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# The evolution of sex differences in mate-attracting signalling

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## ABSTRACT

**Question:** To attract mates, many insects dance, have conspicuous plumage, call vocally, and emit signals such as pheromones. Mate-attracting signals are produced predominantly by males in some species and by females in others. We ask, which sex should evolve to produce mate-attracting signals?

**Method:** We used a quantitative genetic model for the signal-sending and signal-receiving efforts of the two sexes. Mate-finding success is assumed to be a product of power functions of the signal sender's and signal receiver's investments.

**Results:** If mate-finding success strongly depends on the investments of both senders and receivers, only one sex evolves to send the signals; otherwise, both sexes evolve to emit signals. Males evolve to assume the role that more strongly affects mate-finding success, and to engage in mate-finding activities with more investments than females.

*Keywords*: mate-attracting signal, sex role, elasticity, quantitative genetic dynamics.

## INTRODUCTION

For many insects, the habitats of larvae and pupae are spatially distributed, and adults must find each other to encounter individuals of the opposite sex. Using only random searching, it would be difficult to achieve sufficiently high mate-finding success within a limited time. Many insects send signals to indicate their presence and location to individuals of the opposite sex. Signals may be chemical [i.e. pheromones (Svensson, 1996; Wyatt, 2003; Johansson and Jones, 2007)], auditory [i.e. vocal calls or vibrations (Gwynne, 1987; Cade and Cade, 1992; Cooley, 2001)] or visual [i.e. body and wing coloration, or dance (DeRivera *et al.*, 2003)]. The cost of producing such signals may be enhanced by predators or parasites that use them to identify and locate the senders of the signals, especially signals that can be easily detected (Walker, 1964). Similarly, the cost of searching for the signal sender can be large for the receiver (Lloyd, 1965; Eberhard, 1977; Gwynne, 1987), because it is often laborious to search by flying and walking.

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The sex that emits a mate-searching signal varies among species. For example, in cicadas and crickets, males produce loud vocal calls and females search for males (Gwynne, 1987; Cade and Cade, 1992; Cooley, 2001). In contrast, among insect species that produce mate-attracting pheromones, the females commonly emit the pheromones and males search for females (Svensson, 1996). In these species, females tend to produce a relatively small amount of pheromones, and males react to these signals with very sensitive sensory organs. In other insects, males produce a large amount of pheromones to attract females.

The cost and effectiveness of producing and responding to mate-attracting signals may be important in determining the sex that emits them. The energetic cost of producing signals may be heavier for vocal calls than for pheromone production (Wyatt, 2003). Many insects that use vocal signals, such as cicadas and crickets, have a large body size that is needed to produce sufficiently loud calls. In contrast, the cost of producing pheromones is relatively small (Hedin *et al.*, 1974). The cost difference between auditory and chemical signals may be even larger if we consider the risk of being detected by dangerous predators. Chemical signals are detectable only by those individuals equipped with specific receptor molecules, so they may remain undetected by generalist predators (Svensson, 1996). Although signal sending (producing mate-attracting signals) and signal receiving (detecting and responding to signals) may both be costly, males commonly perform the role that is more costly or dangerous (Svensson, 1996; Johansson and Jones, 2007).

In this study, we investigate the evolutionary process that determines which sex sends mate-attracting signals, to indicate presence and location, to individuals of the opposite sex, by assuming that the individual successfully detecting the signals is attracted to the sender. This is quite different from many past theoretical studies of sex differences in mating behaviour, which have focused on mate choice. Typically, each female encounters multiple potential mates and chooses among them, and males compete with each other in the mate-acquisition process (Parker, 1978; Davies and Halliday, 1979; Real, 1990; Wiley and Poston, 1996; Kokko and Johnstone, 2002). In the present study, we focus on the process of mate searching, rather than mate choice.

We adopt a simple, quantitative genetic model for four quantitative traits: males' signal-sending effort, females' responding effort, females' signal-sending effort, and males' responding effort. The evolutionary outcome is strongly affected by the dependence of signal performance on the investments by the signal sender and the signal receiver. Depending on the sensitivity of signal effectiveness on signal-sending and -receiving efforts, both males and females or just one of them may evolve to send mate-attracting signals. In general, males tend to be the senders and females the receivers and searchers, if sending signals is more effective in improving mate-finding success than searching for the opposite sex; in contrast, females tend to be the senders and males the receivers and searchers in the opposite case. Furthermore, it has been observed in many species that males generally evolve to invest more effort in mate-finding processes than females.

## MODEL

We consider a population of organisms with two sexes: male and female. Individuals may emit signals to attract individuals of the opposite sex, and signals produced by males are different from those produced by females. When an individual receives a signal produced by an individual of the opposite sex, it begins searching for the signal sender. The searching activities of a signal receiver can be quite costly due to locomotion and navigation.

