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PERSPECTIVE: SEXUAL CONFLICT AND SEXUAL SELECTION: CHASING AWAY PARADIGM SHIFTS

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Abstract.—Traditional models of sexual selection propose that partner choice increases both average male and average female fitness in a population. Recent theoretical and empirical work, however, has stressed that sexual conflict may be a potent broker of sexual selection. When the fitness interests of males and females diverge, a reproductive strategy that increases the fitness of one sex may decrease the fitness of the other sex. The chase-away hypothesis proposes that sexual conflict promotes sexually antagonistic, rather than mutualistic, coevolution, whereby manipulative reproductive strategies in one sex are counteracted by the evolution of resistance to such strategies in the other sex. In this paper, we consider the criteria necessary to demonstrate the chase-away hypothesis. Specifically, we review sexual conflict with particular emphasis on the chase-away hypothesis; discuss the problems associated with testing the predictions of the chase-away hypothesis and the extent to which these predictions and the predictions of traditional models of sexual selection are mutually exclusive; discuss misconceptions and mismeasures of sexual conflict; and suggest an alternative approach to demonstrate sexual conflict, measure the intensity of sexually antagonistic selection in a population, and elucidate the coevolutionary trajectories of the sexes.

Key words.—Fitness, promiscuity, reproduction, sexual antagonism, sexual coevolution, sexual mutualism.

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Traditional models of sexual selection explain the evolution of sexual traits (mainly in males) and preference for reproductive partners displaying such traits (mainly in females; Andersson 1994; see Appendix). Although these models differ in how sexual selection operates, they share one critical assumption: female choice of partners is adaptive to females. Genes that confer a reproductive advantage to males are assumed to translate simultaneously into fitness gains to females copulating with and/or having their eggs fertilized by males carrying these genes. Therefore, the coevolution between male sexual traits and female preference is largely mutualistic, simultaneously increasing the average fitness of each sex until checked by natural selection (Fig. 1a).

An alternative view of sexual selection that is currently gathering much momentum predicts antagonistic, rather than mutualistic, coevolutionary trajectories of the sexes. This view suggests that reproductive traits can evolve in response to conflict between the sexes over reproductive decisions (hereafter referred to as sexual conflict). Some genes that confer a

reproductive advantage to males may translate into a negative fitness payoff in females copulating with and/or having their eggs fertilized by males carrying these genes. Although the fact that sexual reproduction and sexual selection generate sexual conflict was recognized over 20 years ago (Trivers 1972; Parker 1979), the possibility that this conflict may fuel antagonistic intersexual coevolution and act as a catalyst of the evolution of male and female reproductive traits has only recently received theoretical (Clutton-Brock and Parker 1995; Gowaty 1997; Rice and Holland 1997; Holland and Rice 1998; Parker and Partridge 1998; Gavrillets 2000; Johnstone and Keller 2000; Gavrillets et al. 2001; Pizzari and Birkhead 2002) and empirical (e.g., Partridge and Hurst 1998; Rice 1998; Chapman 2001; Birkhead and Pizzari 2002; Hosken et al. 2001; Knowles and Markow 2001; Moore et al. 2001; Pitnick et al. 2001a,b; Arnqvist and Rowe 2002) attention.

The “chase-away” hypothesis (CA) draws the explicit causal link between sexual conflict and sexual selection. CA provides an alternative hypothesis to traditional models of sexual selection by proposing that sexual traits have evolved as a response to sexually antagonistic, rather than mutualistic, selection. When an increase in the average fitness in one sex

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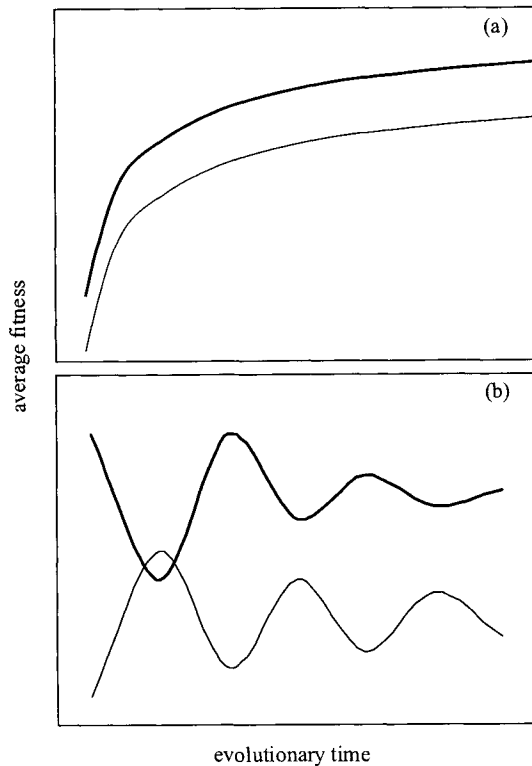


