

SEXUAL CONFLICT AND SEXUAL SELECTION: LOST IN THE CHASE

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Abstract.—The emergent field of evolutionary biology that studies disparities between the evolutionary interests of alleles expressed in the two sexes, or sexual conflict, promises to offer novel insights into male-female coevolution and speciation. Our theoretical understanding of basic concepts is, however, still incomplete. In a recent perspective paper, Pizzari and Snook provided a framework for understanding sexually antagonistic coevolution and for distinguishing this process from other models of male-female coevolution and suggested an experimental protocol to test for sexually antagonistic coevolution. Here, I show that the framework is flawed, primarily because it is built upon the mistaken assumption that male and female fitness can evolve independently. Further, while the empirical strategy advocated has indeed offered important insights in the past, it does not allow unambiguous discrimination between competing hypotheses.

Key words.—Coevolution, fitness, reproduction, sex ratio, sexual selection, sperm competition.

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The study of sexual conflict is a rapidly expanding field in evolutionary biology. Because males and female play different roles in reproduction, we sometimes expect the sexes to evolve sexually antagonistic adaptations and counter-adaptations that reflect differences in the genetic interests of alleles expressed in the two sexes. This can lead to perpetual cyclical or escalating coevolution of reproductive traits in the two sexes, or to highly polymorphic stationary states, in a process known as sexually antagonistic coevolution (SAC; Rice 1996, 2000; Gavrillets et al. 2001; Gavrillets and Waxman 2002). Although thinking in this area has a fairly long history (Trivers 1972; Dawkins 1976; Parker 1979; Dawkins and Krebs 1978, 1979), it is still in several ways a young field. It should therefore come as no surprise (Kuhn 1970) that the study of sexual conflict suffers from conceptual ambiguities, and that confusion and debate is rife (e.g., Cameron et al. 2003; Chapman et al. 2003; Cordero and Eberhard 2003). In particular, the fact that intersexual selection by female choice is an integral part of SAC (i.e., female resistance will bias reproductive success among males toward more persistent, or manipulative, males; Rowe et al. 1994; Holland and Rice 1998; Gavrillets et al. 2001) has led to a debate over whether and how empirical data can help us distinguish this form of intersexual selection from other coevolutionary scenarios (e.g., Getty 1999; Rice and Holland 1999; Rosenthal and Servedio 1999; Cameron et al. 2003; Chapman et al. 2003; Kokko et al. 2003).

Pizzari and Snook (2003), henceforth PS, in a recent Perspective in *Evolution*, focused on two main points relating to sexual conflict as a generator of female choice. First, they presented a conceptual framework for understanding and studying SAC. Second, they provided a detailed critique of the various empirical approaches that have been used to separate sexual conflict from other generators of male-female coevolution, and outlined an experimental protocol that they suggested can help separate different coevolutionary processes. Here, I point to the fact that the framework presented by PS is flawed and show that the protocol they suggest has both important limitations and a deeper historical foundation than they appreciated.

On Sexual Conflict and the Evolution of Male and Female Fitness

Students of sexual conflict have often portrayed SAC as an evolutionary process in which the fitness of one sex increases at the expense of the other, and the framework presented by PS is built entirely upon this notion. However, this portrayal of SAC is incorrect. As pointed out already by Fisher (1930), males gain their fitness through females, and male and female fitness therefore cannot evolve independently (cf. fig. 1b in PS). In a sexually reproducing organism with an even primary sex ratio (i.e., 1:1), average male and female fitness is equal. In the context of sexual conflict, this has been pointed out in several earlier contributions and is also the reason why one sex cannot be said to win sexual conflict (e.g., Getty 1999; Rice and Holland 1999; Rowe and Arnqvist 2002). The logical cornerstone of the framework presented by PS is therefore flawed. For example, consider their pivotal equation on page 1231. Since $\partial W_m = \partial W_f$, this expression reduces to the standard deviation of female fitness divided by the standard deviation of male fitness. This approximates the relative net opportunity for selection in the two sexes, but is not a measure of the “intensity of sex specific directional selection” (p. 1231). Further, this variance ratio cannot be less than zero, a condition required by PS for the demonstration of sexually antagonistic selection.