Let $x_m$ and $x_f$ be the investments in signal-sending activities of males and females, respectively. Let $y_m$ and $y_f$ be the investments of males and females, respectively, in the activities of signal receiving, including detecting the signal, and searching for and encountering the sender. Therefore, males produce a signal at an intensity of $x_m$, which is received by females with a sensitivity of $y_f$. Similarly, females produce a signal at an intensity of $x_f$, which is received by males with a sensitivity of $y_m$. The number of encounters between the sexes increases with the investments of the signal sender and the signal receiver.

Let $F(x_m, y_m; x_f, y_f)$ be the probability for a male with phenotype $(x_m, y_m)$ and a female with phenotype $(x_f, y_f)$ to encounter each other. Here, we assume that the probability for a male and a female to encounter each other is: $F = F_1 + F_2$, where $F_1(x_m, y_f)$ is the probability of an encounter resulting from the male sending mate-attracting signals and the female searching for them, and $F_2(x_f, y_m)$ is the probability of an encounter resulting from the female sending mate-attracting signals and the male searching for them.

We assume that the number of encounters resulting from one sex sending a signal and the other receiving it is expressed as a product of two power functions:

$$\begin{bmatrix}\text{probability of encounters}\\ \text{between the two}\end{bmatrix} \propto \begin{bmatrix}\text{signal sender's}\\ \text{investment}\end{bmatrix}^{\alpha} \times \begin{bmatrix}\text{signal receiver's}\\ \text{investment}\end{bmatrix}^{\beta},$$

where the sensitivity of the receiver includes not only the sensitivity of sensory organs, but also the activities of searching for and locating the signal sender. If, for example, $\alpha$ is very close to zero, the number of encounters is almost independent of the signal sender's activities, but if $\alpha$ is large, the number of encounters should depend strongly on the signal intensity. Therefore, $\alpha$ indicates how the number of encounters depends on the signal sender's activities, while $\beta$ indicates how the number of encounters depends on the signal receiver's sensitivity. These are called 'elasticities' in sensitivity analysis. The above functional form is called the Cobb-Douglas production function in economics (Douglas, 1976). Specifically, we assume the following functional forms:

$$F_1 = g_1 x_m^{\alpha} y_f^{\beta} \qquad \text{and} \qquad F_2 = g_2 x_f^{\alpha} y_m^{\beta}, \tag{1}$$

which imply that the number of encounters is a power function of both the signal sender's activities and signal receiver's ability.

We consider that males and females search for mates within a region, or mating group, which contains $Q$ males and $R$ females. The average number of matings per male is $R \bullet F(x_m, y_m; \bar{x}_f, \bar{y}_f)$, where $x_m$ and $y_m$ are the focal individual's traits, while $\bar{x}_f$ and $\bar{y}_f$ are the population averages. Investments in signal-sending and signal-receiving activities are accompanied by incurred costs. We assume the following function for survivorship: $\exp[-b_m x_m^2 - c_m y_m^2]$. Thus, we have the following expression of male fitness:

$$W_m(x_m, y_m) = \lambda_m R \bullet F(x_m, y_m; \bar{x}_f, \bar{y}_f) \exp[-b_m x_m^2 - c_m y_m^2], \tag{2a}$$

which indicates that male fitness increases in proportion to the expected number of encounters with females.

In contrast, the average number of encounters with males for a female is $F(\bar{x}_m, \bar{y}_m; x_f, y_f)$, which leads to the probability for a female to be mated, $1 - \exp[-Q \bullet F(\bar{x}_m, \bar{y}_m; x_f, y_f)]$, where $x_f$ and $y_f$ are the focal individual's traits, while $\bar{x}_m$ and $\bar{y}_m$ are the population averages.

If the cost of a female sending mate-attracting signals is $b_f$, and a female's mate-searching cost is $c_f$, we have the following expression for female fitness:

$$W_f(x_f, y_f) = \lambda_f\{1 - \exp(-Q \bullet F(\bar{x}_m, \bar{y}_m; x_f, y_f))\} \exp[-b_f x_f^2 - c_f y_f^2]. \quad (2b)$$