FIG. 1. Diagram outlining the basic differences between traditional and antagonistic models of sexual selection. (a) Traditional models propose mutualistic intersexual coevolution, in which the spread of a gene conferring a reproductive advantage to the carrier males (upper line), is catalyzed by the fact that their reproductive partners (lower line) also obtain fitness benefits, resulting in parallel trajectories of average male and female fitness, typically rising to an asymptote set by natural selection. Imagine a locus g segregating for two sex-limited alleles, g^+ and g^- , controlling reproductive success in males. The evolutionary fate of the two alleles will depend on the relative advantage conferred to g^+ - and g^- -expressing males (g^+ and g^- males). Suppose that g^+ conveys superior reproductive success so that $W(g^+) > W(g^-)$ where W is the fitness of an allele. Traditional models of sexual selection assume that females benefit by preferring g^+ males and resisting g^- males, implying a conflict between g^- males and females. However, since g^+ males outcompete g^- males and benefit females, sexual selection will tend to eradicate g^- from the population promoting the mutual coevolution of g^+ and the genes underlying female preference for g^+ males. (b) When sexual conflict drives sexual selection, mutations conferring a reproductive advantage to males (upper line) reduce the fitness of their partners (lower line), creating potential for the evolution of female counteradaptations, in effect generating cyclic and opposite fitness profiles. In contrast to traditional models, sexually antagonistic selection implies that g^+ confers a reproductive advantage to males while reducing the fitness of either g^+ -expressing females (intralocus conflict) or the copulation partners of g^+ -expressing males (interlocus conflict). g^+ is at a selective advantage and reduces female fitness so that: $W(\text{females reproducing with } g^+ \text{ males}) < W(\text{females reproducing with } g^- \text{ males})$. When g^+ reduces the average fitness of the females of the population, its spread favors the increase in frequency of genes that allow females to reduce the costs imposed by g^+ , by avoiding g^+ males and/or reducing the cost of mating with them. To the extent to which these female adaptations constrain the reproductive success of the prevalent, g^+ -expressing male type there will be potential for the evolution of male adaptations with counteracting effect.

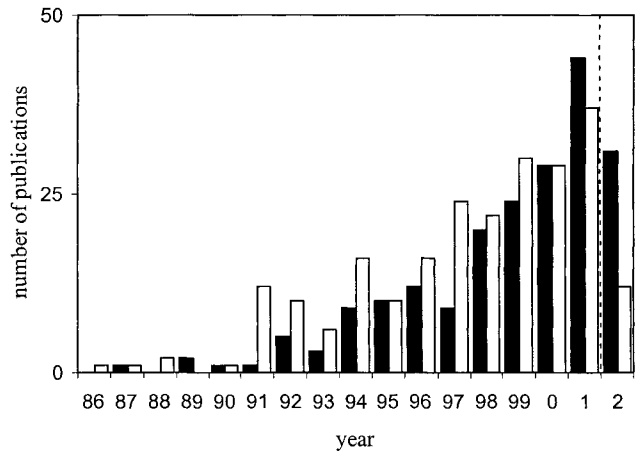


FIG. 2. Studies referencing sexual antagonism have become progressively more common and have recently become more numerous than studies testing traditional models of sexual selection. Frequency distribution of publications with "good genes" or "sexy son*" (empty bars) and with "sexual conflict" or "sexually antagonistic" (filled bars) in their title, keywords, or abstract cited in Web of Science (ISI 2002; available via <http://isiknowledge.com>) for every year from 1986 to 2001, and until 22 July for 2002 (beyond dotted line). Asterisk allows searching for any word starting with "son" (e.g., "sons," "son's," etc.).

translates into a reduction in the average fitness of the other, sexual conflict acts as a broker of sexual selection operating through intersexual antagonism rather than mutualism (Rice and Holland 1997; Holland and Rice 1998). CA predicts that males manipulate female reproductive decisions in ways that are beneficial to average male reproductive fitness but detrimental to average female fitness through the sex-limited expression of genes in males (Rice and Holland 1997; Holland and Rice 1998). Antagonistic manipulation of female reproductive decisions in turn selects for female-limited genes that allow females to resist such manipulation and for a subsequent selection on males to develop more extreme or different forms of manipulation of their partners. Thus, a cyclic chase-away process between the sexes occurs (Fig. 1b). At any point of the cycle, the model predicts that the average fitness of one sex will increase at the expense of the other sex, or, in other words, there will be a negative intersexual fitness relationship.

CA is an appealing alternative to traditional mutualistic models for three reasons. First, the negative fitness function between the sexes predicted by CA and the positive fitness relationship predicted by traditional sexual selection models (Appendix) are mutually exclusive. Second, CA provides a functional explanation for maladaptive reproductive behaviors like super- and suboptimal remating frequency (reviewed in Arnqvist and Nilsson 2000) and potentially maladaptive partner choice (see Holland and Rice 1998) that are unaccounted for by traditional models. Third, sexually antagonistic coevolution proposed by CA constitutes an alternative mechanism through which sexual selection may increase speciation rates (Rice 1998; Arnqvist et al. 2000; Gavrillets 2000; Gavrillets and Waxman 2002; but see Parker and Partridge 1998; Tregenza et al. 2000; Gage et al. 2002).

The appeal of CA has generated enormous interest in un-

covering sexual conflict as a broker of sexual selection, an interest that is notable because it appears that for the past couple of years we have been witnessing a shift in the sexual selection paradigm. More studies are now being published that consider how partners may harm rather than benefit each other through traditional mechanisms of sexual selection (Fig. 2). At the same time, the observed enthusiasm for sexual conflict is limiting our understanding of sexual selection. Increasingly, more studies appear to assume, rather than test, that sexual conflict translates into sexually antagonistic coevolution, thus accepting CA and ignoring traditional models of sexual selection. Nevertheless, there is no a priori reason to assume that either CA or traditional models will better explain reproductive strategies or that they do not interact (Holland and Rice 1998); for example, by operating during different selection episodes (Brooks and Jennions 1999). Additionally, there appears to be confusion associated with sexual conflict, sexually antagonistic coevolution, and consequently with experimentally distinguishing CA from traditional models.

Our aims in this paper are to: (1) review the mechanism of sexually antagonistic coevolution proposed by CA and compare it with traditional models of sexual selection, (2) analyze the different approaches currently adopted to test CA predictions and outline where misconceptions about sexual conflict may generate ambiguity, and (3) suggest an approach to test CA that focuses on its primary prediction: a negative intersexual fitness relationship between reproductive partners.

SEXUALLY ANTAGONISTIC EVOLUTION AND EPISODES OF SEXUAL SELECTION

Sexual selection promotes an increase in the frequency of alleles conferring a reproductive advantage and its action occurs over several discrete selective episodes targeting different phenotypic traits (Arnold and Wade 1984a; Andersson 1994). These episodes are: intrasexual selection, the competition between members of the same sex during precopulatory (e.g., mating contests) and/or postcopulatory (e.g., sperm competition) competition; and intersexual selection, the selection by one sex of reproductive partners during either precopulatory (e.g., female choice) and/or postcopulatory choice (e.g., cryptic female choice, male choice through differential sperm allocation; Andersson 1994; Birkhead and Pizzari 2002; Wedell et al. 2002). Within different episodes of sexual selection, gene frequencies can be changed by different selective mechanisms (see Appendix for examples of potential mechanisms proposed by traditional models of sexual selection). Under genetic lifetime monogamy only precopulatory episodes of sexual selection are relevant since monogamy generates the same postcopulatory fitness landscapes for both sexes. However, most species are to some extent sexually promiscuous (e.g., Birkhead and Møller 1998), providing scope for postcopulatory selection through sperm competition (Parker 1970) and cryptic female choice (Eberhard 1996, reviewed in Birkhead and Pizzari 2002). Moreover, after fertilization, females may bias the performance of the young by differentially investing in progeny fathered by different males (differential maternal investment; Sheldon 2000).

