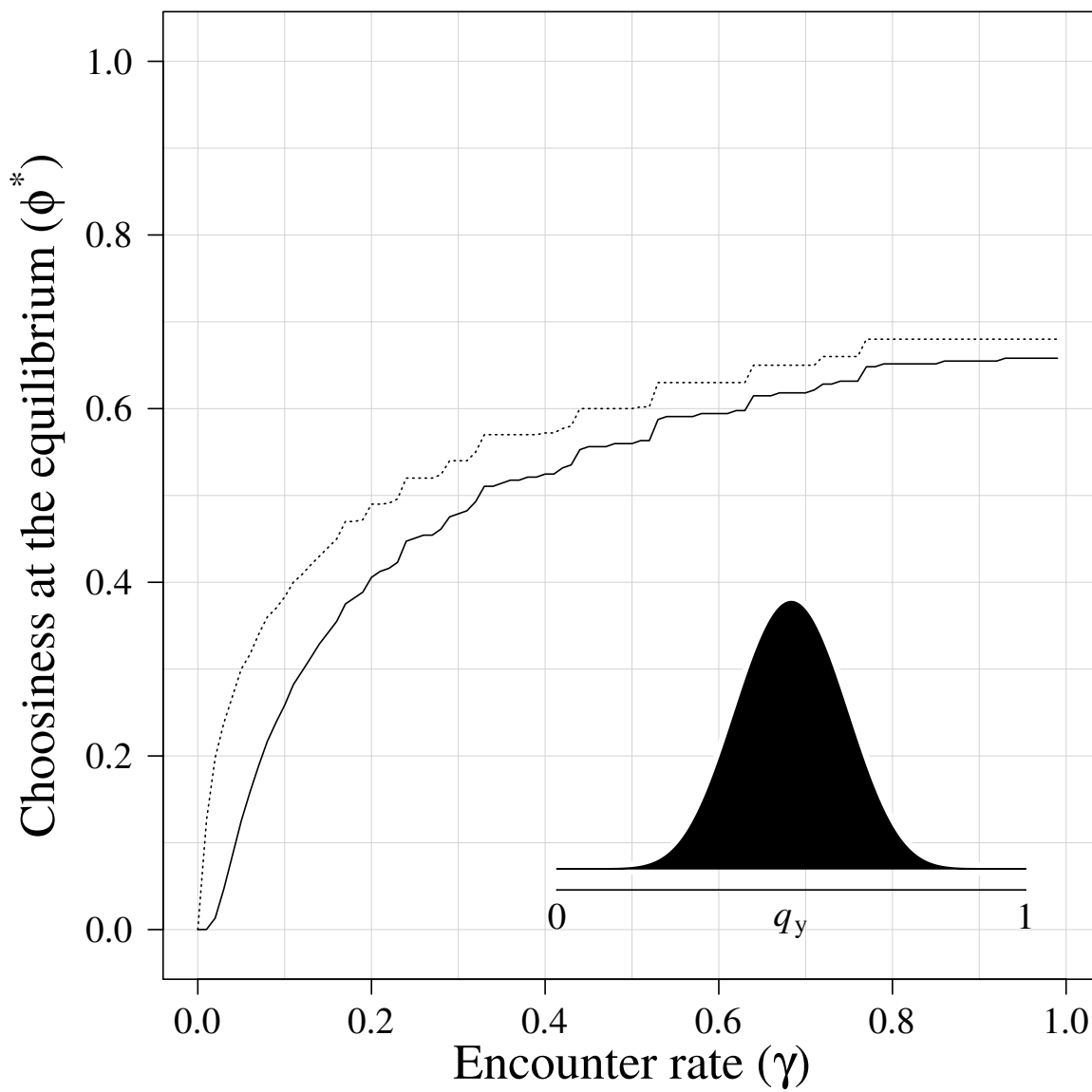


Figure 3:

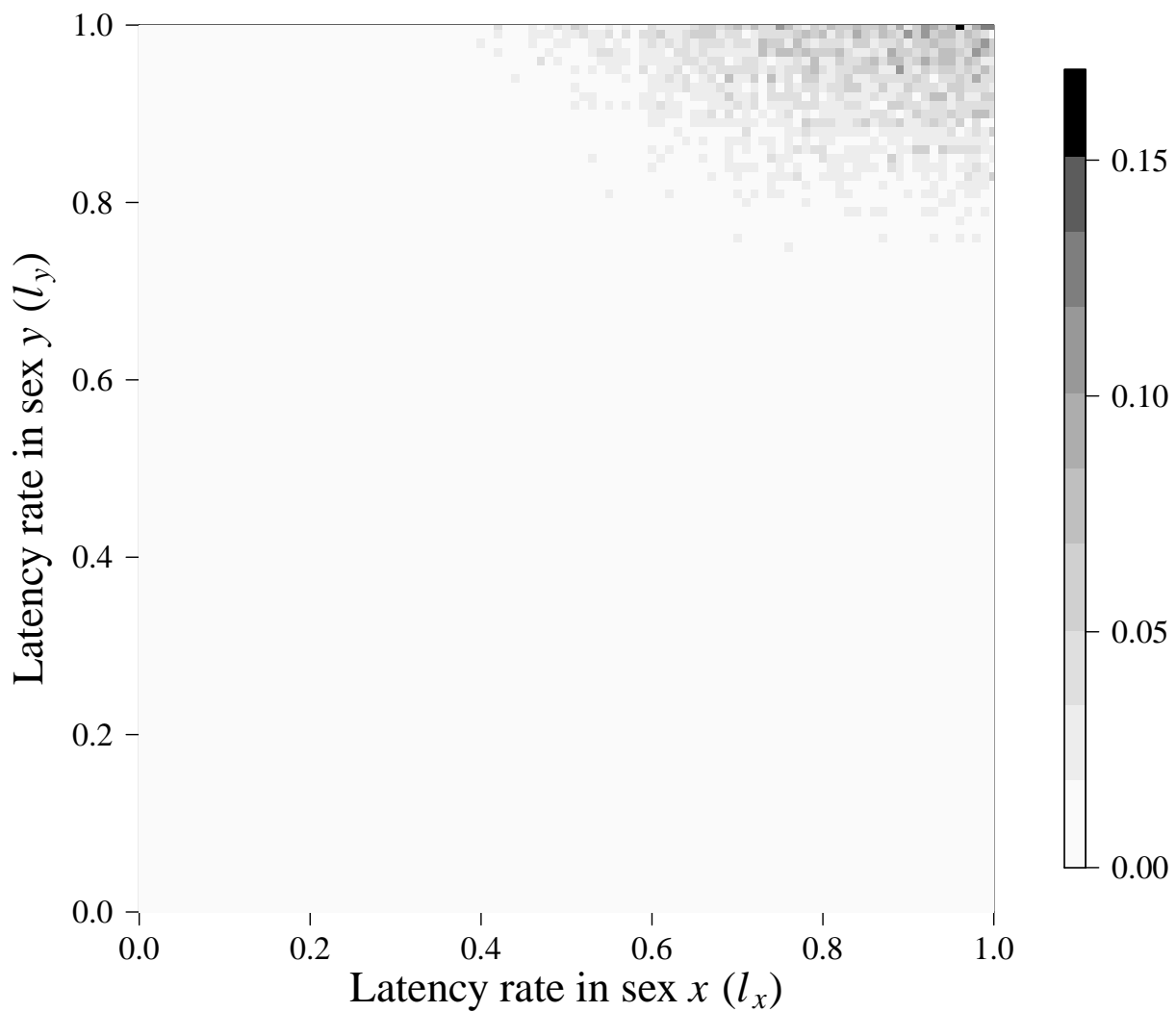


Figure 4:

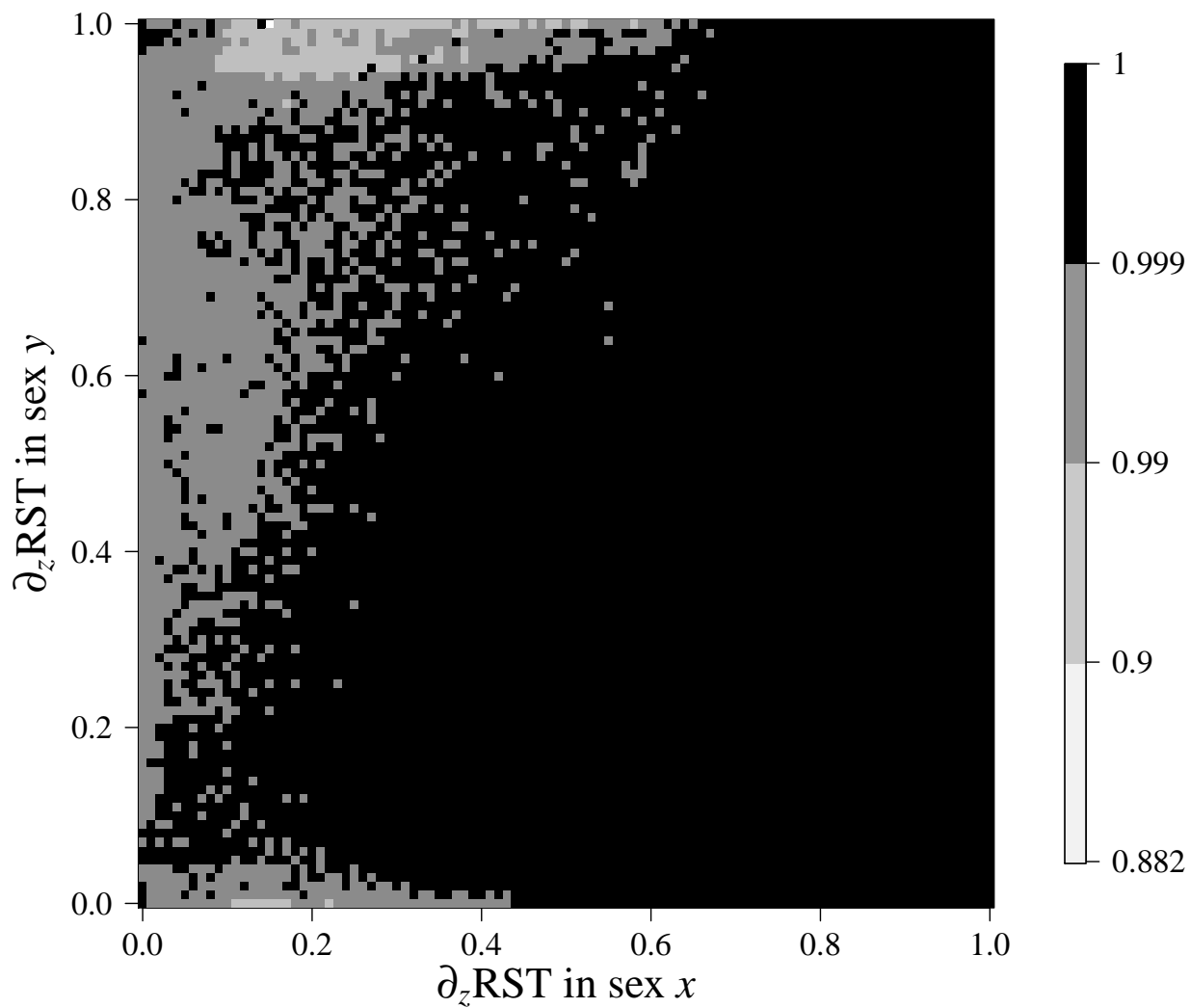


Figure 5: