Appendix A from A. Courtiol et al., "The Evolution of Mutual Mate Choice under Direct Benefits"
(Am. Nat., vol. 188, no. 5, p. 000)

Model Analysis

Joint Convergence Stability of Choosiness

We first determined the equilibrium choosiness, defined as the choosiness values where the selection gradients vanish in each sex. Since the population is of constant size, the lifetime fecundity is an appropriate measure of fitness (e.g., Caswell 2001). Furthermore, the selection gradients are independent of mutant allele frequency and can be deduced from the fecundities of each sex (see Rousset 2004, p. 80) as the joint solution of

$$
\begin{cases}
\left. \dfrac{\partial F_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}}} \right|_{\phi_{x,\mathrm{m}} = \phi_{x,\mathrm{p}} = \phi_x^*} = 0, \\[2em]
\left. \dfrac{\partial F_{y,\mathrm{m}}}{\partial \phi_{y,\mathrm{m}}} \right|_{\phi_{y,\mathrm{m}} = \phi_{y,\mathrm{p}} = \phi_y^*} = 0,
\end{cases}
\tag{A1}
$$

where $F_{x,\mathrm{m}}$ is the expected lifetime fecundity of a mutant representative of a mutant lineage in sex x, hereafter called the mutant of sex x as defined in equation (10), and $F_{y,\mathrm{m}}$ is the expected lifetime fecundity of a mutant representative of a mutant lineage in sex y, hereafter called the mutant of sex y, which can be obtained from exchanging x and y in $F_{x,\mathrm{m}}$. The joint solution (ϕ_x^*, ϕ_y^*) of this system, if it exists, corresponds to a joint equilibrium for choosiness.

From equations (12) and (14), we deduced that the fecundity is computed differently according to whether mutant choosiness is lower or higher than resident choosiness. However, we show in box 1 (eqq. [A2]–[A6]) that left and right derivatives cancel at the same point. This implies that we can always use a single partial derivative in the following computations. We chose the right one, which we denote $\partial_+ F_{x,\mathrm{m}}/\partial \phi_{x,\mathrm{m}}$ and assessed the existence of the equilibrium in each sex numerically.

Box A1

Demonstration of Differentiability of $F_{x,\mathrm{m}}$

The fecundity is computed differently according to whether focal choosiness is lower or higher than resident choosiness (eqq. [12] and [14]). We thus have to ensure that if an equilibrium exists, fecundity is derivable at this equilibrium. To that aim, we distinguished the left and right derivatives at $\phi_{x,\mathrm{m}} = \phi_{x,\mathrm{p}}$, respectively denoted by ∂_- and ∂_+. For either derivative, at this point, we have $\partial \log F_{x,\mathrm{m}}/\partial \phi_{x,\mathrm{m}} = r'_{x,\mathrm{m}}/r_{x,\mathrm{m}} + b'_{x,\mathrm{m}}/b_{x,\mathrm{m}} = 0$ (from eq. [18]). We then found that the right derivative $\partial_+ F_{x,\mathrm{m}}/\partial \phi_{x,\mathrm{m}}$ vanishes when

$$
\frac{\partial_+ b_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}}} = \frac{a_{x,\mathrm{m}} b_{x,\mathrm{m}}}{1 - \phi_{x,\mathrm{m}}}
\tag{A2}
$$

and that the left derivative $\partial_- F_{x,\mathrm{m}}/\partial \phi_{x,\mathrm{m}}$ vanishes when

$$
\frac{\partial_- b_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}}} = \frac{b_{x,\mathrm{m}}}{1 - \phi_{x,\mathrm{m}}}.
\tag{A3}
$$

Thus, the condition for both derivatives to vanish simultaneously is

$$
\frac{\partial_- b_{x,\mathrm{m}}}{\partial \phi_{x,\mathrm{m}}} = \frac{\partial_+ b_{x,\mathrm{m}}}{a_{x,\mathrm{m}} \partial \phi_{x,\mathrm{m}}}.
\tag{A4}
$$

We now show that this condition is always satisfied. The right derivative is that of $b_{x,\mathrm{m}}$ as given by the first equation in expression (15). Only the last fraction therein depends on $\phi_{x,\mathrm{m}}$. It can be written as u_+/v_+, where $v_+ = 1 - \phi_{x,\mathrm{m}} =$

1

$\int_{q_y(\phi_{x,m})}^{1} f_y(q) \, dq$. The standard expression for the derivative of a ratio, $(u/v)' = (vu' - uv')/v^2$, reduces here to

$$\frac{\partial_+ b_{x,m}}{\partial \phi_{x,m}} = \frac{u'_+ - \bar{q}_y v'_+}{v_+} \tag{A5}$$

because $u_+/v_+|_{\phi_{x,m} = \phi_{x,p}} = \bar{q}_y$.