Sexual conflict occurs because partners are genetically unrelated (Dawkins and Krebs 1979) and because the differ-

ential investment in male and female gametes (anisogamy) creates diverging phenotypic optima for males and females, especially over mating frequency (Bateman 1948; Trivers 1972). Thus, sexual conflict can arise over several different reproductive decisions, such as with whom to copulate; when, where, and how often to copulate; and how much to invest in a partner and each reproductive event (Partridge and Hurst 1998; Lessells 1999; Pitnick et al. 2001b). Any trait used by one sex to increase its fitness by manipulating the decisions of its reproductive partners at their expense will be sexually antagonistic. Sexual antagonism may thus be an automatic byproduct of sexual conflict arising over these different reproductive decisions (Lessells 1999; Pitnick et al. 2001b): traits conferring a reproductive advantage to members of one sex will necessarily constrain the fitness of their reproductive partners. In addition, sexually antagonistic traits may also evolve precisely because of their antagonistic nature. By harming and/or imposing costs, an individual may discourage his/her partners from making reproductive decisions that reduce that individual's fitness (Clutton-Brock and Parker 1995; Gowaty and Buschhaus 1998; Johnstone and Keller 2000). Sexually antagonistic coevolution occurs between loci that are sex-limited in their expression and that confer a reproductive advantage to the carriers but have deleterious effects on their reproductive partners, creating potential for the spread of alleles with counteracting effects at different loci (interlocus conflict; Parker 1979; Lessells 1999; Fig. 1b).

Sexual conflict is not specific to CA. Conflict between the sexes is implicit in all traditional models (e.g., Williams 1966; Gowaty 1997) because some individuals of one sex (e.g., males) will be discriminated against by individuals of the other sex (e.g., females) in precopulatory and postcopulatory episodes of sexual selection (Fig. 1a). In this case, conflicts between the sexes over with whom and when to copulate do not generate sexually antagonistic coevolution because the average male fitness does not change in a direction that is opposite to that of the average female fitness in the population (see Fig. 1a). Sexually antagonistic coevolution will occur when, following the spread of a trait, the average fitness will increase in one sex and decrease in the other relative to *before* the spread of the trait, leading to one sex approaching its phenotypic optimum while simultaneously driving the other sex away from its own optimum (Fig. 1b).

The ability to distinguish between CA and traditional models of sexual selection therefore hinges on determining the consequences of reproduction for the fitness of partners and that of their offspring. This will allow us to quantify relative direct and indirect selection acting on female reproductive decisions and to control for the possibility that females lose fitness through male manipulation but their offspring enjoy a fitness advantage that more than outweighs female fitness costs. Indirect sexual selection through increased offspring performance is predicted by several traditional models of sexual selection (Appendix; Table 1; see also Kirkpatrick and Barton 1997). Although the strength of indirect selection on female reproductive decisions may be small (Kirkpatrick and Barton 1997), the relative contribution of direct and indirect selection has not been quantified (Hall et al. 2000). Since females mated to reproductively more efficient males may produce sons that will experience superior reproductive suc-

TABLE 1. Potential effects on some components of female fitness following mating with reproductively successful male type relative to mating with less successful male type (female fitness payoff following mating with successful male minus fitness payoff following mating with less successful male). Different outcomes are consistent with several models of sexual selection including models of sexual conflict.

Female fitness component		Fitness payoff
Longevity	-	
Current fecundity	+	
Future fecundity	-	
Sons' longevity	+	+
Daughters' longevity	+	-
Sons' reproductive success	+	+
Daughters' reproductive success	+	-
Consistent models	Differential maternal investment, Fisherian run-away, Sexually selected sperm, Chase-away (interlocus conflict)	Differential maternal investment, Sexually selected sperm, Intralocus conflict

cess (e.g., Keller and Reeve 1995; Pizzari and Birkhead 2002), positive indirect selection on female preference for reproductively superior but harmful males may outweigh negative direct selection for such preference. Despite a direct cost of mating to females, this female preference would generate mutualistic rather than antagonistic coevolution.

