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Research article

Interaction between sexually antagonistic selection and mate choice in the evolution of female responses to male traits

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Abstract. Theoretical analyses of selection on mutations affecting female responsiveness to male traits suggested that sexually antagonistic selection and traditional female choice are not exclusive alternatives. They can act simultaneously on the same female traits, and can either reinforce or act against each other. These analyses do not yield theoretical predictions regarding the relative frequency and importance of the two types of selection on female responsiveness, as the balance between them is affected by complex factors, including the frequency distribution of male traits, and the mechanisms of male action. Male–female interactions differ from many other evolutionary interactions involving potential evolutionary conflict, in that male and female genomes are irretrievably mixed in their offspring, thus increasing the possibility of indirect payoffs to one participant from the traits of its partner.

Key words: cryptic female choice, sexual selection, sexually antagonistic coevolution

Introduction

Analysis of evolutionary interactions in terms of conflicts between the reproductive interests of participating parties has a long and distinguished record of providing useful insights (e.g., Trivers, 1972, 1974; Eberhard, 1980, 1990; Haig, 1993; Drummond, 2001; Rice and Chippindale, 2002). It is thus logical to attempt to analyze the reproductive interactions between males and females during sexual reproduction in terms of potential conflicts in their reproductive interests (Parker, 1979; Holland and Rice, 1998; Chapman *et al.*, 2003). But there is some uncertainty regarding the importance and ubiquity of such conflict (Cameron *et al.*, 2001; Cordero and Eberhard, 2003; Kokko *et al.*, 2003; Pizzari and Snook, 2003).

Traditional explanations of why females accede to some males but not others have invoked female choice on the basis of direct gains (often in terms of

greater numbers of offspring produced) and/or indirect gains (greater genetic quality of offspring, produced) (Andersson, 1994). However, females can suffer a variety of costs resulting from sexual interactions – including reduced oviposition, longevity and food intake, and increased predation – that could generate a coevolutionary process of antagonistic adaptation and counter-adaptation between males and females (Holland and Rice, 1998; Chapman *et al.*, 2003; Pizzari and Snook, 2003). Recent discussions of sexually antagonistic selection (SAS) (and the resulting sexually antagonistic coevolution) have emphasized a particular type of payoff to the female – the benefit of reducing direct male-inflicted damage to her ability to produce offspring (Rowe *et al.*, 1994; Holland and Rice, 1998; Chapman *et al.*, 2003).

Whereas models of SAS have focused on possible direct benefits to females, several traditional female choice models have emphasized indirect payoffs (Fisher, 1958; Andersson, 1994; Kokko *et al.*, 2003). While some recent authors have questioned on theoretical grounds whether the magnitude of indirect payoffs can be sufficient to offset direct costs (Gavrilets *et al.,* 2001; Cameron *et al.,* 2001; Chapman *et al.,* 2003), this issue is still in doubt, as there is recent evidence from both theoretical (Kokko *et al.,* 2003, in preparation; H. Kokko, in preparation.) and empirical studies (Tallamy *et al.,* 2003; Pai and Yan, 2002) that indirect payoffs can be substantial. This, and the likely graded nature of direct costs which can be negligible under some conditions, justify further theoretical exploration of the possible effects of indirect payoffs such as the one presented here.

Many of the traits mentioned in recent discussions of SAS, such as male courtship behavior, genitalic morphology, and male seminal products that affect female reproductive processes, were previously thought to have evolved under sexual selection by female choice (Eberhard, 1985, 1996; Andersson, 1994; Cordero, 1995, 1998; Eberhard and Cordero, 1995; Birkhead and Møller, 1998). The two types of selection act on different aspects of female fitness, so they are not strict alternatives (Cordero and Eberhard, 2003; Kokko *et al.*, 2003). Determing the selective value of particular patterns of female response to "antagonistic" male traits requires taking into account both direct and indirect costs and benefits to the female (Parker, 1979; Andrés and Morrow, 2003; Cordero and Eberhard, 2003; Kokko *et al.*, 2003; Pizzari and Snook, 2003).