Likewise, the left derivative is that of $b_{x,m}$ as given by the second equation in expression (15). Again, only the last fraction therein depends on $\phi_{x,m}$. It can be written as u_-/v_-, where $u_-/v_-|_{\phi_{x,m} = \phi_{x,p}} = \bar{q}_y$ so that in $\phi_{x,m} = \phi_{x,p}$, $(u_-/v_-)' = (u'_- - \bar{q}_y v'_-)/v_-$. Here $u'_- = u'_+$, both being the derivative of $\int_{q_y(\phi_{x,m})}^{1} q f_y(q) \, dq$. Likewise, $v'_- = v'_+$, both being the derivative of $-\phi_{x,m}$. Moreover, in $\phi_{x,m} = \phi_{x,p}$, $v_- = a_{x,m} v_+$. Hence,

$$\frac{\partial_- b_{x,m}}{\partial \phi_{x,m}} = \frac{u'_- - \bar{q}_y v'_-}{v_-} = \frac{u'_+ - \bar{q}_y v'_+}{a_{x,m} v_+} = \frac{\partial_+ b_{x,m}}{a_{x,m} \partial \phi_{x,m}}. \tag{A6}$$

We conclude that the left and right derivatives of $F_{x,m}$ vanish at the same value of $\phi_{x,m} = \phi_{x,p}$. The same proof holds for the other sex y. $F_{x,m}$ and $F_{y,m}$ are thus derivable at equilibrium—if an equilibrium exists.

For a given parameter setting, we first computed the value of focal-sex mutant choosiness $\phi_{x,m}$ that satisfies the following condition for any fixed value of other-sex choosiness:

$$\frac{\partial_+ F_{x,m}}{\partial \phi_{x,m}} = 0. \tag{A7}$$

This gave us the value of focal-sex choosiness at the singular point for each value of other-sex choosiness, which graphically corresponds to a curve (fig. A1). Then we computed the same curve for other-sex choosiness. If the two curves cross, then equation (A1) is satisfied and there is an equilibrium. We repeated this as well as other numerical analyses for 3.2×10^6 different parameter sets representing the whole range of parameters (see "Numerical Analysis" in the main text). We also checked that there is always one single equilibrium for each parameter set considered.

Second, we tested, also numerically, whether the equilibrium obtained is convergence stable (see Eshel 1996). Convergence stability was examined by checking that the gradients for each choosiness are positive below and negative above the equilibrium value in each sex.

Third, we evaluated the joint convergence stability of the joint equilibrium for choosiness. To accomplish this step, we have to assume that the mutational effects on each choosiness are independent. Under this assumption, the joint convergence stability is determined by the Jacobian matrix of the selection gradients (see Leimar 2009).

Finally, in the case of a null choosiness in sex y at equilibrium, it is possible to determine the evolutionary stability by checking that the following equation is true at equilibrium (e.g., see Metz et al. 1996):

$$\left. \frac{\partial_+^2 F_{x,m}}{\partial \phi_{x,m}^2} \right|_{\phi_{y,m} = \phi_{y,p} = 0} < 0. \tag{A8}$$

The joint evolutionary stability is determined by the Hessian matrix of the fecundities of both sexes (see Leimar 2009). If the equilibria are convergence and evolutionarily stable, the only allele favored by selection in sex x (y) is the one coding for the choosiness ϕ_x^* (ϕ_y^*). We numerically checked the joint evolutionary stability and the joint convergence stable equilibria.

Effect of Ecological Variables on the Joint Equilibrium for Choosiness

The expected fecundity of the mutant of sex x (i.e., $F_{x,m}$) is expressed as the product of the mating rate $r_{x,m}$, the expected benefits per mating $b_{x,m}$, and the expected lifetime (see eq. [10]). Because lifetime is not related to choosiness, at equilibrium we have

$$0 = \left.\frac{\partial_+ \ln(F_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{m}}}\right|_{\phi_{x,\mathrm{m}} = \phi_x^*} = \overbrace{\left.\frac{\partial_+ \ln(r_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{m}}}\right|_{\phi_{x,\mathrm{m}} = \phi_x^*}}^{R_x^*} + \overbrace{\left.\frac{\partial_+ \ln(b_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{m}}}\right|_{\phi_{x,\mathrm{m}} = \phi_x^*}}^{B_x^*}, \tag{A9}$$

where R_x^* represents the relative change in mating rate in sex x at equilibrium and B_x^* the relative change in expected benefits per mating at equilibrium. We obtain from the previous equation

$$R_x^* = -B_x^*. \tag{A10}$$

To understand how a change in a given biological or ecological variable influences the joint equilibrium for choosiness, one has therefore to analyze how a change in an individual's choosiness $\phi_{x,\mathrm{m}}$ influences its mating rate and/or the expected benefits per mating near the joint equilibrium choosiness.

Effect of Variables Influencing the Mating Rate of the Mutant of Sex x

Let us consider z_r, a given biological or ecological variable affecting the mating rate $r_{x,\mathrm{m}}$ of the mutant of sex x without affecting its expected benefits per mating $b_{x,\mathrm{m}}$. To study the effect of a change in z_r on the evolution of choosiness, we relied on a graphical method (Maynard Smith 1982, p. 46). We first need to represent the trade-off between the decrease in mating rate and the increase in expected benefits per mating (i.e., the fundamental trade-off of mate choice; see the introduction in the main text). We do so by plotting the curve $T(\phi_{x,\mathrm{m}}, \phi_{x,\mathrm{p}}, \phi_{y,\mathrm{p}}) \equiv [b_{x,\mathrm{m}}(\phi_{x,\mathrm{m}}, \phi_{x,\mathrm{p}}, \phi_{y,\mathrm{p}}), r_{x,\mathrm{m}}(\phi_{x,\mathrm{m}}, \phi_{x,\mathrm{p}}, \phi_{y,\mathrm{p}})]$ for all possible levels of mutant choosiness $\phi_{x,\mathrm{m}}$ and for given resident values in each sex (fig. A2). Because of the trade-off between $r_{x,\mathrm{m}}$ and $b_{x,\mathrm{m}}$, the slope of T is always negative. Moreover, we have numerically found that choosiness in a given sex always admits a single convergence stable strategy regardless of choosiness in the other sex (see result 1 in the main text), which implies that T is concave (Maynard Smith 1982). The slope of T is thus increasingly negative when $\phi_{x,\mathrm{m}}$ increases.

Then we plotted T when the variable z_r takes value z_{r1} and when it takes value z_{r2} (with $z_{r1} \neq z_{r2}$). Let us denote these curves T_1 and T_2, respectively. Precisely, in the curve $T_1 \equiv T(\phi_{x,\mathrm{m}}, \phi_x^*(z_{r1}), \phi_y^*(z_{r1}))$, resident choosiness is fixed to the convergence stable strategy in both sexes ($\phi_{x,\mathrm{p}} = \phi_x^*(z_{r1})$ and $\phi_{y,\mathrm{p}} = \phi_y^*(z_{r1})$). In the curve $T_2 \equiv T(\phi_{x,\mathrm{m}}, \phi_x^*(z_{r2}), \phi_y^*(z_{r1}))$, the focal-sex resident choosiness is fixed to its new convergence stable strategy ($\phi_{x,\mathrm{p}} = \phi_x^*(z_{r2})$) after a change in z_r from z_{r1} to z_{r2}, but choosiness remains unchanged in the other sex ($\phi_{y,\mathrm{p}} = \phi_y^*(z_{r1})$). Because the curves are represented on a log-log scale, the equilibrium for focal choosiness corresponds to the point where the slope of the curves equals -1, that is, when $R_x^* = -B_x^*$ (eq. [A10]).