PREDICTIONS OF THE CHASE-AWAY HYPOTHESIS

The chase-away hypothesis generates four critical predictions, two to be tested within a population (predictions 1 and 2) and two between populations (predictions 3 and 4; Holland and Rice 1998).

Within-Population Predictions Generated by CA

(1) Males that experience superior reproductive fitness do so through sexually antagonistic manipulation subsequently imposing fitness costs on their mating partners (i.e., there is a negative intersexual fitness relationship); and (2) When one sex is winning, counteracting traits in the other sex will evolve.

Evidence consistent with both predictions has come from the work of W. R. Rice and his laboratory using the sexually promiscuous fruit fly, *Drosophila melanogaster* (Rice 1996; Holland and Rice 1999).

Holland and Rice (1999) experimentally removed the potential for sexual conflict by imposing social and genetic monogamy on a *D. melanogaster* population. Strict monogamy should promote intersexual mutualism thus reducing male antagonistic manipulation of females and correspondingly, decreasing female resistance to male manipulation. After 32–47 generations of enforced monogamy, control promiscuous females mated to monogamous males lived longer and produced more progeny than promiscuous females mated to promiscuous males. This result is consistent with prediction 1 in that monogamous males became less harmful to females. In addition, monogamous females mated to promiscuous males had shorter life spans relative to promiscuous females mated with promiscuous males (Holland and Rice 1999). This result is consistent with prediction 2 because it suggests that under promiscuity male deleterious manipulation was counteracted by female resistance (see also Rice 1996).

These findings generated much enthusiasm for sexually

antagonistic coevolution as a new paradigm in sexual selection. However, there are some problems with the experimental design that may confound the interpretation of these results (Snook 2001). As in most artificial selection experiments, there are unmeasured latent variables that may account for correlated responses to selection (Snook 2001; Pitnick and García-González 2002), and the sample size is limited to few selection lines. Additionally, the direct or indirect *benefits* that females gain from mating with promiscuous compared to monogamous males were not measured. For example, there may be differential fitness payoffs derived from the reproductive performance of offspring fathered by each male. Females that mated with deleterious males died younger and produced fewer eggs (Rice 1996; Holland and Rice 1999) but presumably also produced sons that in turn experienced high reproductive success. If indirect benefits can compensate for direct costs, the potential for sexually antagonistic coevolution is eliminated.

Rice (1996) also supported a corollary of prediction 2. If males are free to evolve in the absence of counteracting evolution in the other sex, then they should evolve greater antagonistic manipulation compared to a population in which the sexes can coevolve. Rice (1996) prevented female genotypes from evolving with promiscuous males and showed that males became more harmful to these females, an effect that was attributed to increased toxicity of seminal fluid. Because seminal fluid components also play an important role in sperm competition (Chapman 2001), it is possible that these males increased their reproductive success consistent with prediction 1.

Prediction 2 is generally difficult to test primarily because it is not possible to predict when in the future the next step in the antagonistic coevolutionary process will occur, and how rapidly its effect will vanish, counteracted by yet another response in the other sex. Predicting the evolutionary response of one sex to sexually antagonistic traits expressed in the other sex depends on both the relative fitness payoffs at stake for each sex ("value of winning"; Parker and Partridge 1998) and the costs of one sex to respond to sexual antagonism by evolving counteracting traits ("power of winning"; Parker and Partridge 1998). At an evolutionary level, the power of winning depends on the evolvability or capacity to generate heritable phenotypic variation (Wagner and Al-

tenberg 1996; Kirschner and Gerhart 1998) in female resistance and harmful male manipulation that is constrained by the available genetic material and mutation rate of the sexes. The assumption that females can counteract negative male manipulation may be weakened by the fact that the effective mutation rate in males may be higher than in females, due to a higher number of functional cells generated during spermatogenesis (four) compared to oogenesis (one; Ellegren and Fridolfsson 1997; Montell et al. 2001; Makova and Li 2002; but see McVean and Hurst 1997). On the other hand, females may have more physiological and morphological tools to control processes between insemination and fertilization, and possibly beyond (Eberhard 1996). The evolvability of a trait is difficult to measure (Brookfield 2001).