For instance, a mutant female with increased susceptibility to the more manipulative males in her population may pay higher direct costs (lower number of offspring) as well as indirect costs through her female offspring (increased direct costs paid by her female offspring; this cost would be small if more "manipulative" males are rare, but it will have increasing importance as the frequency of these males increases). But this same female will also bias the paternity of her offspring more strongly in favor of manipulative males; if

differences in male ability to inflict damage are due to genetic differences between males, she will produce sons with above average manipulative abilities and will thus obtain indirect benefits through her male offspring. Similarly, a female mutant with an overall reduction in susceptibility to male manipulation could also experience mixed results: a direct gain in terms of more offspring, and an indirect cost in terms of lower manipulative capabilities of male offspring due to her reduced ability to bias paternity. Indirect and direct selection resulting from female choice and SAS could also act in the same direction, both favoring the same types of female responses (see below). SAS and traditional female choice have usually been considered as alternatives, and there are few discussions of the possible interactions between the two types of selection (Cordero and Eberhard, 2003; Kokko *et al.*, 2003; Pizarri and Snook, 2003).

Here we explore some ways in which female choice and SAS could interact during the origin of female traits. We are fully conscious of the short useful life of most theoretical discussions of sexual selection (Andersson, 1994) and that we are making certain simplifying assumptions (see below), and are attempting to make only a partial exploration of possible interactions between the two types of selection in order to discern the lay of the land, rather than a large-scale overview or synthesis.

Interaction between sexually antagonistic selection and mate choice in the origin of female responses

To illustrate the possible simultaneous action of the two types of selection, consider the mode of action of a sexually antagonistic male trait depicted in Figure 1. Because we are interested in the very early stages of the evolution of female traits, we will assume that the male trait is constant (obviously, it may change at later stages). The left panel shows the effect of a male trait (A) "displayed" during sexual interactions on a female sexual response (R). For example, A could be the size of spines on the male genitalia of an insect which abrade the internal lining of the female's reproductive tract and thus increase the access of male seminal products to her hemolymph, thereby increasing their action on her CNS to decrease her receptivity to remating (a common seminal trait – see Chen, 1984; Eberhard, 1996). R could be the length of the female refractory period (i.e., the time until her next mating). As a result of its influence on R, A has a positive effect on male reproductive success (RS_m) (Fig. 1, upper right panel). If, as we will assume in this discussion, differences in male ability to inflict damage are due, at least in part, to genetic differences between males, selection will favor males with greater A. Trait A is sexually antagonistic because it also has a negative effect on what we will call the direct