Note that z_r affects $r_{x,\mathrm{m}}$ but not $b_{x,\mathrm{m}}$ and that $b_{x,\mathrm{m}}$ is not a function of $\phi_{x,\mathrm{p}}$ (and thus of ϕ_x^*) when $\phi_{x,\mathrm{m}}$ is higher than or equal to $\phi_{x,\mathrm{p}}$ (which is the case here because we consider the right derivatives in eq. [A9]). Thus, for a small change of z from z_{r1} to z_{r2}, each point of the T_1 curve moves (for fixed $\phi_{x,\mathrm{m}}$ and $\phi_{y,\mathrm{p}}$) along the $r_{x,\mathrm{m}}$ axis but not along the $b_{x,\mathrm{m}}$ axis. Hence, the change in the slope of T with respect to $\phi_{x,\mathrm{m}}$ is entirely determined by the change in slope of $\ln(r_{x,\mathrm{m}})$, which can be written

$$\frac{\partial(\partial_+ \ln(r_{x,\mathrm{m}})/\partial \phi_{x,\mathrm{m}})}{\partial z_r} + \frac{\partial \phi_x^*}{\partial z_r}\frac{\partial(\partial_+ \ln(r_{x,\mathrm{m}})/\partial \phi_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{p}}} = \frac{\partial R_x^*}{\partial z_r} + \frac{\partial \phi_x^*}{\partial z_r}\frac{\partial(\partial_+ \ln(r_{x,\mathrm{m}})/\partial \phi_{x,\mathrm{m}})}{\partial \phi_{x,\mathrm{p}}}. \tag{A11}$$

Here R_x^* is the notation introduced in equation (A9), and all derivatives of $\ln r_{x,\mathrm{m}}$ are evaluated in $z_r = z_{r1}$, $\phi_{x,\mathrm{m}} = \phi_x^*(z_{r1})$, and $\phi_{x,\mathrm{p}} = \phi_x^*(z_{r1})$. The total variation encompasses two effects on the slope of the trade-off curve. The first effect corresponds to the partial variation in the slope of the trade-off curve due to a change in z_r while resident choosiness remains fixed at the equilibrium value for z_{r1} ($\phi_x^*(z_{r1})$ in sex x and $\phi_y^*(z_{r1})$ in sex y); therefore, it represents only the change in the functional relationship of T to each choosiness. The second effect corresponds to the partial variation in the slope of the trade-off curve due to a change in focal-sex resident choosiness around $\phi_{x,\mathrm{p}} = \phi_x^*$ while other-sex resident choosiness remains fixed.

If the slope of T_2 at $\phi_{x,\mathrm{m}} = \phi_x^*(z_{r1})$ is higher than -1 on the log-log scale, as in figure A2, then the value of $\phi_{x,\mathrm{m}}$ where the slope of T_2 equals -1 is higher than $\phi_x^*(z_{r1})$, that is, $\phi_x^*(z_{r2}) > \phi_x^*(z_{r1})$. Conversely, if the slope of T_2 at $\phi_{x,\mathrm{m}} = \phi_x^*(z_{r1})$ were lower than -1, $\phi_x^*(z_{r2})$ would be lower than $\phi_x^*(z_{r1})$. This means that we can deduce the sign of the effect of z_r on

the value of choosiness at equilibrium in sex x by studying its effect on the slope of the trade-off curve on the log-log scale. Hence,

$$\text{sgn}\left(\frac{\partial \phi_x^*}{\partial z_r}\right) = \text{sgn}\left(\frac{\partial R_x^*}{\partial z_r} + \frac{\partial \phi_x^*}{\partial z_r}\frac{\partial(\partial_+ \ln(r_{x,m})/\partial \phi_{x,m})}{\partial \phi_{x,p}}\right). \tag{A12}$$

If for some real numbers A (where $A \neq 0$), B, and C, $\text{sgn}(A) = \text{sgn}(B + AC)$ and $C < 0$, then $\text{sgn}(B) = \text{sgn}(A)$. Hence, the signs of $A = \partial \phi_x^*/\partial z_r$ and $B = \partial R_x^*/\partial z_r$ are identical if

$$\frac{\partial(\partial_+ \ln(r_{x,m})/\partial \phi_{x,m})}{\partial \phi_{x,p}} < 0. \tag{A13}$$

From the fact that the mixed derivative of the product $(1 - \phi_{x,m})a_{y,p}$ vanishes, the mixed derivative of $\ln r_{x,m}$ depends only on the mixed derivative of the denominator in the first expression for $r_{x,m}$ in equation (12), which reduces to

$$\left.\frac{\partial_+^2 \ln r_{x,m}}{\partial \phi_{x,m}\partial \phi_{x,p}}\right|_{\phi_{x,m} = \phi_x^*} = -\left.\frac{\partial_+ \ln\left((1 - s_x l_x)/(1 - s_x l_x + s_x \gamma(1 - \phi_{x,m})a_{y,p}l_x)\right)}{\partial \phi_{x,p}}\right|_{\phi_{x,m} = \phi_x^*}. \tag{A14}$$