The evolution of the averages of these traits can be discussed in terms of quantitative genetic dynamics (Lande, 1976; Iwasa *et al.*, 1991), as follows:

$$\Delta\bar{x}_m = \frac{1}{2} G_{xm} \frac{\partial}{\partial x_m} \ln W_m, \qquad \Delta\bar{y}_m = \frac{1}{2} G_{ym} \frac{\partial}{\partial y_m} \ln W_m,$$

$$\Delta\bar{x}_f = \frac{1}{2} G_{xf} \frac{\partial}{\partial x_f} \ln W_f, \qquad \Delta\bar{y}_f = \frac{1}{2} G_{yf} \frac{\partial}{\partial y_f} \ln W_f, \quad (3)$$

where $G_{xm}$, $G_{ym}$, $G_{xf}$, and $G_{yf}$ are additive genetic variances for corresponding quantities. The factors ½ indicate that the traits are sex-limited and are expressed only in one-half of generations. Partial derivatives are evaluated at the population mean ($x_m = \bar{x}_m$, $y_m = \bar{y}_m$, $x_f = \bar{x}_f$, $y_f = \bar{y}_f$). Here we adopt the formalism by Iwasa *et al.* (1991), which is valid under weak selection (while Lande's formalism assumes normality of genetic value distribution and that the derivatives in the selection gradient are different). Here, we neglect the effects of additive genetic covariance between traits and the preference of a trait by the opposite sex, because it is known to be of a magnitude smaller under a weak selection scheme (Pomiankowski and Iwasa, 1993; Tazzyman and Iwasa, 2010).

Figures 1a and 1b illustrate trajectories of the model for two typical cases, with $F_1$ and $F_2$ as axes, and trajectories starting from different initial conditions. The trajectories cross because the figure is a projection of four-dimensional dynamics on a plane. In Fig. 1a, all the trajectories converge to the same equilibrium at which $\bar{x}_m$, $\bar{y}_m$, $\bar{x}_f$ and $\bar{y}_f$ are positive.

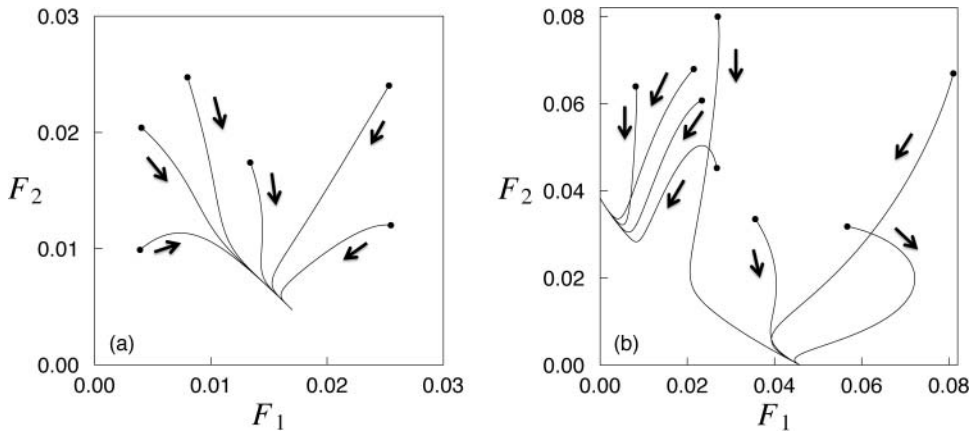


**Fig. 1.** Trajectories of evolutionary dynamics. The projection to a ($F_1$, $F_2$) plane is shown. (a) Starting from any initial conditions, trajectories converge to the equilibrium at which both modes of signalling (males as signal senders and females as signal senders) are used ($F_1 > 0$ and $F_2 > 0$); $\alpha = 1.5$ and $\beta = 0.5$. (b) There are two equilibriums that are locally stable. In one, only the signalling mode in which males are the senders is used ($F_1 > 0$ and $F_2 = 0$). In the second, only the signalling mode in which females are the senders is used ($F_1 = 0$ and $F_2 > 0$); $\alpha = 2.0$ and $\beta = 1.0$. Other parameters: $P = Q = 100$, $g_1 = g_2 = 0.01$, and $b_m = b_f = c_m = c_f = 0.1$.

At this final point, males send signals that attract females, but females also send different signals that attract males ($F_1 > 0$ and $F_2 > 0$). In contrast, Fig. 1b illustrates a case in which some trajectories converge to one equilibrium, but other trajectories converge to a second equilibrium; here, evolutionary dynamics are bistable. At one of the equilibriums, only males send mate-attracting signals ($F_1 > 0$ and $F_2 = 0$), and at a second equilibrium, only females send mate-attracting signals ($F_1 = 0$ and $F_2 > 0$).

