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Escalation, Retreat, and Female Indifference as Alternative Outcomes of Sexually Antagonistic Coevolution

Locke Rowe,[1,*] Erin Cameron,[2,†] and Troy Day[2,3,‡]

1. Department of Zoology, University of Toronto, Toronto, Ontario M5S 3G5, Canada;
2. Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada;
3. Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada

ABSTRACT: Verbal and quantitative genetic models of sexually antagonistic coevolution suggest that coevolutionary arms races should be common. Sexual selection favors exaggeration of male persistence traits that are costly to females, and females, in turn, are selected to resist these traits. The heightened resistance by females is thought to then favor further exaggeration in the male trait, leading to an escalating coevolutionary arms race between persistence and resistance traits. Much of this theory, however, is based on an (implicit) assumption that there are tight constraints on how female resistance can evolve. We develop a theory that identifies and relaxes these constraints, allowing female resistance to evolve in a fashion that better reflects known empirical patterns in the evolution of female preference functions (the resistance trait). Our results suggest that evolutionary arms races that lead to the exaggeration of persistence and resistance will be much less common than formerly predicted. Females sometimes evolve indifference to male traits rather than resistance and can even evolve to discriminate against these traits. These alternative outcomes depend on the existence of genetic variance in the components of the female sensory system underlying female resistance and on the strength of natural selection acting on these components. Female indifference tends to evolve when natural selection on the sensory system is weak, and under these conditions, sexually antagonistic coevolution tends not to reduce female fitness significantly at equilibrium. When natural selection on the female sensory system is strong, however, then arms races are more likely, and female fitness is then sometimes significantly depressed at equilibrium. Sexually antagonistic coevolution is thus likely to have strong deleterious effects on population fitness only when female sensory traits are under strong natural selection to perform functions in addition to those involved with mating. Together, these results suggest that identifying the nature of genetic variation in and the strength of natural selection on female resistance should be a central goal of future studies of sexual conflict.

Keywords: female preference, female resistance, sexual selection, coevolutionary theory.

There is growing evidence that reproductive interactions between the sexes involve conflicts that result from selection operating in different directions on interacting traits in the two sexes (Parker 1979; Holland and Rice 1998; Chapman et al. 2003*b*). For example, higher mating rates are often favored in males relative to females, and this leads to conflicts between individuals over mating (Rowe et al. 1994; Clutton-Brock and Parker 1995; Arnqvist and Nilsson 2000). Analogous conflicts are expected in a wide variety of traits, including female remating rates, oviposition rates, and reproductive allocation. These conflicts may lead to sexually antagonistic coevolution between pairs or suites of traits that affect the outcome of these reproductive interactions.

Multiple lines of evidence suggest that females may suffer direct costs with elevated mating rates (thus accounting for resistance) and that female resistance biases the mating success of males toward males with those persistence traits that overcome resistance (reviewed in Chapman et al. 2003*b*). Recently, there has been debate about the relationship between sexual conflict and the evolution of female mating preferences (e.g., Cameron et al. 2003; Chapman et al. 2003*a*, 2003*b*; Cordero and Eberhard 2003; Kokko et al. 2003). If one focuses on the primary effect of female choice or preference (that it biases mating success toward certain male phenotypes; Halliday 1983; Maynard Smith 1987; Pomiankowski 1988), then female resistance is equivalent to preference (resistance likewise biases mating success of males; Rowe et al. 1994; Kokko et al. 2003). When female resistance biases male mating success toward persistent males, it is exerting sexual selection for male persistence. It is easy then to imagine an escalating coevolutionary trajectory, or arms race, where persistence and resistance traits are increasingly exaggerated (Parker

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[*] E-mail: lrowe@zoo.utoronto.ca.

[†] E-mail: camerone@biology.queensu.ca.

[‡] E-mail: tday@mast.queensu.ca.

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1979). Indeed, evidence from experiments employing laboratory evolution and from comparative studies (e.g., Holland and Rice 1999; Bergsten et al. 2001; Arnqvist and Rowe 2002) suggest that some cases of coevolution between the sexes resemble arms races. Assuming resistance is costly to females, then female fitness, and thereby population fitness, may well decline as a result of this coevolutionary process.

Holland and Rice (1998) presented a compelling verbal model outlining this idea, referring to the process as the "chase-away" hypothesis (see also Parker 1979). More recently, this idea has been explored with a formal coevolutionary model (Gavrilets et al. 2001). The model was designed to explore the dynamics of male/female reproductive traits evolving under sexual conflict over mating rate, but it is equally applicable to intersexual conflict over other variables (Gavrilets et al. 2001). This work is particularly useful as there is relatively little formal theory describing the dynamic nature of sexual conflict (see Parker 1979; Parker and Partridge 1998; Gavrilets 2000; Gavrilets and Waxman 2002 for exceptions) in spite of the rapid accumulation of empirical data related to the topic. The results of Gavrilets et al. (2001) suggest that sexual conflict over mating interactions may commonly lead to arms races where costly persistence and resistance traits are greatly exaggerated and population fitness is reduced.

Gavrilets et al. (2001) model male fitness as an increasing function of mating rate so that males with trait values that induce the highest probability of mating have the highest fitness. Conversely, female fitness is modeled so that it is maximized at some intermediate rate of mating. Mating rate is a function of the difference between the level of male persistence and female resistance; in this model both male persistence and female resistance are each determined by a single quantitative trait. Females are characterized by preference (resistance) functions that are fixed in shape but variable in location across the distribution of male traits. This means that females may resist the increased persistence associated with evolutionary increases in the male trait only by adjusting the threshold amount of male persistence they require for mating (fig. 1*a*). However, since the preference function itself is constant in shape, female sensitivity to changes in the male trait is always the same. Consequently, there is always sexual selection favoring male traits that increase their mating rate, with females being able to respond only by further increasing the threshold amount of persistence required for mating. If there is natural selection on the female threshold, then displacement of the threshold from its optimum during sexually antagonist coevolution will depress population fitness through its cost to females.

Although the above scenario is certainly one possibility, previous authors have distinguished between two components of female resistance: her threshold of acceptability for mating (mating threshold) and her sensitivity to the male trait (Rosenthal and Servedio 1999). These two components are somewhat interrelated, but both the verbal model presented by Holland and Rice (1998) and the quantitative-genetic model of Gavrilets et al. (2001) appear to focus only on the first component of female resistance (the mating threshold), assuming that sensitivity is fixed. In some systems this is probably an appropriate way to quantify resistance, but it is unlikely to be a general feature of most mating systems. Comparative studies have demonstrated that the sensitivity of female preference functions readily evolves (Basolo 1996, 1998; Morris et al. 1996). Likewise, the sensitivity of female preference functions are