When $\phi_{x,p}$ increases, the availability $a_{y,p}$ of other-sex individuals that are of sufficient quality to mate decreases. As a consequence, the partial derivative in the right-hand side of the previous equation is positive, which proves equation (A13), and then

$$\text{sgn}\left(\frac{\partial \phi_x^*}{\partial z_r}\right) = \text{sgn}\left(\frac{\partial R_x^*}{\partial z_r}\right). \tag{A15}$$

This shows that to study the variation in choosiness at equilibrium in a given sex following a change in the mating rate of this sex, we can simply study the variation in the relative change in the mating rate computed in this sex while holding the other-sex choosiness fixed.

Effect of a Variable Influencing the Expected Benefits per Mating of the Mutant

Let us now consider the biological or ecological variable z_b to affect the expected benefits per mating $b_{x,m}$ of the mutant of sex x without affecting its mating rate $r_{x,m}$. By considering graphs of $T'(\phi_{x,p}, \phi_{y,p}) \equiv (r_{x,m}(\phi_{x,m}, \phi_{x,p}, \phi_{y,p}), b_{x,m}(\phi_{x,m}, \phi_{x,p}, \phi_{y,p}))$, where the axes have been swapped relative to T (fig. A3), we can repeat the argument of the previous section and conclude that

$$\text{sgn}\left(\frac{\partial \phi_x^*}{\partial z_b}\right) = \text{sgn}\left(\frac{\partial B_x^*}{\partial z_b}\right). \tag{A16}$$

Variation in Choosiness at Equilibrium and the Sensitivity of RST

The mating rate $r_{x,m}$ of the mutant in sex x equals $1/t_{x,m}$, where $t_{x,m}$ is the mean time of one reproductive event performed by a mutant. The variable $t_{x,m}$ equals the expected time spent searching for a mate (denoted $\tau_{x,m}$) plus the expected time spent in latency after a mating. The partial derivative of the logarithm of $r_{x,m}$ with respect to $\phi_{x,m}$ at equilibrium (i.e., R_x^* in eq. [A9]) can therefore be rewritten as

$$R_x^* = -\left.\frac{1}{t_{x,m}}\frac{\partial_+ t_{x,m}}{\partial \phi_{x,m}}\right|_{\phi_{x,m} = \phi_x^*}. \tag{A17}$$

Because we assume that the time spent in one latency period is not related to choosiness, the above equation becomes

$$R_x^* = -\left.\frac{1}{t_{x,m}}\frac{\partial_+ \tau_{x,m}}{\partial \phi_{x,m}}\right|_{\phi_{x,m} = \phi_x^*}. \tag{A18}$$

The mean time spent searching for a mate $\tau_{x,m}$ can be written as the inverse of the probability that a mutant mates given that it is available for mating, which equals the inverse of $s_x \gamma (1 - \phi_{x,m}) a_{y,p}$ (from eq. [1]). Then equation (A18) takes the form

$$R_x^* = -\frac{1}{1 - \phi_{x,m}} \frac{\tau_{x,m}}{t_{x,m}}, \tag{A19}$$

where the ratio $\tau_{x,m}/t_{x,m}$ corresponds to the relative searching time (RST, following Etienne et al. 2014; i.e., the proportion of one reproductive event [or lifetime] that is devoted to searching for mates). The partial derivative of the previous equation with respect to z_r (a given biological or ecological variable affecting the mating rate of the mutant of sex x but not its mating benefit) is

$$\frac{\partial R_x^*}{\partial z_r} = -\frac{1}{1 - \phi_{x,m}} \frac{\partial \mathrm{RST}_x^*}{\partial z_r}. \tag{A20}$$

From equation (A15) and $\phi_{x,m} \leq 1$, this yields

$$\mathrm{sgn}\left(\frac{\partial \phi_x^*}{\partial z_r}\right) = -\mathrm{sgn}\left(\frac{\partial \mathrm{RST}_x^*}{\partial z_r}\right). \tag{A21}$$

