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The evolution of female mate choice by sexual conflict

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Although empirical evidence has shown that many male traits have evolved via sexual selection by female mate choice, our understanding of the adaptive value of female mating preferences is still very incomplete. It has recently been suggested that female mate choice may result from females evolving resistance rather than attraction to males, but this has been disputed. Here, we develop a quantitative genetic model showing that sexual conflict over mating indeed results in the joint evolution of costly female mate choice and exaggerated male traits under a wide range of circumstances. In contrast to traditional explanations of costly female mate choice, which rely on indirect genetic benefits, our model shows that mate choice can be generated as a side-effect of females evolving to reduce the direct costs of mating.

Keywords: sexual selection; sexual conflict; evolution of female mate choice; mathematical models

1. INTRODUCTION

In many species, females prefer mates with extreme characteristics that are apparently useless or deleterious for survival, such as bright colours, elaborate ornaments and conspicuous songs (Darwin 1871; Andersson 1994). Such female mate choice can be understood as a means for females to increase their immediate fecundity whenever females receive direct benefits, such as improved territory quality or paternal care, by choosing certain males over others as mates (Price *et al.* 1993; Iwasa & Pomiankowski 1999). Females of most species, however, do not seem to receive any appreciable direct benefits from exercising mate choice, and the evolutionary mechanisms responsible for the origin and maintenance of such female mate choice remain an evolutionary enigma despite several decades of intensive research (Kirkpatrick & Ryan 1991; Andersson 1994). Logic suggests that the costs paid by females for being choosy and by males for having exaggerated traits must somehow be compensated. Traditional explanations of costly female mate choice are cast in terms of indirect genetic benefits, which have been theoretically studied within the frameworks of Fisher's 'runaway' process (e.g. Lande 1981; Kirkpatrick 1982; Iwasa & Pomiankowski 1995) or 'good genes' models (e.g. Pomiankowski *et al.* 1991; Iwasa *et al.* 1991). It is, however, not clear whether costly female mate choice can be maintained by these processes, since the suggested indirect benefits of female mate preferences often seem trivial relative to the costs associated with mate choice (Kirkpatrick & Ryan 1991; Andersson 1994). In contrast, it has recently been suggested that sexual conflict over mating may result in the evolution of mate choice (Arnqvist & Rowe 1995; Rice 1996, 1998; Rice & Holland 1997; Holland & Rice 1998, 1999). In this scenario, males evolve to entice females into mating and females evolve resistance, rather than attraction, to males in order to reduce direct costs associated with mating.

Conflicts of interest between the sexes are manifest at all levels from behaviour to molecules, and such conflicts are key to our understanding of reproductive biology. Sexual conflict over, for example, mating rates, mating durations, the effects on females of male ejaculates and relative parental effort, is of fundamental importance for the evolutionary dynamics of mating systems, and many intriguing components of the reproductive behaviour of both sexes can be understood as sexually antagonistic and coevolving adaptations (Trivers 1972; Parker 1984; Arnqvist & Rowe 1995; Clutton-Brock & Parker 1995; Chapman & Partridge 1996; Rice 1996, 1998; Choe & Crespi 1997; Rice & Holland 1997; Stockley 1997; Holland & Rice 1998, 1999; Howard *et al.* 1998; Parker & Partridge 1998; Partridge & Hurst 1998; Arnqvist & Nilsson 2000). However, the idea that female mate choice may result from females evolving to avoid direct costs imposed by males, rather than to gain some indirect benefits, has not yet been formalized, and is still controversial (Brooks & Jennions 1999; Getty 1999; Rosenthal & Servedio 1999; Rice & Holland 1999).

Here, we develop the first formal model of the coevolution of female mate choice and a male display trait under sexual conflict. An assumption of standard population genetic models is that fitness of both sexes increases with mating rate (e.g. Arnold & Duvall 1994). In contrast, we study the coevolutionary dynamics of male and female traits under sexual conflict over mating rate by assuming that female fitness is maximized at an intermediate mating rate, and any deviation from this optimal rate causes a fitness decline due to direct costs in terms of reduced longevity and/or offspring production. There are many reasons to believe that such situations are very common. Consider the direct net effect on female fitness of increased mating rate. Most of the beneficial effects of mating will generate a gain curve which is asymptotic with increased mating rate, due to the diminishing rewards of, for example, receiving viable or compatible sperm. The costs of mating, in contrast, are likely to be more linearly or even exponentially related to mating rate, due to the additive or multiplicative effects of such

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costs. There is ample evidence for the fact that mating indeed is associated with a variety of costs to females (for reviews, see Daly 1978; Choe & Crespi 1997). Some of these derive from the ecology of mating (e.g. time and energy expenditure, risk of injury or predation, risk of decreased paternal care) and some result from the physiological processes involved in mating (e.g. risk of infection with various diseases, reception of toxic substances with the ejaculate, decreased immune response). If the direct costs and benefits of mating are then combined, this yields an optimal female mating rate simply reflecting the trade-off between the various direct costs and benefits involved. Such optimal female mating rate has been demonstrated in insects (for a review see Arnqvist & Nilsson 2000), where experimental studies are relatively easy to perform. Because of the generality of many of the costs of mating, however, optimal mating rates may also be common among vertebrates (e.g. Daly 1978; Westneat 1992; Magurran & Seghers 1994; Olsson 1995). Although we model conflicts over the mating rate, or the number of mates, we wish to stress that our model is applicable also to many other forms of sexual conflict over mating (cf. Rice & Holland 1997; Holland & Rice 1998) including conflicts over the environmental setting (Magurran & Seghers 1994; Lutnesky & Kosaki 1995) and the female condition or state (Rowe *et al.* 1996; Neuhaus *et al.* 1999) at the time and place of mating.

2. MODEL

We assume that females are potentially polyandrous and that they are stimulated (in a wide sense) into mating by a certain male stimulus, for example by a process analogous to sensory exploitation (Ryan 1990), which can be thought of as a visual or auditory display trait. We treat this stimulus as a quantitative character y. Its distribution and mean in the population are denoted as $g(y)$ and $\bar{y}$, respectively. Females are characterized by 'response curves' Ψ giving the probability of mating with a male as a function of his stimulus y. This function should have an S-shaped form approaching 1 for very high levels of y and 0 for very small levels of y. Females are different with respect to resistance x defined as the level of the male stimulus at which the probability of mating is 0.5. We use $f(x)$ and $\bar{x}$ for the distribution of resistance x in the population and its mean, respectively. Females with high x require high levels of the male stimulus to accept mating whereas females with low x accept matings at lower levels of stimulation. Resistance x will be treated as a parameter specifying the location of the female's response curve on the y-axis. We also assume that the outcome of sexual interactions is determined solely by the male stimulus and the female resistance. The probability of mating between a male y and a female x can thus be described as $\Psi(y-x)$. In summary, males are characterized by a single number whereas females are characterized by response curves which are similar in shape but differ in location (see figure 1).

Let

$$P(x) = \int \Psi(y-x)g(y)\mathrm{d}y \qquad (1a)$$

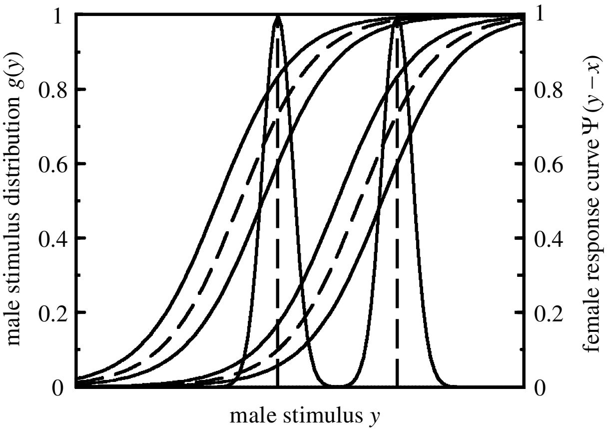

Figure 1. Graphical description of male and female subpopulations, to illustrate the interplay between male stimulus and female resistance. Two different male subpopulations are presented by two bell-shaped curves describing the normalized frequency distribution of the stimulus y. The vertical dashed lines describe the 'average males'. Two different female subpopulations are presented by two families of response curves $\Psi(y-x)$. Each family of S-shaped curves represents the response function for an 'average female' (dashed line) and for two females deviating from the average female by two standard deviations (solid lines). The left male subpopulation would be relatively successful in mating with females from the left subpopulation, but the right female subpopulation would be very reluctant to mate with these males. The right male subpopulation would be relatively successful in mating with females from the right subpopulation and extremely successful in mating with females from the left subpopulation.

be the average proportion of males that can stimulate a female x into mating, and

$$Q(y) = \int \Psi(y-x)f(x)\mathrm{d}x \qquad (1b)$$

be the average proportion of females that would mate with male y. These values, which reflect female and male mating rates, determine the fitness components resulting from sexual selection. Female fitness should be an increasing function at small values of $P(x)$ (the more acceptable males the higher the probability of fertilization). However, because of the various costs of mating, high values of $P(x)$ should depress female fitness and fitness should thus be optimized at some intermediate $P(x)$ (see § 1). The simplest form of a function having these properties is a quadratic function with a maximum at P_{opt} $(0<P_{\mathrm{opt}}<1)$:

$$W_{\mathrm{f,sex}}(x) = 1 - a[P(x) - P_{\mathrm{opt}}]^2, \qquad (2a)$$

where a can be seen as a measure of how important it is for females to succeed in optimizing their mating rate (Gavrilets 2000). More formally, a will be determined by the shape of the cost and benefit functions discussed in § 1. In contrast, male fitness should be a monotonically increasing function of male mating success Q. The simplest form of a function having this property is a linear function:

$$W_{\mathrm{m,sex}}(y) = 1 + 2bQ(y), \qquad (2b)$$

where b is a positive parameter measuring the intensity of sexual selection in males (and the constant 2 is merely for mathematical convenience). Note that both males' and females' fitness components resulting from sexual selection are frequency dependent. Finally, we assume that both traits are under direct natural selection. For males, costs of producing elaborate display traits can arise for a variety of documented reasons (Andersson 1994; Arnqvist 1994; Grether & Grey 1996; Rowe & Houle 1996). For females, natural selection will act on x whenever the perception system which detects the male stimulus also affects survival and/or fecundity. Imagine, for example, that the tuning of the female sensory system influences their ability to detect food and/or predators. To describe the corresponding fitness components we use quadratic functions

$$W_{\mathrm{f,nat}}(x) = 1 - s_x(x - \theta_x)^2, \tag{3a}$$

$$W_{\mathrm{m,nat}}(y) = 1 - s_y(y - \theta_y)^2. \tag{3b}$$

Parameters s_x and s_y measure the strength of natural selection whereas parameters θ_x and θ_y specify optima under natural selection for the traits. Note that the case of directional selection against a trait can be incorporated by assuming that the corresponding optimum is at a boundary of possible trait values (e.g. at zero).

Throughout the paper we will use a standard weak selection approximation assuming that parameters a,b,s_x and s_y are small and that function Ψ changes weakly over the range of males and females present in the population. Note that assuming weak selection implies that linkage disequilibrium is negligible. We will assume that the genetic covariance between male and female traits is absent (but see Appendix A). The dynamic equations for the changes in the mean trait values between two subsequent generations are

$$\Delta\bar{x} = V_x[a\Psi'(\Psi - P_{\mathrm{opt}}) - s_x(\bar{x} - \theta_x)], \tag{4a}$$

$$\Delta\bar{y} = V_y[b\Psi' - s_y(\bar{y} - \theta_y)], \tag{4b}$$

where V_x and V_y are the corresponding additive genetic variances and both $\Psi(z)$ and its first derivative, $\Psi'(z)$, are evaluated at $z = \bar{y} - \bar{x}$. Note that the variable z can be thought of as a measure of relative mating success of males: high (low) values of z imply that females have low (high) resistance to the males present in the population. Equations (4) were derived using a method developed in Gavrilets (2000). Details and generalizations of our approach, including analyses of the influence of covariance between male trait and female resistance, are described in Appendix A.

(a) *No natural selection*

First, let us assume that there is no natural selection (i.e. $s_x = s_y = 0$). Although this assumption is unrealistic, the resulting model can be viewed as an approximation for initial stages of evolutionary dynamics when mean trait values are still in the neighbourhood of the optima θ_x and θ_y. With no natural selection there are two different dynamic regimes. If sexual selection in males is sufficiently strong relative to that in females (precisely, if $bV_y > (1 - P_{\mathrm{opt}})aV_x$), then z always increases. This means that males continuously increase both absolute ($\Delta\bar{y} > 0$) and relative ($\Delta z > 0$) mating success. Females will increase their absolute resistance ($\Delta\bar{x} > 0$) but to an insufficient degree. One might say that in this case males win the sexual conflict. If sexual selection in males is not sufficiently strong relative to that on females (precisely, if $bV_y < (1 - P_{\mathrm{opt}})aV_x$), then z evolves to a stable equilibrium $\hat{z}$ at which

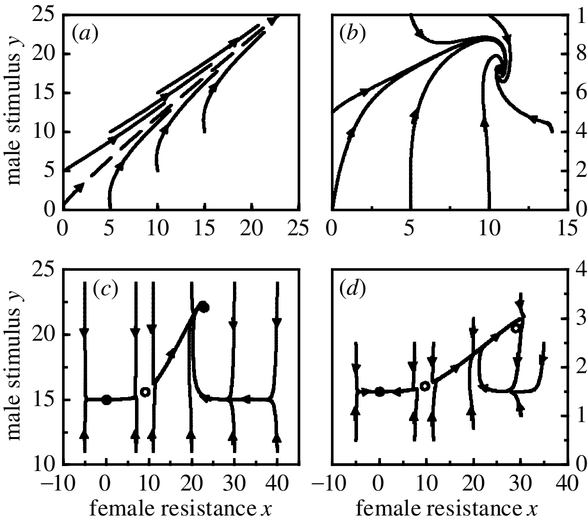

Figure 2. Coevolutionary dynamics in the phase-plane $(\bar{x},\bar{y})$ with $\Psi(y - x) = (\tanh(\varepsilon(y - x)) + 1)/2$. (*a*) 'Run-away' evolution with no natural selection ($\varepsilon = 0.2$, $V_x = V_y = 1$, $a = 0.1$, $b = 0.05$, $s_x = s_y = 0$, $\theta_x = 0$, $\theta_y = 4$, $P_{\mathrm{opt}} = 0.2$). (*b*) Evolution towards a stable equilibrium (the black circle) with natural selection in males only (parameters are the same as in (*a*) but with $a = 0.05$, $s_y = 0.001$). (*c*) Evolution towards one of the two equilibria (black circles) with natural selection in both sexes. The white circle shows the location of an unstable equilibrium ($\varepsilon = 0.3$, $V_x = 0.1$, $V_y = 1$, $a = 0.1$, $b = 0.05$, $s_x = 0.0001$, $s_y = 0.001$, $\theta_x = 0$, $\theta_y = 15$, $P_{\mathrm{opt}} = 0.22$). (*d*) Evolution towards an equilibrium (black circle) or a stable limit cycle with natural selection in both sexes. The white circles show the location of unstable equilibria (parameters are the same as in (*c*) but with $s_y = 0.0005$, $P_{\mathrm{opt}} = 0.15$).

$$\Psi(\hat{z}) = P_{\mathrm{opt}} + \frac{bV_y}{aV_x}. \tag{5}$$

Equation (5) implies that the mating rate between an average male (with $x = \bar{x}$) and an average female (with $y = \bar{y}$) is intermediate between the values optimal for females($= P_{\mathrm{opt}}$) and males ($= 1$). The fact that z reaches an equilibrium does not mean, however, stationarity in $\bar{x}$ and $\bar{y}$. Both mean values keep increasing at a constant rate (per generation)

$$R = bV_y\Psi'(\hat{z}) \tag{6}$$

along a line $\bar{y} = \bar{x} + \hat{z}$ (see figure 2*a*). This scenario describes an endless coevolutionary chase between the sexes in which males' evolution of higher and higher stimulus is exactly counterbalanced by females evolving higher and higher resistance to males. Neither sex can be said to win the sexual conflict here.

(b) *Natural selection in males only*

Next, we introduce natural selection on the male trait. With $s_y > 0$ but $s_x = 0$, the system has a unique equilibrium

$$\bar{x}_0 = \bar{y}_0 - z_0, \tag{7a}$$

$$\bar{y}_0 = \theta_y + \frac{b}{s_y} \Psi'(z_0), \tag{7b}$$

where z_0 satisfies to

$$\Psi(z_0) = P_{\mathrm{opt}}. \tag{7c}$$

Equation (7*c*) means that 'average' females mate at the optimum rate, whereas equation (7*b*) implies that the average male trait is exaggerated (i.e. is larger than the optimum θ_y; figure 2*b*). Depending on the parameter values this equilibrium can be locally stable or unstable. In the latter case, there is a stable limit cycle surrounding the equilibrium, and the mean trait values will change in a cyclical fashion. Here, the cycles arise via Poincaré–Andronov–Hopf bifurcation (e.g. Glendinning 1994). In general, the equilibrium (equations (7)) is stable if natural selection on the male trait is not too weak (specifically, if s_y is order $b\Psi'(z_0)$ or larger). The equilibrium is also stable if the second derivative $\Psi''(z_0)$ is negative. Note that if function Ψ has an inflection point only at $\Psi = 1/2$ and $P_{\mathrm{opt}} > 1/2$, then $\Psi''(z_0) < 0$. If $\Psi''(z_0) > 0$ and natural selection on the male trait is very weak (specifically, if s_y is much smaller than $b\Psi'(z_0)$), then the equilibrium is stable if sexual selection in females is sufficiently strong relative to that in males (precisely, if $aV_x > bV_y\Psi''(z_0)/(\Psi'(z_0))^2$). Otherwise, the equilibrium is unstable, and the system cycles.

(c) *Natural selection in both males and females*

Finally, with natural selection on both traits (with $s_x > 0, s_y > 0$), the mean trait values at equilibrium are

$$\bar{x}^* = \theta_x + \frac{a}{s_x} \Psi'[\Psi - P_{\mathrm{opt}}], \tag{8a}$$

$$\bar{y}^* = \theta_y + \frac{b}{s_y} \Psi', \tag{8b}$$

where both Ψ and Ψ' are evaluated at z^* that satisfies to an equation

$$z = \theta_y - \theta_x + \Psi'(z)\left[\frac{b}{s_y} - \frac{a}{s_x}(\Psi(z) - P_{\mathrm{opt}})\right]. \tag{8c}$$

Equations (8*a*) and (8*b*) show that at equilibrium female resistance is costly ($\bar{x}^* \neq \theta_x$) and the male stimulus is exaggerated ($\bar{y}^* > \theta_y$). The degree of exaggeration increases with increased intensity of sexual selection (b), decreased intensity of natural selection in females (s_x), and increased steepness of the female response curve (Ψ'). Generically, equation (8*c*) can have one or three solutions, and the dynamic system (equations (4)) can thus have one or three equilibria. (i) If the difference between the optima under natural selection $|\theta_y - \theta_x|$ is sufficiently large, there is only one equilibrium with $\bar{x}^* \approx \theta_x, \bar{y}^* \approx \theta_y$, which is stable. (ii) If the difference between the optima $|\theta_y - \theta_x|$ is sufficiently small, the system has only one equilibrium which can be stable or unstable depending on the parameter values. If the equilibrium is unstable, it is surrounded by a stable limit cycle, and the mean trait values change in a cyclical fashion. (iii) For intermediate values of $|\theta_y - \theta_x|$, the system has three equilibria. At one of these equilibria, which is always locally stable, $\bar{x}^* \approx \theta_x, \bar{y}^* \approx \theta_y$. Intuitively, in a neighbourhood of this equilibrium $\Psi'(z)$ is so small that neither females nor males 'feel' sexual selection and the dynamics are controlled by natural selection. Another equilibrium can be stable or unstable depending on the parameter values. In the latter case, it is surrounded by a locally stable limit cycle. The third equilibrium, which is located between the first and the second equilibria, is always unstable. This equilibrium separates the domains of attraction of the first locally stable equilibrium and the second locally stable equilibrium (or the locally stable limit cycle that surrounds the second equilibrium if it is unstable). Thus, for intermediate values of $|\theta_y - \theta_x|$, the system can have two locally stable equilibria (figure 2*c*) or a locally stable limit cycle and a locally stable equilibrium (figure 2*d*). In this case, the dynamics depend on initial conditions.

Stabilizing natural selection on female choosiness is often assumed to be much weaker than on the male stimulus (Pomiankowski *et al.* 1991; Iwasa & Pomiankowski 1995). With $0 < s_x \ll s_y$, the conditions for the existence of a locally stable limit cycle in the general case are similar to those for the case of $s_x = 0$. With small s_x, small changes in s_x can significantly affect $\bar{x}^*$. As stated above, with no stabilizing selection in females, average females mate at the optimum rate P_{opt}. With weak stabilizing selection in females, average females mate at a rate that is higher or lower than P_{opt} depending on whether the optimum θ_x is larger or smaller than the value of $\bar{x}_0$ defined by equations (7) (see § (d) of Appendix A).

Our analysis assumed no covariance between x and y in the population. Allowing for a covariance will not affect the location of the equilibria. As in other models of sexual selection (Pomiankowski *et al.* 1991; Iwasa & Pomiankowski 1995), however, the conditions for stability of the equilibria and, consequently, for the existence of stable limit cycles will be affected. If the covariance is not too strong, however, the changes in these conditions will be small. Introducing a covariance does not result in any new qualitative regimes or effects (see § (e) of Appendix A).

3. DISCUSSION

Our model demonstrates that the coevolution of costly female mate choice and male traits does not need to rely on a positive genetic covariance between these traits (Lande 1981; Kirkpatrick 1982; Pomiankowski *et al.* 1991; Iwasa & Pomiankowski 1995), condition-dependent expression of male traits (Rowe & Houle 1996; Iwasa & Pomiankowski 1999), spatial structure (Day 2000) or biased mutations (Iwasa & Pomiankowski 1995). Sexual conflict over mating patterns alone can indeed result in rapid coevolution of male display traits and costly female resistance to these traits. The model generates several novel and general insights. Female mate choice and the male trait are predicted to coevolve in a run-away fashion only in the absence of natural selection. When costs to males or to both sexes are incorporated, the system will evolve towards a stable equilibrium or, more rarely, a stable limit cycle. The intensity of sexual conflict relative to the strength of natural selection is of key importance for the outcome of this coevolutionary interaction. Under some conditions natural selection can prevent coevolution locally (i.e. for a set of initial conditions) or globally (i.e. for any initial condition). However, commonly, the male trait is exaggerated and female choice is costly at equilibrium. Male display traits are predicted to become greatly elaborated and exaggerated in cases where the female response curve is steep. These traits, however, are expected to be relatively ineffective in the sense that they will not cause females on average to deviate greatly from their optimum mating pattern (cf. 'a graveyard of ineffectual display traits'; Holland & Rice 1998). Depending on the strength of different factors female mating rate can be higher or lower than the optimal rate. Under certain conditions, sexual conflict is predicted to drive cyclical changes in male and female traits in a way similar to that previously observed in both Fisherian and 'good genes' models (Iwasa & Pomiankowski 1995). Cycling thus seems to be a general property of sexual selection models and, more generally, of coevolving systems with antagonistic interactions (Gavrilets 1997). Under sexual conflict, different dynamic attractors can be present simultaneously (e.g. two equilibria or an equilibrium and a cycle) and, thus, the behaviour of the system will depend on initial conditions.

Most models of the evolution of female mate choice are based on the assumption of a largely additive and autosomal inheritance of both male display traits and female choice, and our model is no different. This assumption may not always be upheld, since theory predicts that genes with sexually antagonistic effects should be disproportionally located on the sex chromosomes (Rice 1984). Recent studies have also indicated that this might be true for various sex-related genes (see Hurst & Randerson 1999; Roldan & Gomendio 1999). An analysis of whether and how the chromosomal location of genes coding for male and female traits affects the coevolution of these traits is, however, beyond the scope of the current contribution.

Empirical research has demonstrated that sexual conflict can generate costly female mate choice in systems involving sexual harassment (for an example involving insects see Rowe *et al.* 1994; Arnqvist 1997; Watson *et al.* 1998), by a process similar to the scenario modelled above. In such systems, male ability to coerce (rather than stimulate) females into mating is under sexual selection and female resistance is represented by their ability to thwart harassing males. However, our model shows that differences in the interests of the sexes may be a much more general generator of female mate choice (Holland & Rice 1998). In any system where males commonly stand to gain from mating but females do not, antagonistic coevolution between male stimuli or signals and female perception of these can result in the evolution of costly female mate choice. We wish to stress that a wide range of elaborated male traits, with corresponding features of the female perception system, could result from such evolutionary processes. Visual and acoustic signals are obvious candidates, but behavioural, tactile, hormonal and chemical stimuli may also be involved. A potentially restrictive key assumption of our model is that females exhibit an optimal mating pattern of some kind, and that deviations from this optimum convey direct fitness costs for females. Given the great diversity of mating costs (see § 1), however, optimal female mating patterns (e.g. mating rate, number of partners, ecological setting, timing, female condition) may be much more common and consequential than previously believed.

There is considerable confusion around the terms 'female preference' and 'female resistance' (Brooks & Jennions 1999; Getty 1999; Rosenthal & Servedio 1999; Rice & Holland 1999). However, these terms are clearly identical in that they both describe situations where there are biases in the probabilities that females mate with different kinds of males, and both result in sexual selection by female mate choice among males. They only differ with regards to which female fitness component is assumed to be affected by the mating bias. The term female preference implies either that the mating bias is neutral (Lande 1981; Kirkpatrick 1982) or that there is only indirect selection on this bias, generated by differential reproductive success (e.g. Pomiankowski *et al.* 1991) or viability (e.g. Iwasa *et al.* 1991) of offspring. Female resistance, in contrast, implies that there is direct selection on this bias, propelled by sexual conflict. Thus, it seems that the only route to a proper understanding of the evolution of female mate choice is empirical studies designed to quantify selection acting on female mating biases (Kirkpatrick 1987). In situations where the assumptions of our model apply, and mate choice results from female resistance, females should often suffer direct costs as a result of being stimulated into mating suboptimally when exposed to highly 'attractive' males (Holland & Rice 1998). Future empirical tests of this key assumption can reveal how general such conditions might be.

Our findings also have important implications for the evolution of reproductive isolation. The model predicts that relatively small differences in initial conditions or natural selection in females between populations (caused by food availability, predators etc.) can lead to large differences in evolving patterns of mate choice facilitating the evolution of reproductive isolation. This is especially likely since multiple dynamic attractors can exist, and since multiple male and female traits may often be involved in these coevolutionary systems. Sexual conflict may, thus, be an important engine of speciation (Holland & Rice 1998; Rice 1998; Gavrilets 2000; Arnqvist *et al.* 2000). However, antagonistic adaptations in males will tend to push females away from their optimum sensory tuning under natural selection, by exploiting features of the female perception system. Our model confirms that such costs of resistance to males can be significant at equilibrium (see Rice 1992; Holland & Rice 1999), and sexual antagonisms may thus severely compromise adaptation in both sexes. Remarkably enough, female mate choice generated by sexual conflict is thus also expected to lower overall population fitness and ultimately increase the risk of extinction (cf. Parker & Partridge 1998).

APPENDIX A

(a) *Derivation of the dynamic equations for the means with polynomial fitness functions*

Let $p(x,y)$ be the distribution of a pair of quantitative traits x and y in the population with the means $\bar{x}$, $\bar{y}$ and central moments M_{ij} $(=\int\int(x-\bar{x})^i(y-\bar{y})^j p(x,y)\mathrm{d}x\mathrm{d}y)$. Let the fitness function be represented as a polynomial

$$w(x,y)=\sum_{i,j}A_{ij}(x-\bar{x})^i(y-\bar{y})^j, \tag{A1}$$

where coefficients A_{ij} are allowed to depend on the moments of $p(x,y)$ but not on x and y. Taking the mathematical expectation of both sides of the last equation one finds that the mean fitness $\bar{w}$ can be represented as

$$\bar{w}=\sum_{i,j}A_{ij}M_{ij}.$$

The mean trait value after selection

$$\begin{aligned}
\bar{x}' &= \left[\iint xw(x,y)p(x,y)\mathrm{d}x\mathrm{d}y\right]\Big/\bar{w}\\
&= \left[\iint (x-\bar{x}+\bar{x})w(x,y)p(x,y)\mathrm{d}x\mathrm{d}y\right]\Big/\bar{w}\\
&= \left[\iint (x-\bar{x})\left[\sum_{i,j}A_{ij}(x-\bar{x})^i(y-\bar{y})^j\right]p(x,y)\mathrm{d}x\mathrm{d}y\right.\\
&\qquad \left.+\,\bar{x}\iint w(x,y)p(x,y)\mathrm{d}x\mathrm{d}y\right]\Big/\bar{w}\\
&= \left[\sum_{i,j}A_{ij}\iint (x-\bar{x})^{i+1}(y-\bar{y})^j p(x,y)\mathrm{d}x\mathrm{d}y+\bar{x}\,\bar{w}\right]\Big/\bar{w}\\
&= \left[\sum_{i,j}A_{ij}M_{i+1,j}\right]\Big/\bar{w}+\bar{x}.
\end{aligned}$$

Thus, the within-generation change in $\bar{x}$ is

$$\Delta_s\bar{x}=\frac{\sum_{ij}A_{ij}M_{i+1,j}}{\bar{w}}. \tag{A2a}$$

In a similar way,

$$\Delta_s\bar{y}=\frac{\sum_{ij}A_{ij}M_{i,j+1}}{\bar{w}}. \tag{A2b}$$

Note that the first three terms in the numerators are $0+A_{1,0}M_{2,0}+A_{0,1}M_{1,1}$ and $0+A_{1,0}M_{1,1}+A_{0,1}M_{0,2}$ where $M_{2,0}$, $M_{0,2}$ and $M_{1,1}$ are the (phenotypic) variances and covariance of the distribution of x and y in the population. For traits with sex-limited expression (such as considered here) $\Delta_s\bar{x}$, $\Delta_s\bar{y}$ will be equal to one-half of the values predicted by the above equations. If the traits under consideration are additive and linkage disequilibrium can be neglected, then to find the changes, $\Delta\bar{x}$ and $\Delta\bar{y}$, in the mean values between two subsequent generations one needs to multiply the changes, $\Delta_s\bar{y}$ and $\Delta_s\bar{y}$, within the generation by the corresponding heritabilities $V_x/M_{2,0}$ and $V_y/M_{0,2}$.

(b) ***Derivation of equations*** (*4*)

Here, we first approximate $P(x)$ and $Q(y)$ defined by equations (1). First, expand $\Psi(y-x)$ in a bivariate series at $x=\bar{x}, y=\bar{y}$:

$$\begin{aligned}
\Psi(y-x) &= \Psi+\Psi'_x(x-\bar{x})+\Psi'_y(y-\bar{y})+\tfrac{1}{2}\Psi''_{xx}(x-\bar{x})^2\\
&\quad+\Psi''_{xy}(x-\bar{x})(y-\bar{y})+\tfrac{1}{2}\Psi''_{yy}(y-\bar{y})^2+\ \ldots .
\end{aligned}$$

Note that $\Psi'_y=-\Psi'_x=\Psi'$. After integrating

$$P(x)=\Psi-\Psi'(x-\bar{x})+\tfrac{1}{2}\Psi''\ V_y+\tfrac{1}{2}\Psi''(x-\bar{x})^2+\ \ldots .$$

In a similar way,

$$Q(y)=\Psi+\Psi'(y-\bar{y})+\tfrac{1}{2}\Psi''\ V_x+\tfrac{1}{2}\Psi''(y-\bar{y})^2+\ \ldots .$$

Below we will neglect $\Psi''V_x$ and $\Psi''V_y$ relative to Ψ. This is justified by our assumption that 'function Ψ changes weakly over the range of males and females present in the population' (§ 2, above equations (4)).

To derive the dynamic equations (4), one substitutes the above approximations for $P(x)$ and $Q(y)$ into the general fitness function $w(x,y)=W_{\mathrm{f,sex}}W_{\mathrm{f,nat}}W_{\mathrm{m,sex}}W_{\mathrm{m,nat}}$, then identifies the coefficients $A(i,j)$ of the polynomial expansion (equation (A1)), and finally keeps only the dominant terms in equations (A2).

(c) ***Analyses of the dynamic equations*** (*4*)

(i) *No natural selection* ($s_x=s_y=0$)

Because the function Ψ is monotonically increasing, its first derivative Ψ' is always positive. Thus, if $s_y=0$, then equation (4b) tells us that $\bar{y}$ never settles down to an equilibrium but keeps increasing.

Taking the difference of $\Delta\bar{y}$ and $\Delta\bar{x}$ one finds that the change in z ($=\bar{y}-\bar{x}$) in one generation is

$$\Delta z=\Psi'(z)aV_x[\Pi-\Psi(z)], \tag{A3}$$

where

$$\Pi=P_{\mathrm{opt}}+\frac{bV_y}{aV_x}. \tag{A4}$$

Equation (A4) shows that there are two different dynamic regimes. Because the probability of mating Ψ cannot be greater than one, if $\Pi>1$, then z always increases. If $\Pi<1$, then z evolves to a stable equilibrium $\hat{z}$ at which

$$\Psi(\hat{z})=\Pi. \tag{A5}$$

(ii) *Natural selection in males only* ($s_x=0, s_y>0$)

Note that the equilibrium values do not depend on genetic variances V_x and V_y. These values will affect the rate of approach to the equilibrium though (and its stability properties). The stability of equilibrium (equations (7)) depends on the eigenvalues of matrix

$$S=\begin{pmatrix}-aV_x(\Psi')^2 & aV_x(\Psi')^2\\ -bV_y\Psi'' & V_y(b\Psi''-s_y)\end{pmatrix},$$

where Ψ'' is the second derivative of $\Psi(z)$. The trace and determinant of S are

$$\begin{aligned}
\mathrm{Tr}S &= -s_yV_y-aV_x(\Psi')^2+bV_y\Psi'',\\
\det S &= as_yV_xV_y(\Psi')^2.
\end{aligned}$$

Because $\det S>0$ always, the equilibrium will be stable if $\mathrm{Tr}S<0$ that is if

$$-s_yV_y-aV_x(\Psi')^2+bV_y\Psi''<0, \tag{A6}$$

where both the first, Ψ', and the second, Ψ'', derivatives of Ψ are evaluated at z_0. Depending on parameter values $\mathrm{Tr}S$ can be positive or negative and, thus, the equilibrium can be stable or unstable.

We consider three special cases. Let $\Psi''(z_0) < 0$. Then the equilibrium is stable because all three terms in the left-hand side of equation (A6) are negative. Let $\bar{y}^*$ have the same order as θ_y, which implies that $b\Psi'(z_0)$ and s_y have similar order. Then the term $-s_y V_y$ must dominate in the expression for the trace because it will have order Ψ' and will be much larger than terms proportional to $(\Psi')^2$ and Ψ''. In this case the equilibrium is stable. Let $\Psi''(z_0) > 0$ and natural selection be very weak so that s_y is much smaller than $b\Psi'(z_0)$ resulting in that $\bar{y}^* \gg \theta_y$. Then the term $-s_y V_y$ can be neglected. In this case, the equilibrium is stable if sexual selection in females is sufficiently strong (precisely, if $aV_x > bV_y\Psi''(z_0)/(\Psi'(z_0))^2$). Otherwise, the equilibrium is unstable, and the system cycles. This cycle arises via Poincaré–Andronov–Hopf bifurcation. Note that because $\Psi'(z)$ can be extremely small for large z, the evolution can effectively freeze along some parts of the cycle.

(iii) *Natural selection in both males and females* ($s_x > 0, s_y > 0$)

From consideration of the graph of the function in the right-hand side of equation (8*c*), which we will call $f(z)$, it follows that this graph can intersect with the line $z + \theta_x - \theta_y$ one or three times. A necessary condition for three intersections is $f' > 1$ at some z which will be in a neighbourhood of the intermediate solution, say, z_2^*. Calculating f' one finds that the condition $f' > 1$ is equivalent to

$$s_x s_y + s_y a[(\Psi')^2 + \Psi''(\Psi - P_{\mathrm{opt}})] - s_x b\Psi'' < 0. \tag{A7}$$

Note that if there are three solutions, then at the first and the third one $f' < 1$.

For an equilibrium (equations (8)) the stability matrix is

$$S = \begin{pmatrix} -V_x[a((\Psi')^2 + \Psi''(\Psi - P_{\mathrm{opt}})) + s_x] & aV_x((\Psi')^2 + \Psi''(\Psi - P_{\mathrm{opt}})) \\ -bV_y\Psi'' & V_y(b\Psi'' - s_y) \end{pmatrix},$$

with the trace and determinant

$$\mathrm{Tr}S = -s_x V_x - s_y V_y - aV_x[(\Psi')^2 + \Psi''(\Psi - P_{\mathrm{opt}})] + bV_y\Psi'', \tag{A8a}$$

and

$$\det S = V_x V_y (s_x s_y + s_y a[(\Psi')^2 + \Psi''(\Psi - P_{\mathrm{opt}})] - s_x b\Psi''). \tag{A8b}$$

One can immediately see that if there are three solutions, the determinant is positive at the first and third, and is negative at the second (compare equation (A7) with equation (A8*b*)). Thus, the second equilibrium is always unstable, and the stability of the first and the third equilibria depends on the sign of Tr*S*. If there is only one solution, the determinant of *S* is always positive, and stability again depends only on the sign of Tr*S*. That is the equilibrium is stable if

$$-s_x V_x - s_y V_y - aV_x[(\Psi')^2 + \Psi''(\Psi - P_{\mathrm{opt}})] + bV_y\Psi'' < 0. \tag{A9}$$

Different sufficient conditions for stability can be found in a similar way as above. A major difference is that if there are three equilibria two of them can be stable simultaneously. Another possibility is that a limit cycle and an equilibrium can be simultaneously stable. In these situations the dynamics will depend on initial conditions.

(d) *Equilibrium with $s_x \ll s_y$*

We will use the perturbation techniques (e.g. Holmes 1995). Equation (8*c*) can be rewritten as

$$s_x(z + \theta_x - \theta_y) + a\Psi'(\Psi - P_{\mathrm{opt}}) - s_x\frac{b\Psi'}{s_y} = 0. \tag{A10}$$

If $s_x = 0$,

$$z \to z_0 = \Psi^{-1}(P_{\mathrm{opt}}),$$

$$y \to y_0 = \theta_y + \frac{b\Psi'(z_0)}{s_y},$$

$$x \to x_0 = y_0 - z_0.$$

We will be looking for a solution of equations (1) in the form

$$z = z_0 + As_x^{\alpha},$$

where $s_x \ll 1$ and A and α are to be determined. Substituting this z into equation (A9) one finds that

$$s_x(z_0 + As_x^{\alpha} + \theta_x - \theta_y) + a[\Psi'(z_0)(\Psi(z_0) - P_{\mathrm{opt}}) + (\Psi''(z_0)(\Psi(z_0) - P_{\mathrm{opt}}) + (\Psi'(z_0))^2)As_x^{\alpha}] - s_x\frac{b\Psi'(z_0)}{s_y} = 0$$

Keeping only the dominant terms

$$s_x(z_0 + \theta_x - \theta_y) + aA(\Psi'(z_0))^2 s_x^{\alpha} - s_x\frac{b\Psi'(z_0)}{s_y} = 0.$$

The only choice that keeps all three terms is $\alpha = 1$. Then

$$z_0 + \theta_x - \theta_y + aA(\Psi'(z_0))^2 - \frac{b\Psi'(z_0)}{s_y} = 0,$$

which results in

$$A = \frac{x_0 - \theta_x}{a(\Psi'(z_0))^2}.$$

Thus, the solution of equations (1) for small s_x can be approximated as

$$z = z_0 + \frac{s_x(x_0 - \theta_x)}{a(\Psi'(z_0))^2}.$$

This shows that $z > z_0$ if $x_0 > \theta_x$ and that $z < z_0$ if $x_0 < \theta_x$.

(e) *x and y are correlated*

Let C be covariance of x and y coming from pleiotropy and/or linkage disequilibrium. The system with $C \neq 0$ 'inherits' all equilibria for $\bar{x}, \bar{y}$ that the corresponding system with $C = 0$ has; no new equilibria show up either. However, the stability properties of the equilibria will be modified.

For example, consider a system

$$\Delta x = V_x f, \tag{A11}$$

$$\Delta y = V_y g, \tag{A12}$$

which has a stability matrix

$$S_0 = \begin{pmatrix} V_x f'_x & V_x f'_y \\ V_y g'_x & V_y g'_y \end{pmatrix}.$$

The trace and determinant of S_0 are

$$\mathrm{Tr} S_0 = V_x f'_x + V_y g'_y, \ \det S_0 = V_x V_y (f'_x g'_y - f'_y g'_x).$$

Consider also a system

$$\Delta x = V_x f + Cg, \tag{A13}$$

$$\Delta y = Cf + V_y g. \tag{A14}$$

The stability matrix is

$$S = \begin{pmatrix} V_x f'_x + C g'_x & V_x f'_y + C g'_y \\ C f'_x + V_y g'_x & C f'_y + V_y g'_y \end{pmatrix}.$$

Now, the trace and determinant are

$$\mathrm{Tr} S = \mathrm{Tr} S_0 + C(f'_y + g'_x), \ \det S = \left(1 - \frac{C^2}{V_x V_y}\right) \det S_0.$$

This shows that the sign of the determinant stays the same, but the trace changes by $C(f'_y + g'_x)$. One can see that for the model studied here

$$f'_y + g'_x = a[(\Psi')^2 + \Psi''(\Psi - P_{\mathrm{opt}})] - b\Psi''.$$

Thus, to find a general expression for $\mathrm{Tr} S$ with $C \neq 0$ one has to make the substitutions $V_x \rightarrow V_x - C$ and $V_y \rightarrow V_y - C$ in equation (A7*a*).

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