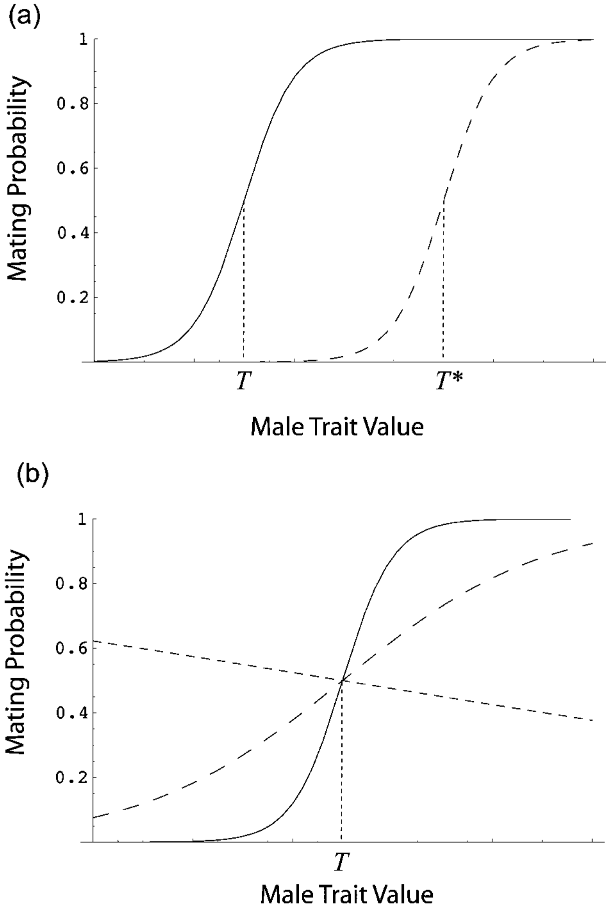

Figure 1: Illustration of the threshold and sensitivity of the female preference function. *a*, Solid and dashed curves represent two preference functions with different thresholds. The threshold T^* is greater than the threshold T, but the sensitivity of the two preference functions is the same. *b*, Solid and dashed curves represent three preference functions with identical thresholds but with different sensitivities. Solid curve has a high, positive sensitivity. Long-dashed curve has a lower but still positive sensitivity. Short-dashed curve has a weak and negative sensitivity.

often quite plastic and can even change sign (Berglund 1993; Hedrick and Dill 1993; Wagner 1998; Johnson and Basolo 2003). If sensitivity can evolve, then females might reduce the rate of mating by either evolving a higher threshold of acceptability to the male trait or by evolving a lower sensitivity to it (fig. 1*b*). In contrast to increasing the threshold, reduced female sensitivity may lead to a reduction in the male trait rather than greater selection for exaggeration. Hence, sexually antagonistic interactions may shut down coevolutionary change rather than fuel escalating arms races.

We develop a theory that relaxes the restrictions placed on the female preference (resistance) function of Gavrilets et al. (2001) by allowing both the threshold and the sensitivity of the preference function to evolve. Our results demonstrate that the evolutionary flexibility of female preference functions is a key factor determining the outcome of male-female antagonistic coevolution. If the sensitivity of preference functions to male stimulus can evolve, then coevolutionary arms races are much less likely to occur. Furthermore, the strength of natural selection operating on the female preference function appears to determine the extent to which female fitness is depressed by antagonistic evolution. Identifying the nature of genetic variation in female preference functions and the strength of natural selection on them should therefore be a central goal of future studies of sexual conflict.

The Model

We consider sexually antagonistic coevolution of male persistence and female resistance resulting from evolutionary conflicts over mating rate, but our results are valid for analogous conflicts over other traits (e.g., oviposition rate). In the case of conflict over mating rate, female costs do not depend on which males they mate with but on how many they mate with. Although these male "phenotype-independent" costs are probably common, there are other cases where the costs to females do depend on the phenotypes of their mating partners because some male phenotypes are more costly to mate with than others (Chapman et al. 2003*b*). Although we have not considered these latter examples specifically, results are expected to be similar in these cases as well.

As in Gavrilets et al. (2001), we assume that male fitness is a linearly increasing function of mating rate and that female fitness has an optimum at an intermediate mating rate. Males possess one persistence trait that affects mating rate. The persistence trait might be a visual signal that exploits some sensory bias in females or any other signal that influences a female's propensity to mate. We suppose that the male persistence trait initially evolves because of a preexisting female preference function (i.e., a preexisting bias in the sensory system) that initially favors its spread. If the evolution of this male trait displaces the mating rate of females from their optimum, then females can evolve to reduce the costs of this elevated rate of mating through changes in either of two resistance traits: the threshold of their preference function (defined as the level of male persistence that would induce a 50% chance of mating; fig. 1), or their sensitivity to the male trait (defined as the slope of the preference function; fig. 1). Although we are imagining coevolution between signal and receiver traits, the model is equally applicable to other suites of traits (e.g., grasping and antigrasping traits).

Equations describing the evolutionary dynamics of the male persistence trait and the two female resistance traits are derived by first specifying fitness functions for males and females. We denote the male persistence trait by P and the female threshold and sensitivity by T and S, respectively. Our analysis is essentially a game-theoretic one in which we formulate a fitness expression for a mutant female with traits T and S in a population where the resident male trait value is $\hat{P}$. Similarly, we formulate a fitness expression for a mutant male with trait value P in a population where the resident female trait values are $\hat{T}$ and $\hat{S}$.

Suppose that the probability of a female mating during any given encounter, $\psi(n)$, increases as a sigmoid function of the net amount of the signal perceived by the female, from 0 to 1 (fig. 1). We use the particular function $\psi(n) = 1/(1 + e^{-n})$. Further, suppose that the net amount of the signal perceived by a female, n, depends linearly on the magnitude of the male persistence trait, P, with the slope and intercept of this relationship being determined by the female sensitivity and threshold, S and T; that is, $n = S(P - T)$. Thus, the probability of mating between a female with traits S and T and a male with trait P is given by $\psi[S(P - T)]$. With this choice, there is a 50% chance of mating in the absence of any signal perception by the female. In other words, if the female perceives no signal (i.e., $n = 0$) then $\psi = 1/2$. These choices are essentially the same as those used by Gavrilets et al. (2001).

We assume that the component of a mutant female's fitness related to sexual interactions is given by $1 - a(\psi - \theta_{\psi})^2$, where the mating function is evaluated using the mutant female's trait values, S and T, and using the resident male trait value, $\hat{P}$; that is, $\psi[S(\hat{P} - T)]$. The parameter θ_{ψ} is the optimal female mating rate, 1 is a baseline fitness, and a is a positive parameter scaling the fitness consequences to females of having their mating probability deviating from its optimum. Similarly, the component of mutant male's fitness related to sexual interactions is given by $1 + 2b\psi$, where the mating function is evaluated using the mutant male's trait value, P, and the resident female trait values, $\hat{S}$ and $\hat{T}$; that is, $\psi[\hat{S}(P - \hat{T})]$. The parameter

b is also positive and scales the fitness consequences to males of increases in the probability of mating. The 2 in this expression is an arbitrary factor included to make the analysis more transparent.