We have seen before that the term $\partial \phi_x^*/\partial z_r$, the partial variation in choosiness, represents the variation in choosiness in sex x caused by a change in z_r while choosiness remains fixed in the other sex. Likewise, the term $\partial \mathrm{RST}_x^*/\partial z_r$ (which is more compactly denoted $\partial \mathrm{RST}$) corresponds to the sensitivity of RST of sex x with respect to z_r, that is, the variation in the RST caused by the change in z_r while choosiness remains fixed in both sexes.
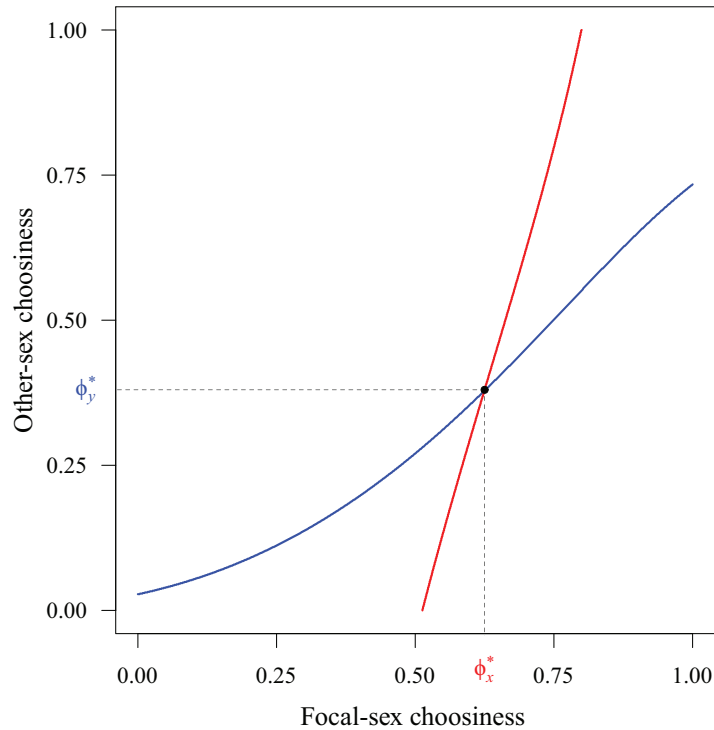