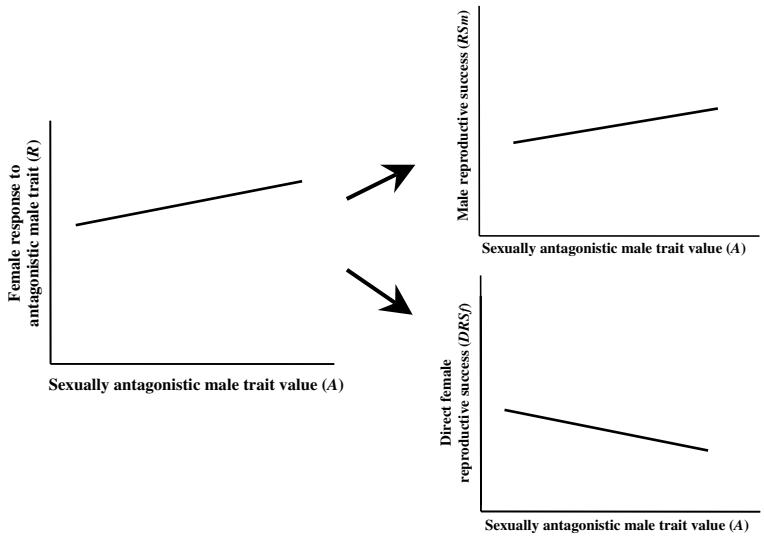

Figure 1. The mode of action of a sexually antagonistic male trait. Left panel: the value of the male trait (A) (say, the amount of a certain chemical in semen or the size of a spine in the penis that damages the female vagina during copulation) has a direct proportional effect on the response of the female (R) (say, on the length of the postcopulatory female refractory period). Two consequences are depicted in the panels at the right. Upper right: As a result of its effect on R, the value of A has a positive effect on male reproductive success (RS_m). Lower right: Trait A is called sexually antagonistic because it has a negative effect on the direct reproductive success of the female (DRS_f = the number of viable offspring, without taking into account possible differences in the "female manipulation" perfomance of male offspring).

reproductive success of the female (DRS_f), defined as the number of viable offspring she produces, without taking into account possible differences in the quality of her male offspring, in terms of their "female manipulation" abilities (Fig. 1, lower right panel). In our hypothetical case, the decrease in DRS_f could result from the negative effects of the damage to the female's reproductive tract that results in lower number of eggs laid, or to the decreased remating frequency on the female's total number of offspring if females gain access through remating to a resource (such as food).

Now consider possible female mutations that affect the response function of the female to the male trait (for instance, changes in the thickness or toughness of the lining of her reproductive tract). We will discuss two types of female mutations: mutations affecting only the intercept of the female response function (Fig. 2) and mutations affecting the intercept and the slope of the response function (Fig. 3). One type of intercept change that will be favored by selection on females is when the intercept of the response function is decreased in comparison with that of wild females (Ra and Rb *versus* Rw in upper panel of Fig. 2); the mutant female will experience a reduced antagonistic effect when interacting with males (lower panel of Fig. 2). Both mutants a and b will be

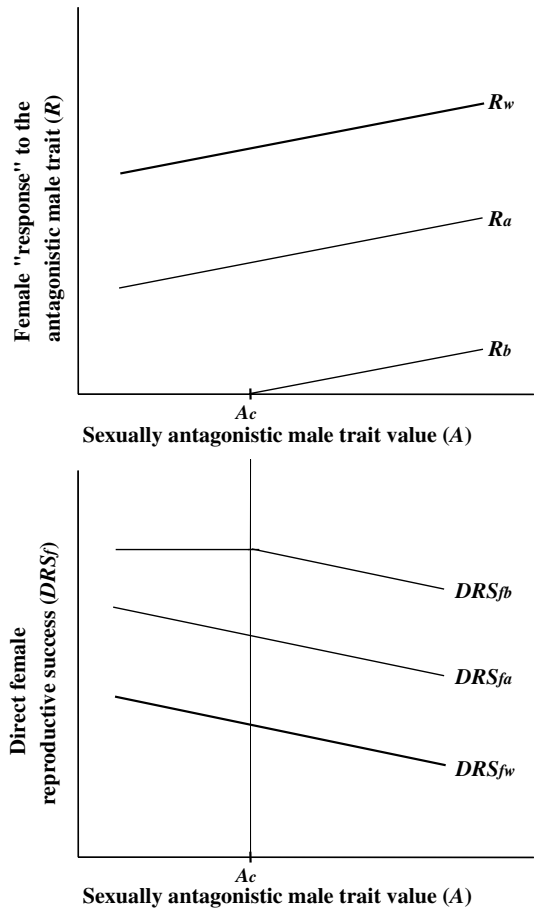

Figure 2. Effect of favorable mutations (when compared with wild type females, *w*) affecting the intercept of the female response function on the direct reproductive success of females (DRS_f). Two mutant females are considered (*a* and *b*). Mutant *a* would be favored by sexual conflict (i.e., because of her increased resistance to male manipulation), whereas mutation *b* would be favored by sexual conflict (i.e., increased resistance) and female choice (i.e., increased quality – "female manipulation" performance – of her male offspring). The magnitude of the indirect benefits of female choice for mutant *b* will depend, among other things, on the distribution of *A* in the population.

favored by SAS because their increased resistance to males (sensu Holland and Rice, 1998) results in increased DRS_f.

However, mutant *b* will also be favored because, as a result of not being manipulated by males with values of A below A_c, she will produce a stronger bias in the paternity of her offspring in favor of males with a higher value of A than do the *w* females (Fig. 2) (in our hypothetical example, damage due to theincreased length of the refractory period of mutant *b* is not produced by males with a sexually antagonistic trait smaller than A_c). As a result, she will

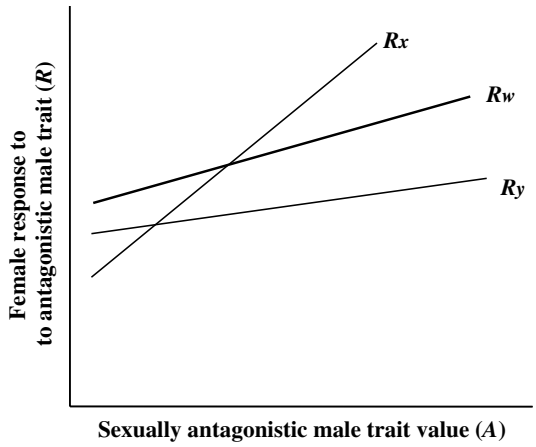

Figure 3. Two hypothetical female mutations (x and y) affecting the intercept and the slope of the female response function. Mutant x, in comparison with wild type females (w), has la decreased response to males with less developed A and an increased response to males with more developed A. Mutant y, in comparison with w females, shows an increased resistance to male manipulation (lower intercept), but a decreased ability to bias, via differential responses, the paternity of her offspring in favor of males with higher values of A (lower slope). The effect of each of these mutations on net female fitness, and therefore whether they will be able to invade the population, will depend on their effects on DRS_f (i.e., resistance) and on the inherited "female manipulation" performance of male offspring (i.e., indirect benefits of female choice), which, in turn, will depend, among other things, on the distribution of A in the population.

produce male offspring with better abilities to manipulate females than those of the male offspring of w females. The magnitude of this indirect benefit to mutant b will depend, among other factors, on the location of A_c with respect to the distribution of trait A in the male population. The indirect benefits to mutant b, compared with w females, will tend to be greater if the distribution is biased toward low values of A because she will have more offspring with the scarce "high A" phenotypes. The expected magnitude of the indirect benefits tomutant b is smaller if the male distribution is biased toward high values of A because her paternity bias toward offspring with the common "high A" phenotypes, relative to that of w females, will be smaller.

Now consider two mutations that affect both the intercept and the slope of the female response function (Fig. 3). Mutant x, in comparison with w females, has a decreased response to males with less developed A and an increased response to males with more developed A (a higher slope). Mutant y shows an increased resistance to male manipulation (lower intercept), but a decreased ability to bias, via differential responses, the paternity of her offspring in favor of males with higher values of A (lower slope). The effects of these mutations on net female fitness, and therefore whether they will be able to invade the population, will depend on the combination of their effects on both DRS_f (i.e.,

resistance), and on the magnitude of indirect benefits of female choice (the relative "female manipulation" performance of male offspring). Mutant female x will bias the paternity of her offspring more strongly in favor of males with a higher A than w females and, therefore, obtain an increased indirect benefit of producing, on average, male offspring with higher values of A (i.e., with better abilities to manipulate female responses). The direct effect of mutation x (on DRS_f) is likely to depend, among other things, on the distribution of A in the male population. For example, if most males have low values of A, mutant x would be more strongly favored over w females because she would have a direct benefit resulting from her increased resistance to the most common types of males. Whereas if the male distribution is biased toward high values of A, the DRS_f of mutant x could be below that of w females because she will be less resistant to the most common types of males. The distribution of A in the male population could have a similar effect on indirect benefits to mutant x. If the distribution of A is biased toward low values, then the indirect benefits to a female x will be relatively large compared with female w. Similarly, if the distribution of A is biased toward high values, then the indirect advantage of x over w will be smaller. The mutant x could thus be either favored or not over w, depending on these factors.

Mutant female y will have increased DRS_f, but her male offspring will have a lower average A (therefore, a lower average ability to manipulate females). Again, the mutant could be, on balance, favored or not favored over w. The distribution of A in the male population could also affect the selection on the y mutant. If the distribution is biased toward low values of the antagonistic male trait, the direct advantage to mutant y would be reduced (it would suffer damage more similar to that of w). At the same time, the indirect disadvantage of y due to its reduced capacity to choose males with higher values of A would be more pronounced. The relative effects of direct and indirect effects on the advantage of y compared to w would be reversed if the distribution of A is biased toward higher values.

Still further factors are likely to be important, and this discussion is simplified in several ways. Female responses were assumed for simplicity to be linear. If, for instance, a mutant female has an originally low but exponentially increasing response function, she could reap higher indirect reproductive benefits while suffering similar or even lower direct reproductive costs than w females (compare such a curvilinear response with R_x in Fig. 3). Male traits were taken to be static instead of evolving in response to changes in the female, as probably often occurs. Changes in males could alter the slopes, intercepts, and shapes of female response curves, and thus set off a new round of selection on females. Our analyses are designed to consider the early stages of female responses (that is, invasions by rare mutants). The indirect benefits to a female from the manipulative abilities of her sons will also depend on the

shape (or rather the distribution of shapes) of the female response functions of the next generation. In general, indirect benefits through sons will be greater when the response curves of females in the next generation have steeper slopes.

Another complication is that the different types of damage that a male may inflict on a female to further his own reproductive interests can have different effects on coevolutionary patterns. One type of male damage involves loss of offspring to the female as a direct result of a change in female behavior or physiology that the male has evolved to manipulate (we will call this "functional damage"). For instance, the male-induced tendency for the female to delay remating in our example is advantageous to the male because it reduces possible sperm competition but it could lower the female's total reproductive output if she loses benefits (e.g., access to food) from remating. A second type of damage involves incidental loss of offspring as a result of the mechanism utilized by the male to achieve his goal of increased paternity (we will call this "incidental mechanism damage"). For instance, in our example, the male's ability to perforate the female genital tract is advantageous to the male because it increases the access of his seminal products to the female's body cavity and thus increases his ability to induce her to avoid remating (see Crudgington and Siva-Jothy, 2000 and Flowers and Eberhard, submitted, on chrysomelid beetles). If the female loses additional offspring due to this damage (e.g., the weakening of her reproductive tract sometimes leads to increased danger of invasion of infectious microbes, or impedes oviposition), this would be "incidental mechanism damage". Still another possibility is "incidental collateral damage". An example would be a male seminal product that evolved because of its poisonous action on the sperm of previous males, but that also, because of its poisonous nature, had an additional negative effect on the female herself (as has been suggested for seminal substances that decrease female *Drosophila melanogaster* longevity) (Wolfner, 1997).

Distinguishing between different types of damage could be important. For example, a female mutant that reduces incidental collateral damage by becoming less susceptible to a male seminal poison evolved for sperm competition, without interfering in its action on the sperm of previous males, will be favored strictly by natural selection. Similarly, a male mutation which maintains the spermicidal effects while reducing the poisonous effects on the female would be favored. These would not be conflict situations, as there would be no selection on the other sex to counteract the new traits. Similarly, evolution of some female adaptations to reduce incidental mechanism damage (e.g., an improved ability to degrade infectious organism that enter through holes in her reproductive tract) would not result in conflict.

Although we have only explored a fraction of the possible interactions between SAS and mate choice, two general points are clear. First, sexually antagonistic selection and mate choice selection can act simultaneously on the

same female traits; in some cases they will reinforce each other, while in others they will oppose each other. Second, there seems no way to evaluate a priori the relative frequency or evolutionary importance of SAS and mate choice in the evolution of female responses, because many complex variables are likely to be involved.

Special properties of sexual interactions with respect to antagonistic coevolution

Although antagonistic coevolution and traditional female choice are not theoretically incompatible, they have not necessarily been equally important in the evolution of male and female traits utilized in sexual interactions. To date, most empirical evidence supporting SAS has come from only two groups – *Drosophila melanogaster* flies and *Gerris* water striders (Chapman *et al.*, 2003). In contrast, a summary of data on genitalic evolution in thousands of species in more than 100 families of insects and spiders suggests that the antagonistic coevolution expected to result from SAS has not been of sufficient importance to leave any trace of the predicted correlation between mating system (the degree of exposure of the female to male harassment) and rapid divergent genitalic evolution (Eberhard, 2004a,b). Thus the general usefulness of conflict analyses (see Introduction) is not clear for sexual interactions (see also Eberhard, 2005). In this section we briefly discuss properties of sexual interactions that could affect their relative importance.

One special aspect of sexual interactions, compared with most other conflict situations, is the combination of complete reproductive dependence of both the male and the female on the same offspring, and the intimate mixing of male and female genomes in these offspring. Not only do both male and female have an equal and fixed genetic representation in each offspring, their genes are generally irretrievably mixed in the offspring. In several other types of evolutionary conflicts of interests, genome mixing does not occur, at least in the short term (organelles and nuclei, plasmids and chromosomes, transposons or driver alleles and the rest of the genome, parasites and hosts), so each genome continues to have its own reproductive interests. An obvious limit on male–female cooperation is that the current male's genes will not be used in any offspring of the female which are sired by previous or future males. Once the female commits to having her eggs fertilized by the sperm of a particular male, however, her interests are in accord with those of that male. The overall expectation, from point of view of the female, may be "selective cooperation" (cooperation with particular males) (see Eberhard, 1997, 2002).

Because of this intimate mixing of male and female genomes in their offspring, the potential for conflict surrounding sexual interactions is reduced, because under certain conditions each of the participants can gain reproduc-

tively from the abilities of the other (for an opposing view, see Cameron *et al.*, 2003). For instance, a female can gain from the manipulative abilities of her partner through obtaining more manipulative sons. An obvious limit on male–female cooperation is that the current male's genes will not be used in any offspring of the female which are sired by previous or future males. Once the female commits to having her eggs fertilized by the sperm of a particular male, however, her interests are in accord with those of that male. From the female's point of view, selective cooperation can be a reasonable tactic.

Parent–offspring interactions have a similar property. An offspring that is particularly effective in inducing its parent to provide extra resources could promote its parent's reproductive success by producing particularly effective manipulative offspring of its own (see West-Eberhard, 1983, for a general discussion of social competition of this sort). Parent–offspring conflict is complicated by the fact that the original offspring will later have to pay a cost for its manipulative abilities when it becomes a parent (unless it can inactivate those particular genes that produce manipulation in its own offspring, via genetic imprinting). Similar conflicting selection can operate on particular sexually selected traits when they are expressed in both males and females (Rice, 1992). While the elaborate and escalated traits of some parent offspring interactions (e.g. mother–fetus interactions in mammals) have generally been discussed as examples of conflict (Haig, 1993), they could also be favored by selection on parents to bias provisioning in favor of particularly manipulative offspring. Conflicts between parents and offspring may be more common and have more evolutionary effect than those between males and females because non-damaging manipulation by males of females may be more feasible than non-damaging manipulations by offspring of their parents (Eberhard, 2005).

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