Finally, we also assume that natural selection can act on all three traits, T, S, and P, such that an intermediate optimum is favored in each. This assumption is meant to reflect the fact that female sensory systems underlying resistance are probably under natural selection to perform functions unrelated to mating interactions. For example, if the signal-receiver interaction is one where male color serves as the trait, P, then not only will a female's response to color be under selection as a result of mating interactions with males but also it will probably be under selection due to its effects on other aspects of a female's reproductive success as well (e.g., foraging). In our model, then, any costs to females of sexually antagonistic coevolution may accrue through a displacement of female mating rate, or a displacement of resistance from its optimum, or both. Similarly, we might expect the male trait, P, to be under natural selection for an intermediate optimum. Using the parameters c_T, c_S, and c_P to describe the strength of natural selection on female and male traits and θ_T, θ_S, and θ_P to specify the optimal value of these traits under natural selection, then we have the two additional terms $1 - c_T(T - \theta_T)^2$ and $1 - c_S(S - \theta_S)^2$ for female fitness and the single additional term $1 - c_P(P - \theta_P)^2$ for male fitness. The fitness of a mutant female with threshold and sensitivity T and S in a population where males have persistence $\hat{P}$ is therefore

$$\begin{aligned} W_{\text{female}}(T, S; \hat{P}) = {} & (1 - a\{\psi[S(\hat{P} - T)] - \theta_\psi\}^2) \\ & + [1 - c_T(T - \theta_T)^2] \\ & + [1 - c_S(S - \theta_S)^2], \end{aligned} \tag{1a}$$

and the fitness of a mutant male with persistence P in a population where females have threshold and sensitivity $\hat{T}$ and $\hat{S}$ is

$$\begin{aligned} W_{\text{male}}(P; \hat{T}, \hat{S}) = {} & \{1 + 2b\psi[\hat{S}(P - \hat{T})]\} \\ & + [1 - c_P(P - \theta_P)^2]. \end{aligned} \tag{1b}$$

The above fitness functions (1) can be used to derive equations that approximate the evolutionary dynamics of the average trait values $\overline{T}$, $\overline{S}$, and $\overline{P}$ using standard techniques (e.g., Iwasa et al. 1991; Abrams 2001). We obtain

$$\frac{d\overline{T}}{dt} = 2v_T[a(\psi - \theta_\psi)\psi'\overline{S} - c_T(\overline{T} - \theta_T)], \tag{2a}$$

$$\frac{d\overline{S}}{dt} = 2v_S[-a(\overline{P} - \overline{T})(\psi - \theta_\psi)\psi' - c_S(\overline{S} - \theta_S)], \tag{2b}$$

$$\frac{d\overline{P}}{dt} = 2v_P[b\overline{S}\psi' - c_P(\overline{P} - \theta_P)], \tag{2c}$$

where v_T, v_S, and v_P are the additive genetic variances of the female and male traits, respectively, and ψ' denotes the derivative of ψ. Indirect evolutionary responses caused by genetic correlations among the traits are not included in equations (2), but they will not affect the equilibria that are attained (Gavrilets et al. 2001; Cameron et al. 2003). Furthermore, we note that these equations are valid only under the assumption that the genetic variances are not too large (Iwasa et al. 1991; Abrams 2001; Gavrilets et al. 2001).

Results

First we consider the case where only the female sensitivity evolves and compare these results with those of Gavrilets et al. (2001) where only the female threshold can evolve. We then briefly discuss the more complete model where both the sensitivity and the threshold evolve. We divide our discussion of the results into a series of cases distinguished by the presence or absence of natural selection on male and female persistence and resistance traits.

Only Female Sensitivity Evolves

In this scenario, the female threshold, T, is fixed. This assumption is analogous to assuming that there is no genetic variance in the threshold or that there is very strong natural selection holding it in place. Thus, the only resistance strategy available to females is an alteration of the sensitivity, S, of their preference function. Females might evolve to better discriminate among males (become more sensitive to male persistence) by increasing the slope of their preference function. Alternatively, if discrimination is too costly, then females might evolve insensitivity by adopting a zero-slope preference function ($S = 0$).

Given the form of selection on mating rate in females, a distinction between three different cases related to the optimal mating rate of females, θ_ψ, must be made. As we mentioned earlier, there is a probability of one-half that mating will occur on any given encounter in the absence of any signal perception (i.e., when $P = 0$ or $S = 0$). In this case, the resulting mating rate of one-half can fall into one of three categories: (1) one-half is the optimal female mating rate, (2) one-half is less than the optimal female mating rate, or (3) one-half is greater than the optimal female mating rate. Mathematically, these correspond to those cases where (1) $1/2 = \theta_\psi$, (2) $1/2 < \theta_\psi$, or (3) $1/2 > \theta_\psi$ respectively. In (1), female fitness related to mating is maximized in the absence of male stimulation, and therefore sexual interactions affecting mating rate can only reduce female fitness. In (2), females are mating at a suboptimal rate in the absence of male stimulation, and in (3), females are mating at a superoptimal rate. In both of these later cases, females can use sexual interactions to bring the mating rate closer to their optimum.

No Natural Selection. With no natural selection (i.e., $c_P = c_S = 0$), the dynamic equations for the model are

$$\frac{d\bar{S}}{dt} = 2av_S\psi'[-(\bar{P} - \bar{T})(\psi - \theta_\psi)], \tag{3a}$$

$$\frac{d\bar{P}}{dt} = 2v_P b\psi' b\bar{S}. \tag{3b}$$

Equation (3b) reveals that male persistence evolves in a direction given by the sign of the female sensitivity, S. If there is no natural selection on the male trait, then it will always continue to evolve in the direction that induces a higher mating rate. The equilibrium of model (3) is

$$\bar{S} = 0,\ \bar{P} = \bar{T}. \tag{4}$$

In fact, the male persistent trait can take on any value at equilibrium if the optimal female mating rate is 1/2. In this case, females obtain the highest possible fitness by being completely insensitive to the male trait ($S = 0$) no matter what males do. As result, all sexual selection on male persistence is then removed.

The stability of equilibrium (4) when the optimal female mating rate is not 1/2 depends on parameter values. If the mating rate at this equilibrium is still too high for females (i.e., if $1/2 > \theta_\psi$), then the stability of this equilibrium cannot be determined through a first order stability analysis (i.e., the eigenvalues are purely imaginary; see appendix). This implies that the directional force of selection near this equilibrium is extremely weak.

It is important to recognize, however, that the modeling approach used in equations (2) assumes that the direction of evolutionary change is predominantly driven by the current average values of the traits but that the shape of the phenotypic distribution plays a negligible role. This assumption is reasonable when strength of selection arising from the average trait values is large, but when it is weak we must determine whether other moments of the phenotype distribution, such as its variance, affect the direction of evolution change. Model (2) cannot be used to address this equation, and in fact extending the model to allow for these sorts of second-order effects can be difficult. Nevertheless, it is relatively easy to reason out the expected effect of variation in trait values on the stability of the equilibrium in this case.

If there is significant variation around both the average female sensitivity and the average male persistence values of $\bar{S} = 0$ and $\bar{P} = \bar{T}$, how will this affect stability? Those females with a slightly positive sensitivity will do worse when encountering males with persistence values higher than $\bar{P} = \bar{T}$ because they will mate too readily. In contrast, these same females will do better when encountering males with persistence values lower than $\bar{P} = \bar{T}$. The net effect will depend on the exact distribution of trait values in the population, but in general these effects will tend to cancel one another. The same is true for females with a slightly negative sensitivity. These findings therefore suggest that the equilibrium will be locally stable in this case.