Between-Population Predictions Generated by CA

Holland and Rice (1998) argue that antagonistic coevolution cannot be demonstrated without a historical perspective, whereby the intersexual fitness relationship in a population at a given coevolutionary stage is compared with the intersexual fitness relationship in the same population at a different coevolutionary stage. Such an experiment would be difficult to perform, so they envisaged a hypothetical scenario in which CA can be tested at a single point in time by comparing *different* populations rather than different evolutionary stages within the same population (Holland and Rice 1998). Imagine two allopatric populations, A and B. In population A, sexually antagonistic manipulation occurs through a specific male trait that has not evolved in B males. The introduction of A alleles coding for the sexually antagonistic trait into the B population is expected to result in the spread of the A trait in this population due to increased male reproductive success. The A trait should also reduce the fitness of B females and because of this, B females should evolve resistance against the introduced trait. There has been no attempt to experimentally test this. However, the idea of using different populations to demonstrate CA generates two additional predictions: (3) Due to population-specific sexually antagonistic coevolution and specialization in allopatry (Fisher 1958), A females will be more efficient at resisting A males than males from an isolated B population (Holland and Rice 1998; Parker and Partridge 1998; Rice 1998); and (4) Females from a population evolving under intense sexual conflict will be more resistant to males from any population than females from a population characterized by less intense sexual conflict.

Although several studies have recently attempted to test these between-population predictions (e.g., Andres and Arnqvist 2001; Knowles and Markow 2001; Hosken et al. 2002), we argue that there are confounding problems associated with the comparison of isolated populations that severely limit the interpretation of these studies. Specifically: (1) the interaction between predictions 3 and 4 limits their testability, (2) assumptions of what traits to examine influence the interpretation of the experimental outcome, (3) predictions 3 and 4 do not discriminate between traditional and the sexually antagonistic CA model, and (4) the experimental outcome may be influenced by differences between populations that are independent from sexual conflict.

The interaction between predictions 3 and 4 limits their testability

In a between-population design, the ability of individuals from population A to manipulate or resist is tested against both A and B partners, generating a so-called $A \times B$ matrix. Because there is no coevolution between A and B, prediction 3 states that females are expected to be more resistant to homo- rather than to heteropopulation males. Thus, compared to A males, B males should be more capable of manipulating (and thus reducing the fitness of) A females. Based on prediction 4, if sexual conflict is more intense in B than A, then we expect B females to be more resistant to manipulation by both homo- and heteropopulation males compared to A females (and vice versa if sexual conflict is more intense in A than B).

Prediction 3 is concerned with differential female response to sympatric and allopatric males, independently from different intensities of sexual conflict between the two populations. Prediction 4, on the other hand, is concerned with how different intensities of sexual conflict affect the response of females from different populations. Prediction 3 is non-directional because it does not associate the intensity of sexual conflict with female response, but assumes conflict to occur in both populations and that females from both populations are affected by sexual conflict in the same way and to the same degree. Prediction 4 is directional in that it implies a positive relationship between intensity of sexual conflict and female response: the greater the intensity of conflict within a population, the more resistant to males females will become. The interaction of these two predictions may limit their testability.

Using analysis of variance, prediction 3 should generate a significant ‘‘male population \times female population’’ interaction effect on variance in female response to males (Fig. 3a). However, prediction 4 should generate a significant difference in the response to homo—and heteropopulation males by A females (exposed to relatively relaxed sexual conflict), but does not allow us to predict whether B females (exposed to more intense sexual conflict) will respond differentially to homo- and heteropopulation males (Fig. 3b,c). We can only predict that the response to *any* male will differ between B and A females, thus, we expect a significant female population effect. Therefore, the combination of predictions 3 and 4 does not indicate whether we should expect a significant interaction between male and female populations, or a significant difference between the response of A and B females to males and, in this case, whether this would depend on the difference between A and B females to just one male population (e.g., A), or to both.