To see how male and female fitness evolve under SAC, consider the following simple example. Sexually antagonistic coevolution can be described as a process typically initiated by the spread of a novel persistence trait/allele in males (P+) which gives bearers a relative reproductive fitness advantage over males lacking this trait/allele (P–; see also Parker 1979; Rice 1984, 1998; Rice and Holland 1997; Partridge and Hurst 1998). When the spread of P+ decreases average female (and thus also average male) fitness, it may pay females to resist the effects of P+. Note that P+ will not spread because of, but may spread despite, its population fitness depressing effects (see Morrow et al. 2003). Females reproducing with P+ males can experience depressed fitness compared to those reproducing with P– males either because (1) reproducing

TABLE 1. Methods employed in empirical studies of sexual conflict.

Type	Examples
Studies of the "economy" of male-female interactions, using naturally occurring phenotypes (many different forms of experiments)	Warner et al. 1995; Watson et al. 1998
Phenotypic manipulation of male persistence and/or female resistance	Thornhill and Sauer 1991; Arnqvist and Rowe 1995
Genetic manipulation of male persistence and/or female resistance	Chapman et al. 1995; Gems and Riddle 1996
Adaptive phenotypic plasticity in persistence/resistance	Arnqvist 1992; Jormalainen et al. 2000
Artificial selection experiments	Rice 1996; Holland and Rice 1999
Crosses between allopatric populations	Clark et al. 1999; Andrés and Arnqvist 2001
Comparative studies of the coevolution of persistence/resistance traits	Bergsten et al. 2001; Arnqvist and Rowe 2002

with P+ males is associated with elevated costs per mating/pairing (Tregenza et al. 2000) or (2) P+ males manipulate females into suboptimal mating rates (Gavrilets et al. 2001). A female resistance trait/allele R+, which counters the negative effects of P+ and thus at least partly restores female fitness, may then spread in the population. This may, in turn, set the stage for novel persistence traits in males and SAC can ensue, during which the spread of female/male resistance/persistence traits will increase/decrease fitness in both sexes to the same degree. Thus, SAC is expected to (1) cause absolute fitness to fluctuate over time and to (2) cause a gradual decay of fitness as a result of an adaptational load caused by the costs of accumulated persistence and resistance traits (Dawkins and Krebs 1979; Rice 1998; Holland and Rice 1999; Gavrilets et al. 2001). In natural populations, these dynamics may of course be offset or diluted by other and simultaneous evolutionary processes.

Sexual conflict is an elusive concept in which levels of selection are easily confused. Ironically, because the evolutionary interests of the sexes (as two discrete classes of individuals) are always identical in terms of the evolution of fitness, characterizing sexual conflict as a conflict between the genetic/fitness/evolutionary interests of the sexes, as has been done by most of us in the past, is imprecise. Yet, traits that benefit individual males can clearly result in net costs to their mates (see e.g. Chapman et al. 2003). Although there is always potential for manipulation and exploitation when two individuals interact (Dawkins and Krebs 1978, 1979; Parker 1984; Lessells 1999), sexual conflict results from the fact that the sexes play different reproductive roles in anisogamous species: traits or alleles that aid in reproductive competition among members of the sex with the higher potential reproductive rate (typically males) can spread despite the fact that they are costly to members of the sex with the lower potential reproductive rate (typically females). A more precise definition of sexual conflict is perhaps a discord between the genetic interests of alleles expressed in the two sexes (cf. Rice 1984, 1998; Rice and Holland 1997). However, this more gene-centered description can also be criticized for being incomplete.

Pizzari and Snook (2003) further claim that "traditional models" of male-female coevolution are "mutualistic" in that they predict that the average fitness of both sexes should increase over time (cf. fig. 1a in PS). Unfortunately, this is also incorrect. While theory has shown that some female choice scenarios can increase the rate of fixation of novel beneficial alleles and/or decrease the frequency of deleterious alleles (Whitlock 2000; Agrawal 2001; Siller 2001; Lorch et

al. 2003), this does not imply that absolute fitness will necessarily increase over time. As a result of the accumulation/elaboration of costly sexual traits in males and costly choice in females (see e.g. Tanaka 1996; Houle and Kondrashov 2001), absolute fitness may increase, decrease, or remain relatively unaffected by such processes (Kokko and Brooks 2003).