Alternatively, if the mating rate at equilibrium (4) is too low for females (i.e., $1/2 < \theta_\psi$), then natural selection will favor those females that use the mating interaction to increase their mating rate. This can be accomplished only by maintaining some sensitivity to the male trait. In other words, when the male trait invades, it increases both the fitness of its bearer and females in general by bringing both closer to their optimal mating rate. However, by maintaining some sensitivity to the male trait, this favors males to exploit this sensitivity with the evolution of greater persistence and thereby drive females beyond their optimal mating rate. Thus, the equilibrium (4) is unstable (see appendix). The overall evolutionary dynamics in this case are such that male persistence escalates indefinitely, while females evolve to become less and less sensitive (fig. 2). Biologically, this leads to a population in which males have extremely exaggerated traits but where females are nearly indifferent to these traits.

Overall, the above results are largely opposite to those obtained when the female mating threshold alone evolves. In that case, no fixed equilibrium value for the male and female traits can be identified (Gavrilets et al. 2001), and instead, indefinite escalation in both male and female traits was found. When sensitivity alone evolves, however, then male persistence can either reach a nonexaggerated equilibrium (if $1/2 > \theta_\psi$) or it can escalate indefinitely (if $1/2 < \theta_\psi$). The former case seems most likely to occur (i.e., in the absence of this trait interaction, females are mating at a higher than optimal rate). In either case, however, females are always expected to evolve insensitivity. This illustrates that rather than the perpetually escalating male and female traits found by Gavrilets et al. (2001), females can evolve toward indifference to the male trait, in some cases halting the coevolutionary process and in others leading to further escalation of the male trait (fig. 2).

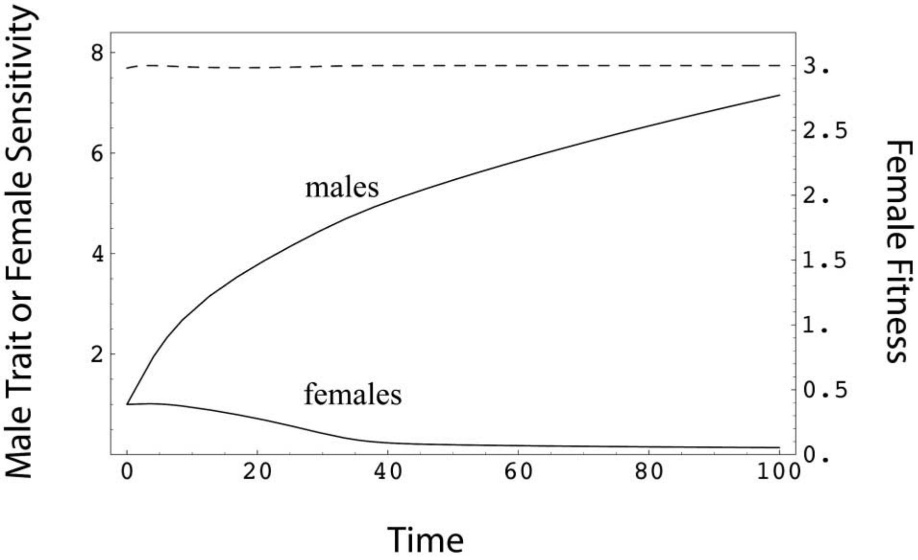

Figure 2: Evolutionary dynamics of the male trait, the sensitivity of the female preference function, and female fitness (*dashed curve*) when there is no natural selection on either female sensitivity or the male trait and the threshold of the female preference function is fixed. In the case shown, female mating rate is below its optimum in the absence of the male trait. Female preference for the trait can then increase mating rate to its optimum and thereby elevate female fitness. Further exaggeration of the male trait is accompanied by reduced female sensitivity so that female fitness stays at its optimum (see "Only Female Sensitivity Evolves: No Natural Selection"). Parameter values: $v_P = 1$, $v_T = 0$, $v_S = 0.5$, $a = 0.5$, $b = 0.5$, $P_{\text{opt}} = 0.7$, $c_P = 0$, $c_T = 0$, $c_S = 0$, $\theta_P = 0$, $\theta_T = 2$, $\theta_S = 3$.

Finally, we can also determine how female fitness is expected to evolve under the above conditions by evaluating female fitness throughout time as the traits coevolve. Interestingly, it appears that female fitness remains near its maximum possible value at equilibrium regardless of which of the above evolutionary outcomes occurs (fig. 2*b*). Intuitively, if females have complete flexibility in their preference function and natural selection does not favor a particular perceptual system, then females can always ensure the highest fitness by being largely unexploitable.

Natural Selection in Males Only. More realistically, there is likely to be natural selection acting, at least on the male traits as they become greatly exaggerated. With natural selection on males only, the dynamical equations become

$$\frac{d\bar{S}}{dt} = 2v_S\psi' a[-(\bar{P} - \bar{T})(\psi - \theta_\psi)], \tag{5a}$$

$$\frac{d\bar{P}}{dt} = 2v_P[b\bar{S}\psi' - c_P(\bar{P} - \theta_P)]. \tag{5b}$$

There are up to three possible equilibria of model (5), and their feasibility along with their stability properties depend on the parameter set chosen (see appendix). Considering the case where $1/2 = \theta_\psi$ (females mate at their optimal rate in the absence of any signal perception), there are then only two equilibria for female sensitivity:

$$\bar{S} = 0,\ \bar{P} = \theta_P, \tag{6a}$$

$$\bar{S} = \frac{4c_S}{b}(T - \theta_P),\ \bar{P} = T. \tag{6b}$$

Equilibrium (6a) is always locally stable, whereas the stability of equilibrium (6b) cannot be determined from a first order analysis (i.e., one of the eigenvalues is 0; see appendix). Again, we must consider the effect of variation in trait values on the stability of this equilibrium. In this case we can reason that such variation will tend to destabilize equilibrium (6b). The reasoning goes as follows. Because the optimal mating rate is 1/2, females cannot do any better than to be completely insensitive to the male trait. In equilibrium (6b) there is a nonzero average female sensitivity. If all males had a persistence value of exactly $\bar{P} = T$, then females would attain their optimal mating rate of 1/2 in this case as well. Any variation in male persistence, however, will result in females mating either too much or too little at this equilibrium. As a result, evolution is expected to move away from this equilibrium and toward that of (6a), where females are guaranteed to always attain their optimal mating rate.

To summarize, with natural selection on the male trait only, we again expect the evolution of female insensitivity and the shutting down of any antagonistic evolutionary process. In this case, however, the male trait evolves to its natural selection optimum (θ_P; fig. 3). Once female sensitivity evolves to be 0, the male persistence trait has no effect on a female's propensity to mate, and thus the male trait reaches equilibrium only when it is at its natural selection optimum (θ_P). In the analogous case of the previous section, when there was no natural selection on either males or females (and when $1/2 = \theta_\psi$), equilibrium was also reached when females are insensitive; however, in this case the male trait evolves to an arbitrary value. Finally, as with the results of the previous section, female fitness tends to evolve to its maximum possible value in this case as well. As a result, sexually antagonistic coevolution is not evidenced by a depression of female fitness at equilibrium.