Figure A1: Computation of the values of choosiness at equilibrium. The red (blue) curve gives the value of focal-sex (other-sex) choosiness at the singular point for all possible values of fixed other-sex (focal-sex) choosiness. The point where both curves cross is the equilibrium, at which choosiness equals ϕ_x^* in the focal sex and ϕ_y^* in the other sex. The parameter setting used to draw this plot is $\gamma = s_x = s_y = l_y = 0.99$, $l_x = 0.999$, and $\alpha_x = \beta_x = \alpha_y = \beta_y = 1$.
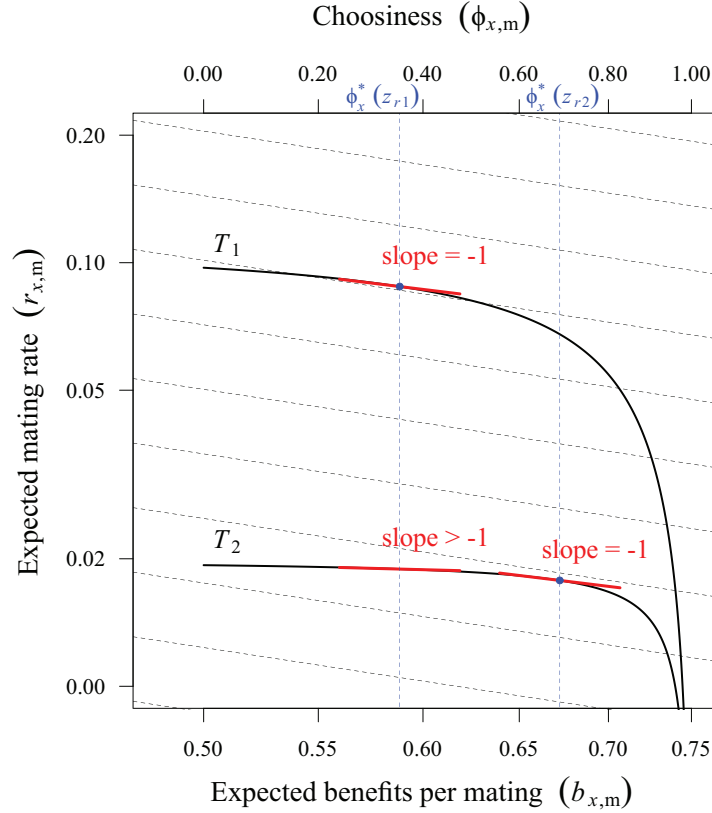
Figure A2: Graphical representation of the effect of z on the fundamental trade-off between direct benefits per mating and lower mating rate. The mating rate of the mutant of sex x ($r_{x,m}$, left axis) is plotted against its expected benefits per mating ($b_{x,m}$, lower axis) for all possible values of its choosiness $\phi_{x,m}$ (upper axis). The curve T_1 corresponds to the case $z_r = z_{r1}$, $\phi_{x,p} = \phi_x^*(z_{r1})$, and $\phi_{y,p} = \phi_y^*(z_{r1})$, whereas the curve T_2 corresponds to the case $z_r = z_{r2}$, $\phi_{x,p} = \phi_x^*(z_{r2})$, and $\phi_{y,p} = \phi_y^*(z_{r1})$. The representation is logarithmic; thus, the equilibrium corresponds to the point on each curve (indicated in blue) where its slope equals -1 (indicated by a red line that is parallel to the dotted gray lines), that is, when $R_x^* = -B_x^*$ (see eq. [A10]). Here $l_{x_1} = 0.9$ and $l_{x_2} = 0.99$. Other parameters are fixed between the curves: $\gamma = 0.5$, $s_x = s_y = 0.99$, $l_y = 0$, and $\alpha_x = \beta_x = \alpha_y = \beta_y = 1$. As $l_y = 0$, $a_{y,p} = 1$ and thus $b_{x,m}$ is not a function of $\phi_{x,p}$ anymore (see eq. [15]), which allows us to represent the variation in $\phi_{x,m}$ on the same axis for the two curves T_1 and T_2. Considering $l_y = 0$ thus makes the geometrical argument described in the text easier to represent, but this argument remains true regardless of the values of the parameters.
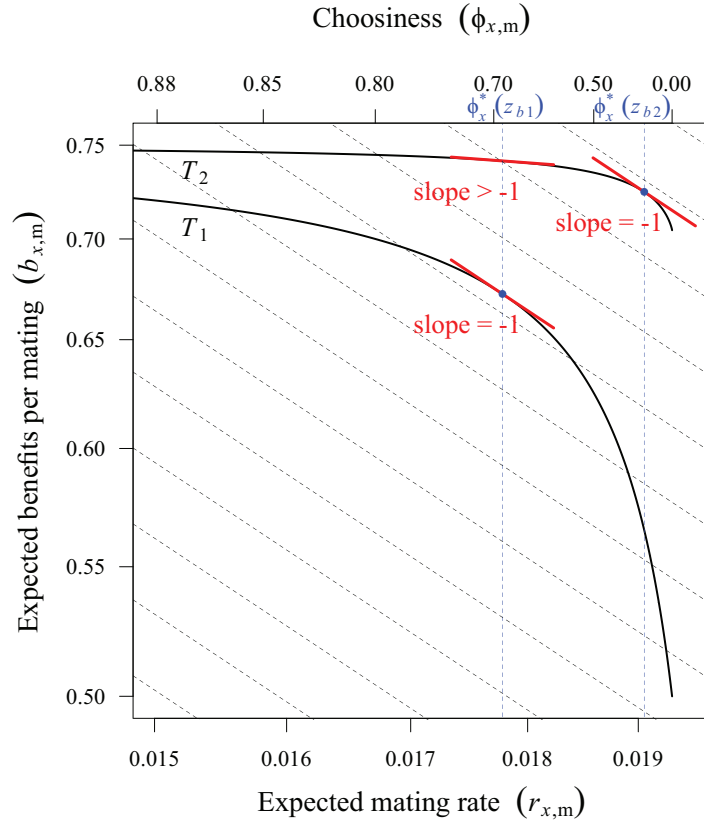
Figure A3: Graphical representation of the effect of z_b on the fundamental trade-off between direct mating benefits and lower mating rate. See the legend of figure A2 for details. Here $\alpha_{y_1} = 1$ and $\alpha_{y_2} = 10$. Other parameters are fixed between the curves: $\gamma = 0.5$, $s_x = s_y = l_x = 0.99$, $l_y = 0$, and $\alpha_x = \beta_x = \beta_y = 1$.