## EVOLUTIONARY EQUILIBRIUM AND SEX DIFFERENCES

We first consider the cases where $\alpha + \beta < 2$. The conditions for the equilibrium are

$$0 = \frac{\partial}{\partial x_m} \ln W_m = \frac{\alpha}{\bar{x}_m} \frac{F_1}{F_1 + F_2} - 2b_m \bar{x}_m, \tag{4a}$$

$$0 = \frac{\partial}{\partial y_m} \ln W_m = \frac{\beta}{\bar{y}_m} \frac{F_2}{F_1 + F_2} - 2c_m \bar{y}_m, \tag{4b}$$

$$0 = \frac{\partial}{\partial x_f} \ln W_f = \frac{\alpha}{\bar{x}_f} QF_2 \frac{e^{-Q(F_1+F_2)}}{1 - e^{-Q(F_1+F_2)}} - 2b_f \bar{x}_f, \tag{4c}$$

$$0 = \frac{\partial}{\partial y_f} \ln W_f = \frac{\beta}{\bar{y}_f} QF_1 \frac{e^{-Q(F_1+F_2)}}{1 - e^{-Q(F_1+F_2)}} - 2c_f \bar{y}_f, \tag{4d}$$

and these become

$$\bar{x}_m = \sqrt{\frac{\alpha}{2b_m} \frac{F_1}{F_1 + F_2}}, \qquad \bar{y}_m = \sqrt{\frac{\beta}{2c_m} \frac{F_2}{F_1 + F_2}},$$

$$\bar{x}_f = \sqrt{\frac{\alpha}{2b_f} \frac{QF_2}{e^{Q(F_1+F_2)} - 1}} \quad \text{and} \quad \bar{y}_f = \sqrt{\frac{\beta}{2c_f} \frac{QF_1}{e^{Q(F_1+F_2)} - 1}}. \tag{5}$$

By replacing these quantities in equations (1), we have the following two equations:

$$F_1^2 = g_1^2 \left( \frac{\alpha}{2b_m} \frac{F_1}{F_1 + F_2} \right)^{\alpha} \left( \frac{\beta}{2c_f} \frac{QF_1}{e^{Q(F_1+F_2)} - 1} \right)^{\beta}, \tag{6a}$$

$$F_2^2 = g_2^2 \left( \frac{\alpha}{2b_f} \frac{QF_2}{e^{Q(F_1+F_2)} - 1} \right)^{\alpha} \left( \frac{\beta}{2c_m} \frac{F_2}{F_1 + F_2} \right)^{\beta}. \tag{6b}$$

The solution of equations (6a) and (6b) gives $F_1$ and $F_2$. For each pair of $F_1$ and $F_2$ satisfying equations (6), we can calculate $\bar{x}_m$, $\bar{y}_m$, $\bar{x}_f$ and $\bar{y}_f$ from equation (5).

Under the condition where $\alpha + \beta < 2$, the evolutionary dynamics (3) with equations (1) and (2) converge to an equilibrium, irrespective of the initial condition (see Fig. 1a). At equilibrium, $\bar{x}_m$, $\bar{y}_m$, $\bar{x}_f$, and $\bar{y}_f$ are positive (see Appendix A for details). From numerical analyses, we confirmed that the endpoint of the dynamics of equations (3) is the same as the equilibrium calculated from equations (5) and (6).

### Relative importance of the two ways of encountering mates

From equations (6a) and (6b), we can derive the following equation:

$$\left(\frac{F_1}{F_2}\right)^{2-\alpha-\beta} = \left(\frac{g_1}{g_2}\right)^2 \left(\frac{b_f}{b_m}\right)^{\alpha} \left(\frac{c_m}{c_f}\right)^{\beta} \left(\frac{e^{Q(F_1+F_2)}-1}{Q(F_1+F_2)}\right)^{\alpha-\beta}. \tag{7}$$

The first factor on the right-hand side of equation (7) indicates that signals from males to females are adopted more than signals from females to males, when signals from males to females are more efficient ($g_1/g_2$ is large), when the cost of males sending signals is lower than that of females sending signals ($b_m/b_f$ is small), or when the cost of the male response is larger than that of the female response ($c_m/c_f$ is large). In summary, signalling by a specific sex is more likely to evolve if it is more efficient and less costly.

The last factor of equation (7) is the most interesting. We note $(e^{Q(F_1+F_2)}-1)/Q(F_1+F_2) > 1$, stating that $F_1/F_2$ is greater if $\alpha > \beta$. This implies that a male-sent signal is more important for finding mates than a female-sent signal if mate-finding success depends more strongly on the magnitude of signal sending than on the sensitivity of signal receiving.

Suppose that there is no intrinsic difference between the sexes with respect to the cost of signalling and mate searching ($b_m = b_f$ and $c_m = c_f$). The relative magnitudes of the two modes of mate finding, $F_1/F_2$ given by equation (7), are independent of cost. A large cost for sending a signal or for mate searching after detecting the signal will not affect which sex sends the signal at the evolutionary equilibrium, given that the costs are equally high for males and females.

### Costs of mate finding to males and females

We consider the magnitude of costs for mate finding to a male and a female. These can be calculated as follows:

$$\begin{bmatrix}\text{cost to a male}\\ \text{for mate finding}\end{bmatrix} = b_m\bar{x}_m^2 + c_m\bar{y}_m^2 = \frac{\alpha F_1 + \beta F_2}{2} \bullet \frac{1}{F_1+F_2}, \tag{8a}$$

$$\begin{bmatrix}\text{cost to a female}\\ \text{for mate finding}\end{bmatrix} = b_f\bar{x}_f^2 + c_f\bar{y}_f^2 = \frac{\beta F_1 + \alpha F_2}{2} \bullet \frac{Q}{e^{Q(F_1+F_2)}-1}. \tag{8b}$$

Since $(e^{Q(F_1+F_2)}-1)/Q(F_1+F_2) > 1$ holds, the second factor of equation (8a) is larger than that of equation (8b). $e^{-Q(F_1+F_2)}$ is the fraction of females that cannot find a mate, and it is often much less than 1. If $\alpha$ and $\beta$ are quantities of the order of 1, a male's mate-finding cost is much larger than that of a female, which is confirmed by the numerical analyses below.

### Numerical analyses

We performed numerical analyses of equilibriums for different sets of parameters: $\alpha = 0.05$, 0.10, 0.15 . . . 1.90, 1.95, 2.00 and $\beta = 0.05$, 0.10, 0.15 . . . 1.90, 1.95, 2.00, but here we focus on the results for $\alpha + \beta < 2$ because the model's behaviour is quite different for $\alpha + \beta > 2$. The initial condition in which $\bar{x}_m$, $\bar{y}_m$, $\bar{x}_f$ and $\bar{y}_f$ follow uniform distributions between 0 and 2 is randomly generated. All trajectories from 20 randomly chosen initial conditions converged to the same equilibrium (within an error of $< 10^{-11}$); we therefore concluded that a globally stable equilibrium exists.

All the conclusions drawn above were confirmed by the numerical analyses. For example, Fig. 2 illustrates the contour map of the ratio, $F_1/(F_1 + F_2)$. We can see that males tend to evolve to be signal senders and females to be signal receivers and mate searchers when $\alpha$ is larger than $\beta$. When $\alpha$ is smaller than $\beta$, females tend to evolve to be signal senders and males to be signal receivers. This confirms the predictions in the last section.

Figure 3 illustrates a contour map for the ratio of male to female costs of mate-finding activities $(b_m \bar{x}_m^2 + c_m \bar{y}_m^2)/(b_f \bar{x}_f^2 + c_f \bar{y}_f^2)$. We can see that males have a larger cost than

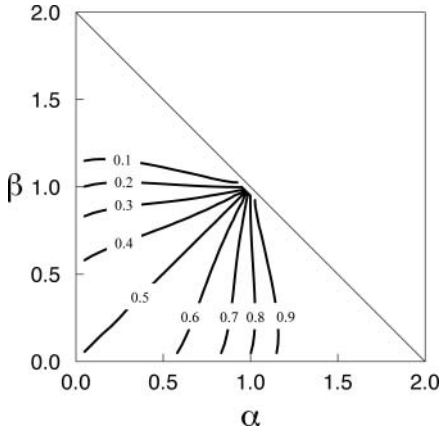


**Fig. 2.** The relative magnitude of mate encounters resulting from males sending the signals, $F_1$. This is shown as $F_1/(F_1 + F_2)$ at the evolutionary equilibrium in a contour map. Horizontal and vertical axes are $\alpha$ and $\beta$, respectively. Here we show the cases where $\alpha + \beta < 2$, in which the system starting from different initial conditions converges to the same equilibrium. The ratio is large when $\alpha$ is larger than $\beta$. This implies that the mode of signalling in which males are the senders is more important than that in which females are the senders, when mate encounter success depends more strongly on signal-sending than signal-receiving activities. Other parameters as in Fig. 1.

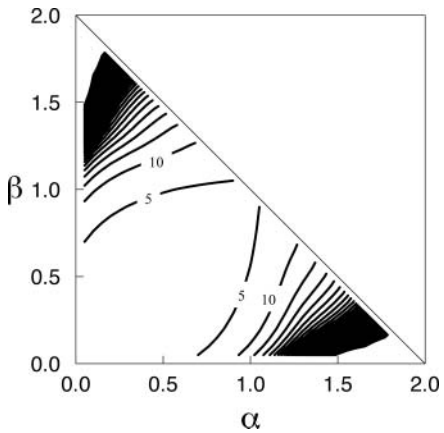


**Fig. 3.** The ratio of the cost of mate-finding activities to males to the cost to females is shown as a contour map. Here, we show the cases where $\alpha + \beta < 2$. Males always invest more into mate-finding activities, but the ratio becomes very high when $\alpha$ is much larger than $\beta$ or when $\alpha$ is much smaller than $\beta$. Other parameters as in Fig. 1.

females. The degree of difference in cost between males and females becomes very large either when α is small and $\beta$ is close to 2, or when α is close to 2 and $\beta$ is small.

## ALTERNATIVE EQUILIBRIUMS, EACH WITH A SINGLE MODE OF SIGNALLING

When $\alpha + \beta > 2$, the system has two stable equilibriums (see Fig. 1b). We numerically examined the location of these stable equilibriums and the size of the domain of attraction of each. The domain of attraction was estimated by the number of trajectories that converged to each equilibrium when initial conditions, in which $\bar{x}_m$, $\bar{x}_f$, $\bar{y}_m$, and $\bar{y}_f$ followed uniform distributions between 0 and 2, were generated randomly.

As explained in Appendix A, we can derive the mathematical formulas for the equilibriums of a single mode of signalling. At one equilibrium, only males send signals, and females receive them and search for males, where $F_1 > 0$ and $F_2 = 0$ hold and $\bar{x}_m > 0$, $\bar{y}_f > 0$, but $\bar{x}_f = \bar{y}_m = 0$. At a second equilibrium, only females send signals, and males receive them and search for females, where $F_1 = 0$ and $F_2 > 0$ hold and $\bar{x}_f > 0$, $\bar{y}_m > 0$, but $\bar{x}_m = \bar{y}_f = 0$. The evolutionary endpoint of the dynamics is consistent with the equilibrium calculated by this method.

From numerical analyses, we can confirm that the equilibrium where both sexes send signals ($F_1 > 0$ and $F_2 > 0$ hold) is unstable, and instead two separate equilibriums, where only one sex sends signals, are locally stable: in one equilibrium $F_1 > 0$ and $F_2 = 0$ hold, and in the second equilibrium $F_1 = 0$ and $F_2 > 0$ hold.

In a contour map with axes α and $\beta$, Fig. 4 illustrates the fraction of trajectories that is attracted to the equilibrium where males are the senders, and the fraction that is attracted to the equilibrium where females are the senders. As mate-finding success becomes more strongly dependent on the sender's effort ($\alpha > \beta$), males tends to expend more effort on sending signals than females. In contrast, if mate-finding success more strongly depends

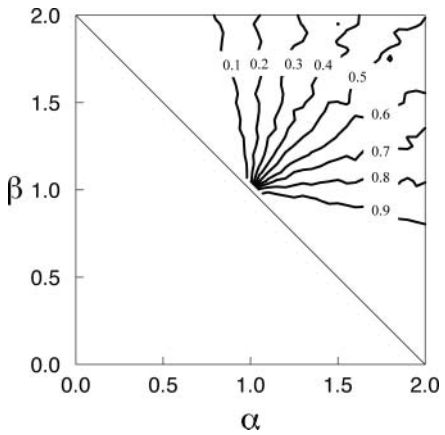


**Fig. 4.** The fraction of initial conditions that lead to the equilibrium in which only males are the signal senders. Horizontal and vertical axes are α and $\beta$, respectively. When $\alpha + \beta > 2$, the system is bistable and trajectories converge either to the equilibrium in which only males are the signal senders or to the equilibrium in which only females are the signal senders. For each set of parameters, 2000 initial conditions were generated randomly, in which $\bar{x}_m$, $\bar{x}_f$, $\bar{y}_m$, and $\bar{y}_f$ follow a uniform distribution between 0 and 2. Other parameters as in Fig. 1.

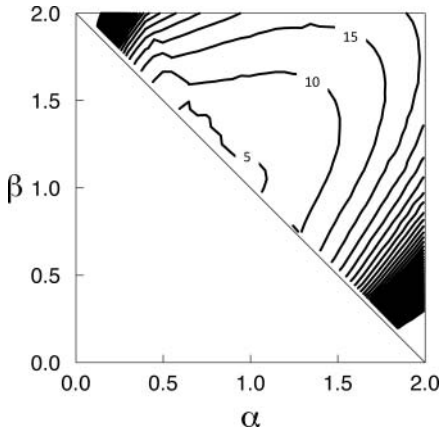


**Fig. 5.** The mean ratio of the cost of mate-finding activities to males to the cost to females. This is shown as contour maps for $\alpha + \beta > 2$. Since the system is bistable, we calculated the ratio of the investments by males and females at the evolutionary equilibrium then averaged over different trajectories with random initial conditions. Males invest more than females for mate-finding activities. The ratio becomes very high when $\alpha$ is much larger than $\beta$ or when $\alpha$ is much smaller than $\beta$. Other parameters as in Fig. 1.

on the receiver's effort (i.e. having good sensory organs, locating the signal sender by flying, and searching for the mate that sent the signal), then males tend to be the signal receivers.

The contours look as if they share the point at which $\alpha = \beta = 1$. This is also the case for $\alpha + \beta < 2$, illustrated in Fig. 2.

Figure 5 illustrates the ratio of mean cost to males to mean cost to females for activities improving mate encounter success. Since the system is bistable, we calculated the averages of male and female investments at the two evolutionary equilibriums using the weighting of the number of trajectories, starting from randomly distributed initial conditions. Again, males expend more effort in mate-finding activities than females at the evolutionary equilibrium. The difference in the mean costs to males and females becomes very large when $\alpha$ is small and $\beta$ is close to 2, or when $\alpha$ is close to 2 and $\beta$ is small (within $\alpha + \beta > 2$).

## DISCUSSION

In this study, we investigated the evolution of the sex that acts as the sender of mate-attracting signals to indicate its presence and location to individuals of the opposite sex. We assumed that when a receiver successfully detects a signal, it begins searching for the sender. We considered two modes of signalling: one where males are the senders and the other where females are the senders, and examined whether both or only one mode have the potential to be adopted. We studied the case when the mate-finding success of a signal is a product of power functions of the investments made by the signal sender and by the signal receiver, as given by equation (1). Given that both the sending and receiving of signals are accompanied by costs that are quadratic functions of the amount of investment, we obtained the evolutionary dynamics. The major results of the analysis follow.

### Total elasticity

The elasticity of signalling performance to signal-sending ability ($\alpha$) and elasticity of signalling performance to signal-responding ability ($\beta$) have a very strong effect on the results. If their sum is less than 2 ($\alpha + \beta < 2$), both modes of signalling – either males or females are the senders – are adopted in the evolutionary equilibrium. Both sexes expend some effort in sending mate-attracting signals and both sexes engage in mate-searching activities. In contrast, if the sum of the two elasticities exceeds 2 ($\alpha + \beta > 2$), only one of the two modes of signalling is adopted in the evolutionary equilibrium. Individuals of one sex (either male or female) send mate-attracting signals, and individuals of the second sex engage in signal detection and mate searching.

### Two elasticities and two costs

When $\alpha + \beta < 2$, the relative importance of males sending signals versus females sending signals is strongly controlled by the relative magnitude of $\alpha$ and $\beta$. If $\alpha$ is larger than $\beta$, mate-finding success depends more on the signal sender's activity than the signal receiver's activity. In these situations, males are more often the signal senders than females. In the opposite case, when $\beta$ is larger than $\alpha$, females are the signal senders and males the receivers, as illustrated in Fig. 2.

In addition, the parameters for costs and efficiencies also affect the final balance of the equilibrium. Suppose that $\alpha + \beta < 2$ and that $\alpha$ and $\beta$ are similar. Then, at the globally stable evolutionary equilibrium, it is more likely for males to be signal senders and for females to be receivers, if this is more efficient than the opposite situation of female senders and male receivers.

If $\alpha + \beta > 2$, the internal equilibrium where both signalling modes are adopted is unstable. The system is bistable and converges to an equilibrium where only males are signal senders, or to an equilibrium where only females are signal senders. Figure 4 illustrates the fraction of trajectories that eventually converge to the signalling mode where males are the senders versus the mode where females are the senders, among randomly generated initial states. Again, the relative magnitude of the two elasticities has a strong effect: If $\alpha$ is larger than $\beta$, a larger fraction of trajectories converges to the signalling mode where males are the senders, and if $\beta$ is larger than $\alpha$, a larger fraction of trajectories converge to the signalling mode where females are the senders. Thus, males tend to evolve to assume the role that has a stronger effect on mate-finding success.

Consider the case in which there is no intrinsic difference between the sexes with respect to the cost of signalling and mate searching ($b_m = b_f$ and $c_m = c_f$). Although the total mate-finding rate, $F_1 + F_2$, depends on the magnitude of the costs (the magnitude of intensity should decline with costs), the relative magnitude of the two modes of mate encountering (ratio $F_1/F_2$) is independent of the cost itself, as shown in equation (7). This implies that even if signalling or mate searching is very costly, it will not affect the sex of the signal sender or mate searcher in the evolutionary equilibrium, because the cost is equally high for both males and females.

### Males expend more effort than females to find mates

In all the cases examined, on average males expend more effort than females for activities that improve mate-finding success. This difference is caused by the assumption that male fitness linearly depends on the expected number of mate encounters, while female fitness increases with the expected number of mate encounters but saturates at very large values, because female fitness is constrained by egg production [see equations (2a) and (2b)]. This difference may not exist in cases where males must provide a large spermatophore or nuptial gifts for mating, as is the case for some butterflies (Rutowski, 1991; Karlsson, 1998).

### Future developments

In this study, we focused on the success of encountering mates, assuming that fitness depends on producing efficient signals, detecting those signals, and searching for signal senders. We did not consider mate choice by a female that chooses one mate out of the multiple males she encounters, or male–male competition through direct fighting, both of which are important for understanding diverse mating systems (Andersson and Iwasa, 1996; Andersson and Simmons, 2006) and sex differences in mating behaviour (Davies and Halliday, 1979; Real, 1990; Wiley and Poston, 1996; Kokko and Johnstone, 2002). The combination of the mate-finding process discussed here with female mate choice and male–male competition is an important theme of future theoretical studies.

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## APPENDIX A

### The analyses of equilibriums

We first consider the equilibrium at which all four variables are positive. From equations (6a) and (6b), we have

$$F_1^{2-\alpha-\beta} = g_1^2 \left(\frac{\alpha}{2b_m} \bullet \frac{1}{F_1 + F_2}\right)^{\alpha} \left(\frac{\beta}{2c_f} \frac{Q}{e^{Q(F_1+F_2)} - 1}\right)^{\beta}, \tag{A1a}$$

$$F_2^{2-\alpha-\beta} = g_2^2 \left(\frac{\alpha}{2b_f} \frac{Q}{e^{Q(F_1+F_2)} - 1}\right)^{\alpha} \left(\frac{\beta}{2c_m} \bullet \frac{1}{F_1 + F_2}\right)^{\beta}. \tag{A1b}$$

*For* $\alpha + \beta < 2$. Let $Z = Q(F_1 + F_2)$. We have:

$$F_1 = Q^{\frac{\alpha+\beta}{2-\alpha-\beta}} g_1^{\frac{2}{2-\alpha-\beta}} \left(\frac{\alpha}{2b_m} \frac{1}{Z}\right)^{\frac{\alpha}{2-\alpha-\beta}} \left(\frac{\beta}{2c_f} \frac{1}{e^Z - 1}\right)^{\frac{\beta}{2-\alpha-\beta}}, \tag{A2a}$$

$$F_2 = Q^{\frac{\alpha+\beta}{2-\alpha-\beta}} g_2^{\frac{2}{2-\alpha-\beta}} \left(\frac{\alpha}{2b_f} \frac{1}{e^Z - 1}\right)^{\frac{\alpha}{2-\alpha-\beta}} \left(\frac{\beta}{2c_m} \frac{1}{Z}\right)^{\frac{\beta}{2-\alpha-\beta}}. \tag{A2b}$$

From these, we have:

$$Z = (g_1 Q)^{\frac{2}{2-\alpha-\beta}} \left(\frac{\alpha}{2b_m}\frac{1}{Z}\right)^{\frac{\alpha}{2-\alpha-\beta}} \left(\frac{\beta}{2c_f}\frac{1}{e^Z-1}\right)^{\frac{\beta}{2-\alpha-\beta}},$$
$$+ (g_2 Q)^{\frac{2}{2-\alpha-\beta}} \left(\frac{\alpha}{2b_f}\frac{1}{e^Z-1}\right)^{\frac{\alpha}{2-\alpha-\beta}} \left(\frac{\beta}{2c_m}\frac{1}{Z}\right)^{\frac{\beta}{2-\alpha-\beta}}. \quad \text{(A3)}$$

From this, we can determine $Z$ as a positive solution, obtain $F_1$ and $F_2$ from equations (6), and then we have $\bar{x}_m$, $\bar{x}_f$, $\bar{y}_m$, and $\bar{y}_f$ from equations (5) in the text. At this equilibrium, all four variables are positive and both modes of signalling are adopted.

*For* $\alpha + \beta > 2$, the numerical analyses of the dynamics suggest that the equilibrium obtained above is unstable and instead two locally stable solutions exist. In one equilibrium, $F_1 > 0$ and $F_2 = 0$ hold. Then, equation (2a) becomes

$$QF_1 = (g_1 Q)^{\frac{2}{2-\alpha-\beta}} \left(\frac{\alpha}{2b_m}\frac{1}{QF_1}\right)^{\frac{\alpha}{2-\alpha-\beta}} \left(\frac{\beta}{2c_f}\frac{1}{e^{QF_1}-1}\right)^{\frac{\beta}{2-\alpha-\beta}}, \quad \text{(A4)}$$

which results in a single positive solution, $F_1 > 0$. Using this, we can calculate $\bar{x}_m$ and $\bar{y}_f$ from equation (5).

In a similar manner, we can derive $F_2 > 0$ and $F_1 = 0$, which determine $\bar{x}_m = \bar{y}_f = 0$, $\bar{x}_f > 0$, and $\bar{y}_m > 0$.

Numerical analyses confirmed that the dynamics of equation (3) converged into the equilibrium calculated above.