Natural Selection in Both Males and Females. The most plausible scenario is where both male and female traits are under natural selection. In this case the analysis becomes more complicated; therefore, we make some simplifying assumptions. First, we examine only the case where females mate at their optimal rate in the absence of any signal perception ($1/2 = \theta_\psi$). Furthermore, because model (2) is structurally symmetrical around 0, we restrict attention to nonnegative male and female trait values only. To do so, we also assume that the fixed female threshold is positive (i.e., $T > 0$) and that optimal female sensitivity is positive (i.e., $\theta_S > 0$). Finally, without loss of generality, we assume that the male trait is measured on a scale where its optimal value is 0 (i.e., $\theta_P = 0$). Under these assumptions, model (2) becomes

$$\frac{d\bar{S}}{dt} = 2v_S\left[-a(\bar{P} - \bar{T})\left(\psi - \frac{1}{2}\right)\psi' - c_S(\bar{S} - \theta_S)\right], \quad (7a)$$

$$\frac{d\bar{P}}{dt} = 2v_P(b\bar{S}\psi' - c_P\bar{P}). \quad (7b)$$

It is no longer possible to obtain explicit expressions for the equilibria of model (7), but we can deduce some information about any equilibrium that might occur. It is possible to show, for example, that the equilibrium of model (7), if one exists, must be such that the male trait is exaggerated (i.e., $\bar{P} > 0$) and the female sensitivity is positive but less than its natural selection optimum (i.e., $0 < \bar{S} < \theta_S$; fig. 4).

As in the model of Gavrilets et al. (2001), where only the female mating threshold was allowed to evolve, increasing the intensity of sexual selection on males, *b*, increases the degree of exaggeration in the male trait. More

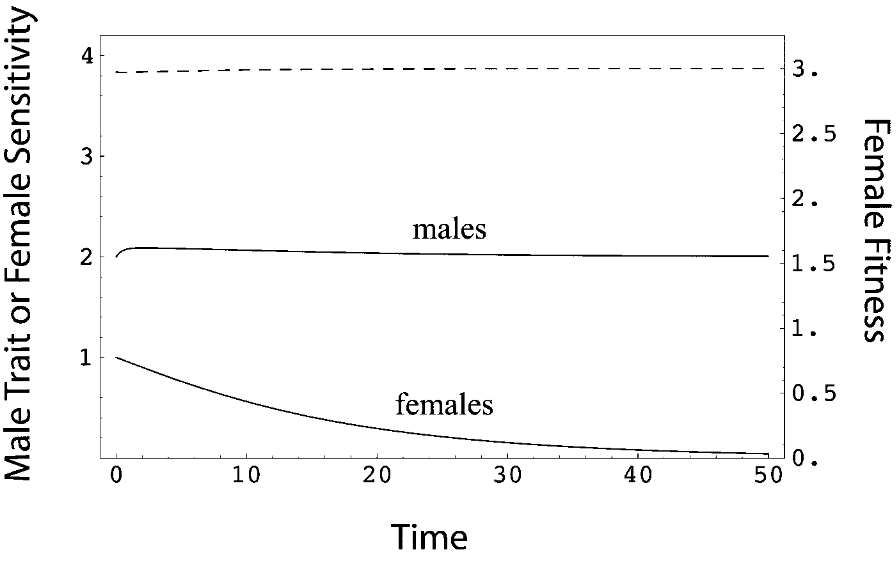

Figure 3: Evolutionary dynamics of the male trait, the sensitivity of the female preference function, and female fitness (*dashed curve*) when there is natural selection on the male trait only. In the case shown, female mating rate is below its optimum in the absence of the male trait. Unlike figure 2, where there was no natural selection on the male trait, reduced sensitivity of females to the male trait is accompanied by retreat of the male trait to its natural selection optimum (see "Only Female Sensitivity Evolves: Natural Selection in Males Only"). Parameter values: $v_P = 1$, $v_T = 0$, $v_S = 1$, $a = 0.5$, $b = 0.5$, $P_{\text{opt}} = 0.5$, $c_P = 1$, $c_T = 0$, $c_S = 0$, $\theta_P = 2$, $\theta_T = 2$, $\theta_S = 3$.

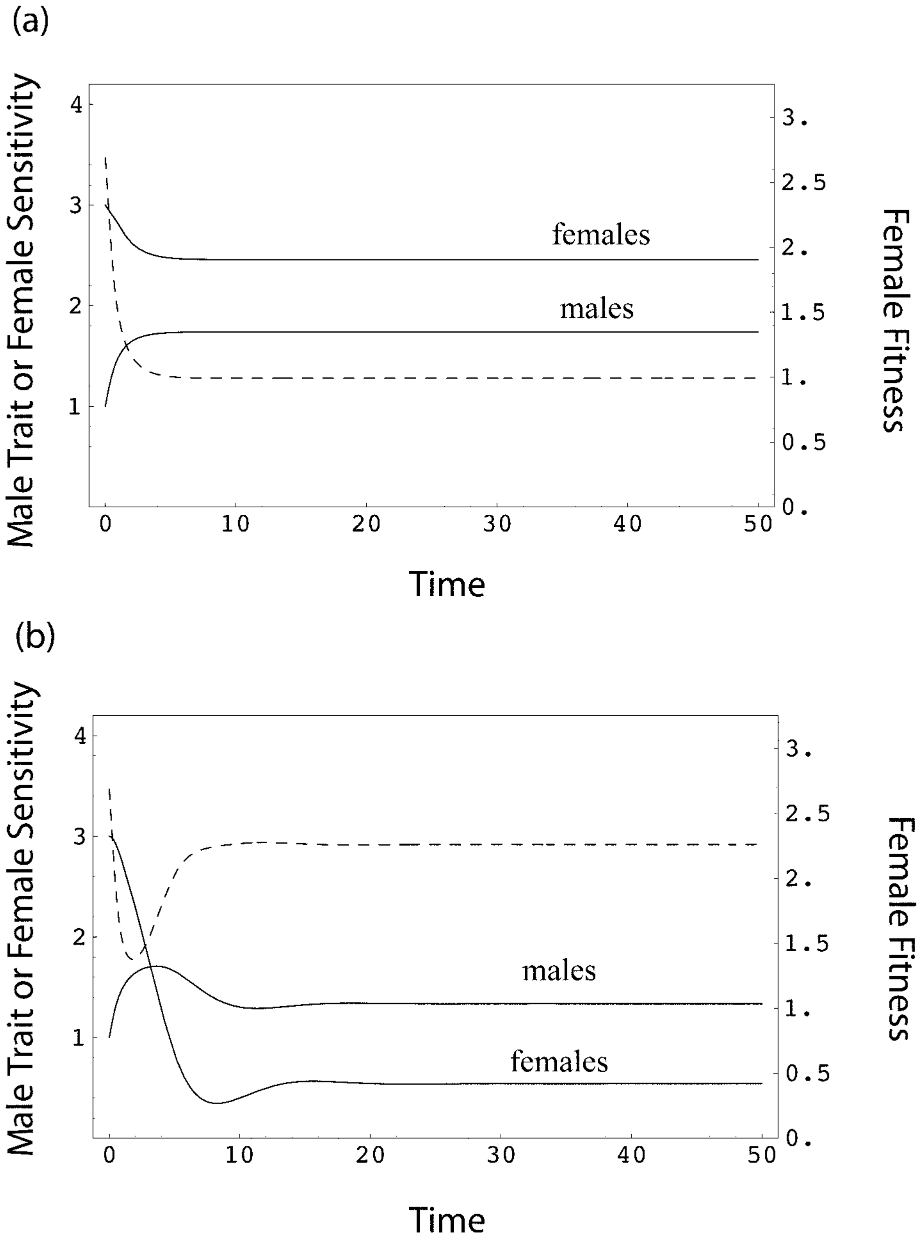

Figure 4: Evolutionary dynamics of the male trait, the sensitivity of the female preference function, and female fitness (*dashed curves*) when there is natural selection on both the male trait and female sensitivity to that trait. *a*, Relatively strong natural selection on female sensitivity (see "Only Female Sensitivity Evolves: Natural Selection in both Males and Females"). Parameter values: $v_P = 1$, $v_T = 0$, $v_S = 1$, $a = 5$, $b = 0.5$, $P_{\mathrm{opt}} = 0.25$, $c_P = 0.1$, $c_T = 0$, $c_S = 0.5$, $\theta_P = 2$, $\theta_T = 2$, $\theta_S = 3$. *b*, Relatively weak natural selection on female sensitivity. Parameter values: $v_P = 1$, $v_T = 0$, $v_S = 1$, $a = 5$, $b = 0.5$, $P_{\mathrm{opt}} = 0.25$, $c_P = 0.1$, $c_T = 0$, $c_S = 0.005$, $\theta_P = 2$, $\theta_T = 2$, $\theta_S = 3$.

significantly, however, decreasing the strength of natural selection on females (i.e., decreasing c_S) now has a markedly different effect. In the model of Gavrilets et al. (2001), decreasing the strength of natural selection on the female resistance trait (i.e., the threshold in that case) led to further discrimination by females (an increased threshold value) and consequently the evolution of increased exaggeration of the male trait. In the present model, however, decreasing the strength of natural selection of the resistance trait (i.e., the sensitivity) leads to decreased exaggeration of the male trait. Intuitively, if only the female resistance threshold evolves, then females must always remain sensitive to male stimulation. Consequently, when natural selection on the threshold is weak, females respond to excessive male stimulation by increasing their mating threshold. This then leads to increased male trait exaggeration as well, and hence, to an escalating arms race. On the other hand, if only the female sensitivity evolves, then weak natural selection on this trait allows females to escape manipulation by evolving insensitivity to manipulation. This lack of sensitivity then results in an evolutionary retreat of the male trait toward its natural selection optimum.

Finally, it is interesting to examine the consequences of the above coevolutionary dynamics on female fitness. In contrast to cases 1 and 2, costs to females caused by the elevation of mating rate cannot be mitigated by a cost-free reduction in sensitivity to the male trait. Here, because of natural selection on sensitivity, any reduction in sensitivity will come at some cost to female fitness. Although no definitive analytical results are possible, numerical simulations suggest the following relatively simple principle: If the strength of natural selection on female sensitivity is strong relative to that on the male trait, then the coevolutionary dynamics tend to substantially depress female fitness at equilibrium (fig. 4*a*). On the other hand, if the strength of natural selection on the female trait is weak relative to that on the male trait, then the coevolutionary dynamics tend to depress female fitness very little at equilibrium (fig. 4*b*). In the first case, strong natural selection on the female trait typically forces females to remain sensitive to some degree, and males then exploit this sensitivity, resulting in depressed female fitness. In the second case, weak natural selection on females allows them to evolve to be nearly insensitive, thereby preventing the substantial depression of their fitness through male exploitation.

Both Female Sensitivity and Threshold Evolve

In natural populations it is unlikely that only the sensitivity or the threshold of the female preference function evolves. More likely, both of these components can evolve to some degree. The situation is naturally even more complex than the previous models, but again, some general principles appear to fall out of numerical simulations. If the strength of natural selection on one of the two female resistance traits, S or T, is strong relative to the other, then this trait tends to be more tightly constrained. As a result, it does not evolve as far from its natural selection optimum (θ_S or θ_T). Provided that the two resistance traits are truly independent, the other trait then evolves to dominate the resistance response and results are very similar to those where only a single trait is allowed to evolve (fig. 5).

Discussion

Although it is commonly suggested that conflict between the sexes over mating may lead to the coevolution of exaggerated male display traits, expensive female preferences, and consequently reduced female fitness (e.g., Parker 1979; Gowaty 1996; Holland and Rice 1998; Partridge and Hurst 1998), little formal theory exists to substantiate these claims, and much of this is verbal theory (e.g., Getty 1999; Holland and Rice 1999; Rosenthal and Servedio 1999). In this article, we assumed sexual conflict over mating rate and then asked how female resistance to costly male traits coevolves with those male traits. Our formulation differs from past models in that we allowed the sensitivity (slope) of the resistance function to evolve instead of the threshold alone. Our results suggest that evolutionary arms races that lead to the exaggeration of persistence and resistance will be much less common than formerly predicted and emphasize the importance of the evolutionary lability of the female sensory system in affecting the pathway of sexually antagonistic coevolution.

The Role of Female Sensitivity in Sexually Antagonistic Coevolution

Our model, which incorporates fewer constraints on the female sensory system underlying resistance, leads to some similar conclusions as previous formal models. However, there are two key conclusions that differ markedly from earlier results. First, Gavrilets et al.'s (2001) analyses suggested that earlier verbal theory by Holland and Rice (1998) was largely correct in predicting the common expectation of escalating arms races resulting from sexual conflict. Our analyses suggest that this outcome is much less likely than previously thought. More specifically, whether an arms race occurs or whether females evolve to be insensitive to male manipulation depends critically on the nature of genetic variation in female preference functions. It also depends critically on the strength and form of natural selection acting on preference functions in contexts unrelated to mating. Evolutionary arms races tend to occur only when the female evolutionary response to male manipulation is tightly constrained by a lack of genetic variation in its shape (i.e., sensitivity) and/or by very strong natural selection to maintain a constant shape. In such cases, the evolutionary response in females is, by necessity, one that induces escalation in males. If the shape of preference functions can readily evolve, however, then arms races are much less likely.

Together, these results suggests that we need to know much more about the evolution of female preference functions before making strong generalizations about arms races. There is no obvious reason to expect that sensitivity

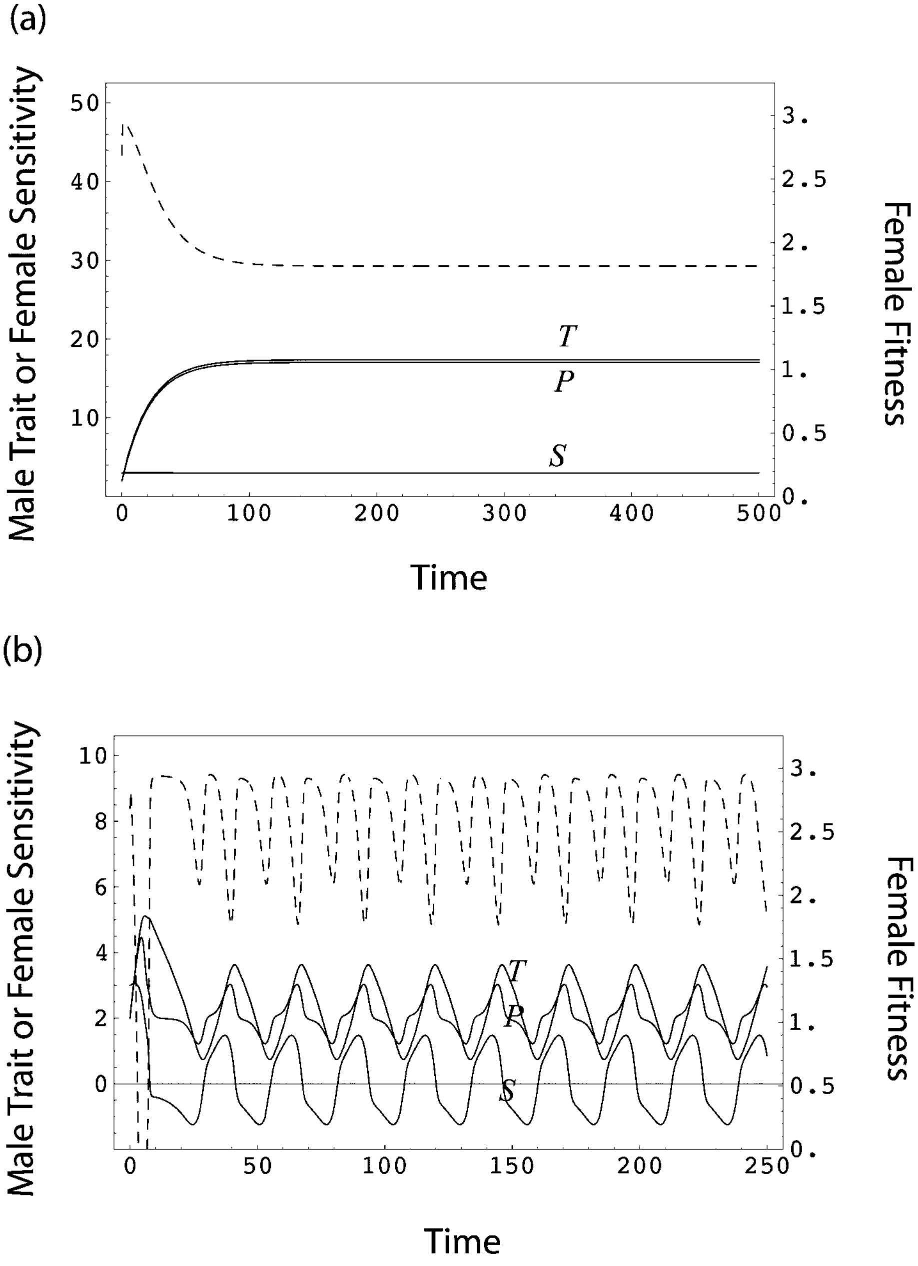

Figure 5: Evolutionary dynamics of the male trait (P), the female threshold (T), the sensitivity of the female preference function (S), and female fitness (*dashed curves*). *a*, Relatively strong natural selection on female sensitivity and weak natural selection on female threshold (see "Both Female Sensitivity and Threshold Evolve"). Parameter values: $v_P = 1$, $v_T = 1$, $v_S = 1$, $a = 5$, $b = 0.5$, $P_{\mathrm{opt}} = 0.25$, $c_P = 0.02$, $c_T = 0.005$, $c_S = 0.5$, $\theta_P = 2$, $\theta_T = 2$, $\theta_S = 3$. *b*, Relatively weak natural selection on female sensitivity and strong natural selection on female threshold. Parameter values: $v_P = 1$, $v_T = 1$, $v_S = 1$, $a = 5$, $b = 0.5$, $P_{\mathrm{opt}} = 0.25$, $c_P = 0.02$, $c_T = 0.5$, $c_S = 0.005$, $\theta_P = 2$, $\theta_T = 2$, $\theta_S = 3$.

is any more likely to be constrained, functionally or by natural selection, than are thresholds. Comparative data demonstrate that both sensitivity and threshold evolve (Basolo 1996, 1998; Morris et al. 1996), and experimental data demonstrate that sensitivities can change and even change sign within a population (Berglund 1993; Hedrick and Dill 1993; Wagner 1998; Johnson and Basolo 2003). Quantifying the genetic variation in female preference functions and the form of natural selection acting on them is therefore a critical area for future research in sexual conflict. Similar calls for more data on the constraints and forces of selection acting on female preference functions have been made for some time (e.g., Kirkpatrick 1987; Kirkpatrick and Ryan 1991). These past calls were aimed at distinguishing between direct and indirect selection acting on the preference, whereas our interest is in determining which components (threshold or slope) of the preference function are evolutionarily labile.

Second, previous work (as well as that presented here) has demonstrated that sexual conflict can result in the evolution of costly female preference for costly male mating traits. Furthermore, the presence of costly preference, in addition to female mating rates being displaced from their optimum, can lead to the depression of female fitness. Some would consider this a hallmark outcome of sexually antagonistic coevolution. Strictly speaking, our results support this notion as well; however, we find important differences in the extent to which female fitness is depressed depending on conditions. If natural selection on the sensitivity of the female preference function is weak relative to natural selection on males, then sexually antagonistic coevolution results in a negligible depression in female fitness (figs. 4*b*, 5*b*). In these cases, females evolve to become insensitive to manipulation because the natural selection cost of doing so is very small. Here, costs of sexually antagonistic coevolution can accrue largely through displacement of female mating rate from its optimum, and females can easily mitigate these costs of mating by reducing their sensitivity to the male trait. It is only when natural selection on female sensitivity is strong that sexually antagonistic coevolution tends to depress female fitness substantially. Here, costs to females accrue through both elevated mating and displacement of the sensory system from its optimum. These results therefore also suggest that quantifying the degree of natural selection acting on the components of female preference functions is critical.

Both sexually selected traits in males and the female preference itself are commonly under natural selection (Kirkpatrick and Ryan 1991; Andersson 1994). When natural selection is moderately strong in all traits, our results are more similar to those of Gavrilets et al. (2001). Sexually antagonistic coevolution leads to equilibria where the male trait is exaggerated and the female preference function is displaced from its optimum (it is costly). However, even in this case, the dynamics of coevolution differ when sensitivities, rather than thresholds, evolve. When females evolve to resist males by altering the slope of their preference function, the degree of exaggeration of the male trait and female sensitivity to that trait at equilibrium increases with increasing natural selection on the female preference (provided that females are at their optimum in the absence of stimulation by males; i.e., when $1/2 = \theta_\psi$). Conversely, when females evolve to resist males by altering their mating threshold only, this result is not observed; the degree of exaggeration in the male trait decreases (Gavrilets et al. 2001). In the case of evolving sensitivity, any reinforcing coevolutionary loop between male persistence and female resistance progressively diminishes as the intensity of natural selection rises, while in the case of evolving thresholds, the potential exists for perpetuation of this loop.

The model presented here only considers the evolution dynamics of a single male trait and female response, and this is admittedly simplistic. In natural populations, females may respond to any number of male characters, making the dynamics of sexually antagonistic coevolution increasingly difficult to understand. It often appears that there are multiple pathways along which males can manipulate females so that divergence between the sexes in isolated populations may proceed along different evolutionary trajectories (e.g., Parker and Partridge 1998; Rice 1998; Gavrilets 2000). Our results suggest that the evolution of female insensitivity during sexually antagonistic arms races may offer an explanation for the apparent rapid divergence of traits evolving under sexually antagonistic selection (Holland and Rice 1998; Chapman et al. 2003*b*). If the advantages of exaggeration in one male persistence trait are quickly nullified by the evolution of female insensitivity to male traits, then alternative traits may invade. If divergence of male manipulation traits proceeds quickly enough, such traits may have not yet had sufficient time to evolve toward their natural selection optima. In other words, although these traits are constantly evolving toward equilibrium, they never actually get there. A system of consistent nonequilibrium conditions is maintained because the equilibria themselves are continuously evolving.