In summary, male and female fitness cannot evolve independently. Unfortunately, PS's description of sexual conflict and the "chase-away" hypothesis is misleading and their representation of the predictions of "traditional models" of male-female coevolution is incorrect. I suggest that the framework advocated by PS should not be adopted. It is difficult to see how the use of this framework to distinguish among alternative hypotheses, as suggested by PS, could be successful. It is also worth noting here that a similar flaw has generated erroneous predictions in parental investment theory in the past (Wade and Shuster 2002; Kokko and Jennions 2003).

Empirical Approaches Used to Study Female Choice Generated by Sexual Conflict

It has proven extremely difficult to unambiguously uncover the processes by which sex-limited traits in males and females coevolve. So far, the absence of rigorous and discriminating empirical predictions has resulted in a lack of consensus even with regard to the relative importance of direct and indirect selection in this process, not to mention the importance of different forms of indirect selection (i.e., "good genes" versus "sexy sons"), despite massive empirical efforts (Kirkpatrick and Ryan 1991; Andersson 1994; Kokko et al. 2003). Adding sexual antagonism as an additional form of direct selection certainly will not make things easier. At least seven different families of empirical avenues have been pursued in an effort to increase our understanding of sexual conflict and/or SAC (see Table 1) (partly reviewed by Lessells 1999; Chapman et al. 2003). All of these methods have both strengths and weaknesses. Given the complexity of the problem, empirical progress in understanding is perhaps most likely to result from the simultaneous application of many different methods to the study of male-female interactions in any given system.

Pizzari and Snook (2003) provide a critique of a few of the empirical approaches used in the past and of selected applications of these, much of which is similar to discussions found elsewhere (e.g., Parker 1979; Eberhard 1996; Tregenza et al. 2000; Brown and Eady 2001; Pitnick and García-Gon-

zález 2002; Chapman et al. 2003; Cameron et al. 2003; Cordero and Eberhard 2003). In particular, they provide a very detailed discussion of the problems they perceive with experiments that attempt to evaluate the importance of SAC by comparing outcomes of crosses between allopatric populations. Although I share some of their concerns (see also Chapman et al. 2003; Rowe et al. 2003), I do believe that such studies will prove helpful in understanding several facets of male-female coevolution especially if (1) formal predictive models are developed, which capture the biological complexity of intersexual communication, and (2) the importance of the degree of genetic divergence between populations is explicitly recognized. However, I also believe the critique of PS to be partly misdirected. First, it is important to note that the prediction that females will be less resistant to males with whom they are not coevolved is a statistical one. Assuming that both persistence and resistance are composite and multidimensional traits, the number of potential coevolutionary trajectories will be very large (cf. Arak and Enquist 1993, 1995). Females can therefore only be expected to be less resistant *on average* to heteropopulation males (see e.g. Clark et al. 1999; Nilsson et al. 2002), and consequently the predictions for specific crosses discussed at some length by PS have limited relevance. Although I suggest that a pattern of females being less resistant on average to males with whom they are not coevolved remains a likely outcome of SAC, it may rely on limited evolvability of the shape of female response functions (see Rowe et al. 2003). Second, the utility of population crosses in this context is not based on the assumption that the same set of persistence/resistance traits evolves in different populations. On the contrary, qualitative differences between diverging populations are expected to accumulate over time as a result of SAC, eventually leading to reproductive isolation (see Parker and Partridge 1998; Rice 1998; Arnqvist et al. 2000). As also recognized by PS, this would result in a pattern where average female resistance (defined as the inverse of average reproductive response) to heteropopulation males first decreases and then rapidly increases with increased time since divergence. This is why the expected outcome depends upon the degree of genetic divergence between populations. Third, whereas the strength of sexual selection can be rigorously defined and empirically estimated, this is unfortunately not true for sexual conflict. Actually, I am unaware of any coherent and general definition of the ‘‘intensity of sexual conflict’’ that can also be measured in extant populations. The use of this concept by PS is therefore unclear and of limited empirical use.

It is also worth noting that the point that sexual conflict is another source of intersexual selection, rather than an alternative to intra- and intersexual selection, has been made repeatedly in the past (e.g., Rowe et al. 1994; Holland and Rice 1998; Gavrillets et al. 2001), as has the obvious fact that overt behavioral aggression between the sexes alone does not demonstrate an evolutionary conflict of interests (e.g., Parker 1979; Crump 1988; Arnqvist 1992; Eberhard 1996). Similarly, several authors have pointed to the possibility that indirect benefits to females may balance direct costs of resistance (e.g. Parker 1979; Arnqvist 1992; Eberhard 1998; Andrés and Morrow 2003) and stressed that empirical estimates

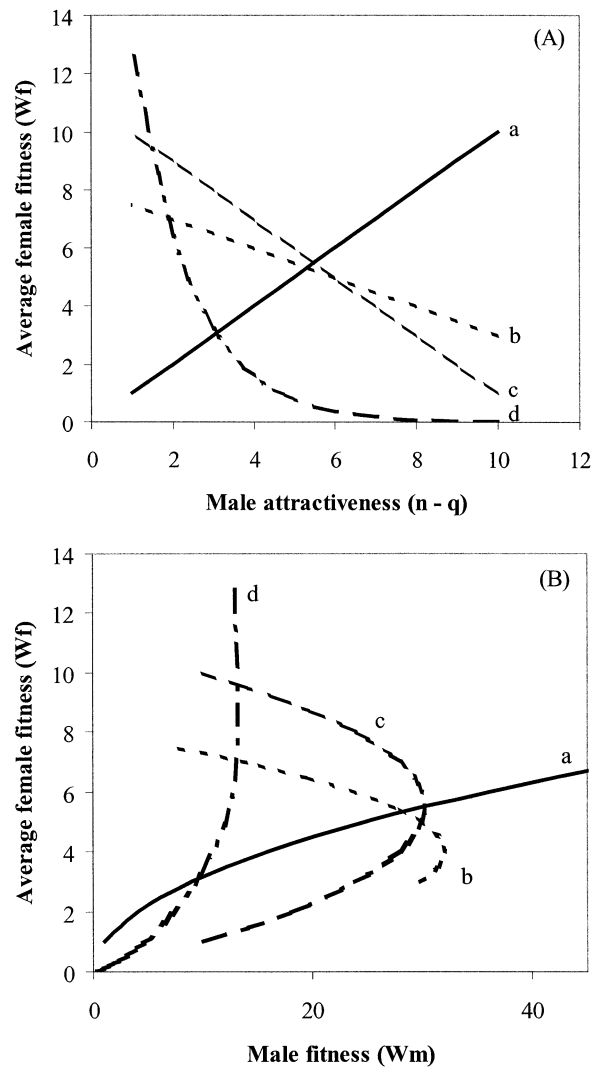


FIG. 1. The particular ‘‘selection differential approach’’ suggested by Pizzari and Snook (2003; PS; see equations on p. 1232) is problematic. One difficulty stems from how sexual conflict is probed. Each of several males is exposed to a total of n females (here $n = 10$) and male mating success (or attractiveness/persistence) is then measured as the number of females that he achieves at least one mating with ($n - q$ in PS). Male fitness (W_m in PS) is then defined as the sum of offspring produced by his mates and female fitness (W_f in PS) as the average offspring production of the females mated to a given male. PS suggest that the resulting fitness slope ‘‘will reveal the extent of sexual conflict in a population’’ (p. 1232). In this figure, panel (A) shows various assumed relationships between male attractiveness and the average fitness of his mates and panel (B) shows the fitness slopes that result from these in the simple case with negligible indirect effects (W_o in PS). Here, a positive relationship between male attractiveness and the average offspring production of his mates will indeed yield a positive fitness slope (a). One of the problems with this approach is that negative relationships can yield either noninformative (c) or even positive (d) fitness slopes. In situations where ‘‘sexy males are bad for females’’ and females are clearly selected to resist persistent males (e.g., [d]; i.e., antagonistic seduction; sensu Holland and Rice 1998), PS’s protocol may lead us to falsely conclude that there is no sexually antagonistic selection. In addition to this problem, it is worth pointing out that a negative fitness slope will not occur if a subset of males have zero fitness, unless such males are simply excluded from the analyses.

of such benefits would be useful (e.g. Eberhard 1996; Cordero and Eberhard 2003; Cameron et al. 2003).

Are Attractive Males Bad for Their Mates?

Pizzari and Snook's (2003) prescription for circumventing limitations of earlier research is an experimental protocol aimed at assessing whether and how standing variation in success in reproductive competition among males (persistence/attractiveness) is associated with the net fitness of their mates. Under ongoing SAC, we expect females to do worse when reproducing with more persistent males. Although not acknowledged by PS, various forms of this type of economic study have previously been advocated by several others (Holland and Rice 1998; Rosenthal and Servedio 1999; Gavrillets et al. 2001) and several relevant applications have also been made (e.g., Slagsvold and Lifjeld 1994; Warner et al. 1995; Brooks 2000; Civetta and Clark 2000; Baker et al. 2001; Pitnick and García-González 2002; Dronev 2003; Friberg and Arnqvist 2003; Moore et al. 2003). Although useful, this approach is no different from the methods disapproved of by PS in that it also suffers from limitations and problems. Here, I highlight two general and two specific points. First, studies testing whether females to do worse when reproducing with more persistent males can at best provide insights into the current maintenance of female resistance. However, different processes are not mutually exclusive and there are good reasons to believe that their relative importance varies over evolutionary time. Consider a population in which, following the invasion of a novel persistence allele expressed in males that exploits a sensory bias in females, females rapidly evolve resistance (Gavrillets et al. 2001). The new persistence/resistance phenotypes may then be maintained at or close to equilibrium for extended periods primarily by other forms of sexual selection (e.g. indirect selection on resistance). If this is true, studies of current selection will commonly fail to recognize the role that SAC has had for the evolution of sexual dimorphism. Second, a related and well-established problem in empirical studies of sexual conflict is the fact that we expect antagonisms to be hidden by continual adaptation and counteradaptation (Rice 1996; Arnqvist and Rowe 2002). Performing experiments with a natural range of phenotypes, as advocated by PS, is problematic, since females might effectively be resistant to male phenotypes encountered under natural circumstances (Holland and Rice 1998; Rice and Holland 1999). For this reason, several contributors have stressed the utility of economic studies that measure the costs and benefits of sexual interactions to both sexes, in which the ranges of persistence and/or resistance traits are experimentally increased (e.g., Thornhill and Sauer 1991; Chapman et al. 1995; Arnqvist and Rowe 1995; Holland and Rice 1998; Rosenthal and Servedio 1999).

The particular protocol advocated by PS also suffers from more specific problems. First, the method implicitly assumes that the direct per mating payoff to females differs between persistent and less persistent males. This assumption is not made in other formulations of the chase-away hypothesis (Holland and Rice 1998; Gavrillets et al. 2001), in which mating suboptimally is costly to females but per mating costs are actually independent of male phenotype (see Tregenza et

al. 2000; Friberg and Arnqvist 2003). This alone means that results from this protocol cannot be used to unambiguously discriminate between hypotheses. For example, despite the fact that direct costs of suboptimal mating rates may select for resistance to male stimuli among females in natural populations, such costs will remain undetected by PS's protocol. Any indirect "sexy sons" effects will instead be relatively inflated. I also note that this problem cannot be easily overcome by modifying their protocol. Second, the analytical path suggested by PS is problematic. The regression involving male fitness and a product of average female fitness (fig. 5a in PS) used to estimate the slope given central importance by PS can be very misleading (see Fig. 1). In short, the particular protocol suggested by PS is unfortunately neither "general" nor "precise."

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