Assumptions of what traits to examine influence the interpretation of the experimental outcome

The ability to test predictions 3 and 4 rests on the assumption that males in both populations use the same set of traits to manipulate and harm females (e.g., specific accessory gland proteins) and that females use the same traits to resist male coercion (e.g., morphology of sperm storage organs). However, there is no a priori reason to predict that male and female traits will be the same between populations. In fact, sexual selection, either mutualistic (Fisher 1958; Boughman

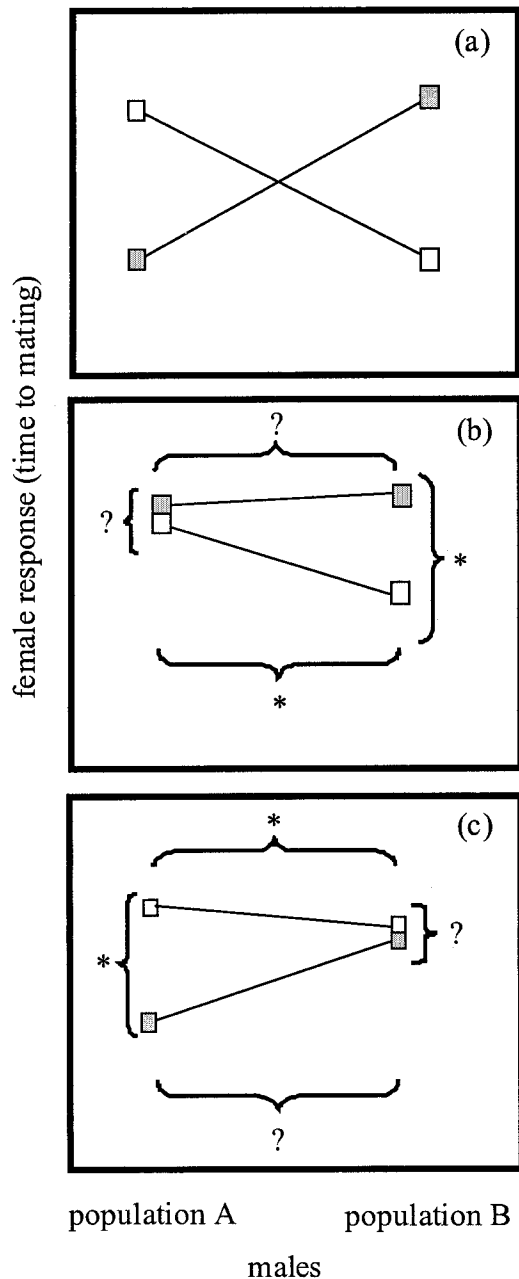


FIG. 3. Theoretical ANOVA results of the between-population CA predictions illustrating the interpretational difficulties outlined in the text. (a) CA prediction 3 proposes that females are more resistant to homo- than heteropopulation males, which would predict an interaction between the male population and female population factors. As in the text, the female response assumed to be symptomatic of sexual conflict is how quickly A (empty boxes) and B (filled boxes) females mate. (b) CA prediction 4 proposes that females from a population in which sexual conflict is more intense (population B) are more resistant to both male types than A females. The combination of predictions 3 and 4 indicates that compared to A females, B females will be more resistant to B males, whereas A females will resist A males more than B males. What predictions can be generated when comparing the resistance of A and B females to A males and the resistance of B females to A and B males is unclear. (c) Reverse scenario of (b). Asterisks indicate post-hoc comparisons that are expected to be significant, whereas question marks denote post-hoc comparisons of more ambiguous interpretation due to the interaction between CA predictions 3 and 4.

2001; reviewed by Masta and Maddison 2002) or antagonistic (Gavrilets 2000; Gavrilets and Waxman 2002; but see Parker and Partridge 1998; Tregenza et al. 2000; Gage et al. 2002), is predicted to promote local intersexual specialization, leading to divergence and ultimately speciation. Thus, sexual conflict is unlikely to target exactly the same set of traits in exactly the same way in isolated populations.

Consider then the more realistic case in which males from each population use different traits to manipulate females: population A males use a courtship display to manipulate female propensity to mate, and population B males use ejaculate products to discourage females from remating. In both populations, males gain paternity by manipulating female decisions against the female interest; they just do this using different traits. The female response will be measured as the length of time it takes for females to mate when exposed to these males (Fig. 3). Exposure of B females to A males (with courtship display manipulation) will result in shorter mating latency because B females are not resistant to A males' display and will be coerced into maladaptive copulation. Population A females will take longer to remate (but not to mate for the first time) following insemination by B males (using ejaculate products to manipulate female remating), because A females are not resistant to B males' ejaculates that inhibit female remating behavior.