Detecting Sexual Conflict

Our analyses of several alternative cases ("Only Female Sensitivity Evolves," "Both Female Sensitivity and Threshold Evolve") suggest that relatively minor differences in the evolutionary lability of male and female traits can have very significant effects on the outcome of sexually antagonistic coevolution between these traits. Females may become more or less discriminating among males, female fitness may increase or decrease, and male traits may escalate or retreat. What ties these cases together is that for some period, usually throughout, the dynamics of coevolution were governed by selection on mating rate being of opposite sign in the two sexes (i.e., it was sexually antagonistic), and this antagonism was driving evolutionary change in resistance and persistence traits. The fact that the outcomes of our sample of cases studies differed so dramatically begs the question: How do we detect a role of sexually antagonistic coevolution in driving male and female traits to their current values?

The short answer is that we cannot with certainty detect sexually antagonistic coevolution in the past by using contemporary studies or retrospective analyses of experimental evolution (see also the discussions of Rice 1998; Arnqvist and Rowe 2002). The reason for this can be seen by contrasting our various case studies, where in most instances sexually antagonistic coevolution has resulted in substantial evolution of both persistence and resistance traits. In cases where natural selection on both components of the female preference function are strong, then at equilibrium, females are mating more frequently than optimum, resistance traits are displaced from their optimum, and greater exaggeration of male traits increases mating costs to females. Each of these elements could in principle be detected with manipulative experiments or selection studies. Likewise, in retrospective analyses of experimental evolution, one would also see a depression of female fitness resulting from sexually antagonistic coevolution. However, when natural selection on the sensory system is weak, quite a different picture emerges. At equilibrium, neither female mating rate nor the resistance trait is substantially displaced from its optimum, and exaggeration of male persistence traits may have relatively little cost to females. Likewise, retrospective analyses of experimental evolution studies would reveal little or no depression of female fitness resulting from sexual antagonistic coevolution. In summary, our ability to detect a role of sexually antagonism in the evolution of resistance and persistence traits rests on the presence of natural selection acting on female preference; when natural selection is weak, any role of sexual antagonism may be obscured.

Direct and Indirect Selection

The coevolutionary patterns that we describe here depend entirely on direct selection on mating rate and the persistence and resistance traits. Our formulation does not include the buildup of genetic covariance among traits and therefore cannot address the role of indirect selection on the dynamics of coevolution. Previous studies of the effects of these covariances alone demonstrate that they can affect dynamics but will not affect equilibria (reviewed in Cameron et al. 2003). The same equilibria would occur had we included these in our models, as has been demonstrated earlier by Gavrilets et al. (2001). It is true that mutation bias, like that which fuels the good genes process, can provide the necessary additional evolutionary force to affect equilibria, but the strength of this force is a matter of debate (Pomiankowski et al. 1991; Kirkpatrick 1996; Cameron et al. 2003). If these effects are strong, then the costs we see to female fitness may be reduced or removed, but they will not change the general coevolutionary patterns, nor will they reduce the role that sexual conflict had in generating them. Nevertheless, good-genes effects will certainly exacerbate the uncertainty in detecting sexually antagonistic coevolution with contemporary studies.

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APPENDIX

Evolution of Female Sensitivity Only

The system of equations describing evolution of female sensitivity only is

$$\frac{d\bar{S}}{dt} = 2v_S[-a(\bar{P} - \bar{T})(\psi - \theta_\psi)\psi' - c_S(\bar{S} - \theta_S)], \quad \text{(A1a)}$$

$$\frac{d\bar{P}}{dt} = 2v_P[b\bar{S}\psi' - c_P(\bar{P} - \theta_P)]. \quad \text{(A1b)}$$

No Natural Selection

When there is no natural selection on either the male or female traits ($c_S = 0$, $c_P = 0$), equilibrium is reached when

$$\bar{S} = 0,\ \bar{P} = \bar{T}, \quad \text{(A2a)}$$

or if $1/2 = \theta_\psi$ when

$$\bar{S} = 0. \quad \text{(A2b)}$$

A local stability analysis of equilibrium (A2a) reveals that the two eigenvalues are given by

$$\left\{-\frac{1}{4}\sqrt{abv_Sv_P\left(\theta_\psi - 1/2\right)},\ \frac{1}{4}\sqrt{abv_Sv_P\left(\theta_\psi - 1/2\right)}\right\}. \quad \text{(A3)}$$

These eigenvalues are purely imaginary when $\theta_\psi < 1/2$. Otherwise, one of them is positive, indicating instability.

Natural Selection in Males

When natural selection acts only on the male trait ($c_S = 0$, $c_P \neq 0$), there are three potential equilibria:

$$\bar{S} = \frac{4c_P(T-\theta_P)}{b},\ \bar{P} = T, \tag{A4a}$$

$$\bar{S} = \frac{c_P(T-\theta_P) + \sqrt{c_P\left[c_P(T-\theta_P)^2 + 4b(1-\theta_\psi)\theta_\psi \ln\frac{\theta_\psi}{1-\theta_\psi}\right]}}{2b(1-\theta_\psi)\theta_\psi}, \tag{A4b}$$

$$\bar{P} = T + \frac{2b(1-\theta_\psi)\theta_\psi \ln\frac{\theta_\psi}{1-\theta_\psi}}{c_P(T-\theta_P) + \sqrt{c_P\left[c_P(T-\theta_P)^2 + 4b(1-\theta_\psi)\theta_\psi \ln\frac{\theta_\psi}{1-\theta_\psi}\right]}},$$

$$\bar{S} = \frac{c_P(T-\theta_P) - \sqrt{c_P\left[c_P(T-\theta_P)^2 + 4b(1-\theta_\psi)\theta_\psi \ln\frac{\theta_\psi}{1-\theta_\psi}\right]}}{2b(1-\theta_\psi)\theta_\psi}, \tag{A4c}$$

$$\bar{P} = T + \frac{2b(1-\theta_\psi)\theta_\psi \ln\frac{\theta_\psi}{1-\theta_\psi}}{c_P(T-\theta_P) - \sqrt{c_P\left[c_P(T-\theta_P)^2 + 4b(1-\theta_\psi)\theta_\psi \ln\frac{\theta_\psi}{1-\theta_\psi}\right]}}.$$

If $1/2 = \theta_\psi$ then this simplifies to the two equilibria,

$$\bar{S} = \frac{4c_P(T-\theta_P)}{b},\ \bar{P} = T, \tag{A5a}$$

$$\bar{S} = 0,\ \bar{P} = \theta_P. \tag{A5b}$$

The eigenvalues of the Jacobian matrix for equilibrium (A5a) are given by

$$\{0,\ -2c_P v_p\}. \tag{A6a}$$

The eigenvalues of the Jacobian matrix for equilibrium (A5b) are given by

$$\left\{-\frac{1}{8} a v_S (T-\theta_P)^2,\ -2c_P v_p\right\}. \tag{A6b}$$

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