Let us analyze this scenario under the assumption of CA predictions 3 and 4 that populations use similar traits, and assume that courtship display mediates sexual conflict in both populations. We then predict that A females exposed to B males should copulate more quickly than when those females are mated to A males and vice versa (i.e., females are more resistant to homopopulation males; Table 2). The observed results, however, would not be consistent with these predictions (Table 2). Because B males use ejaculate display, not courtship display, A females will not vary in their response to either A (to which females are resistant) or B males (which do not use copulation display). Only B females mated to A males will show an increased propensity to mate because B males do not manipulate females through courtship display (Table 2). Without knowing that the populations differ in the traits males use for manipulation, we would come to the erroneous conclusion that A females are not influenced by courtship display or have evolved under greater intensity of sexual conflict. We would also erroneously conclude that B females resisted B males' courtship display (Table 2).

A similar scenario can be constructed with the incorrect assumption that only ejaculates are used for antagonistic manipulation. Here, females would have to be mated to both male types successively; they will initially be mated to either heteropopulation males (to which females are not resistant) or homopopulation males (to which they are resistant) and then exposed to a second mating with homopopulation males. Thus, the first males compete against a constant second male background that is from the same population as the female (Andres and Arnqvist 2001; Table 3). Based on the assumption that sexual conflict is mediated solely by ejaculate manipulation in both populations, we expect A females initially mated to B males to be less likely to remate relative to when these females are first mated to A males, (the reverse applies to B females; Table 3). Once again, however, these predic-

TABLE 2. Assumptions of a single male trait, courtship display, on the outcome and interpretation of a between-population experiment. The experimental mating scheme and predicted and observed results for the time it takes females to mate, assuming that only female response to male courtship display manipulation was assayed, are shown. The results compare how quickly females mate (mating speed) given different mating combinations (identified by their number). $2 > 1$ means that A females mated to B males (2) should mate more quickly compared to A females mated to A males (1). The rationale describes the reasoning for the differences between predicted and observed and their associated conclusions.

Mating (female \times male)	Results		
	Predicted	Observed	Rationale
(1) A \times A (2) A \times B	$2 > 1$	$2 = 1$	Mating speed in mating combinations 1 and 2 are similar because B males do not use courtship display so A females will not differentially respond to males. Erroneous conclusion: no sexual conflict in population A.
(3) B \times B (4) B \times A	$4 > 3$	$4 > 3$	Mating combination 4 results in females mating more quickly because B females are not resistant to A males' courtship display. However, B males use ejaculate display so the B \times B "resistance" does not exist. Erroneous conclusion: B females resist B males' courtship display.

tions will not be supported. B females will remate with the same propensity irrespective of the population of origin of the first partner. This is because A males do not use ejaculate manipulation to influence female mating propensity, and B females are resistant to B males' ejaculates (Table 3). The origin of the first male also does not have any bearing on the propensity to remate of population A females. Although A females will be less willing to remate after exposure to a heteropopulation B male's ejaculate to which they are not resistant, A females are resistant to A males' courtship display. Thus, irrespective of the first mate, A females will resist the courtship display of their second (and homopopulation) mate (Table 3).

Predictions 3 and 4 do not discriminate between mutualistic and antagonistic coevolution

The population matrix approach is also flawed because predictions 3 and 4 do not discriminate between antagonistic and mutualistic models of sexual coevolution. This is because many traditional models of sexual selection do not generate explicit predictions about interpopulation matings. For example, females favoring allopatric males (e.g., allopatric males enjoying higher paternity) is consistent with CA, but is equally consistent with several traditional models. Females from population A may favor B males' sperm in fertilization to avoid inbreeding and promote genetic compatibility (Appendix). Al-

ternatively, if B males evolved under more intense sexual selection, they may be preferred for superior attractiveness, fertilizing efficiency, and possibly viability genes necessary to invest in costly ornaments (Appendix; Table 1). B males may also exploit a female sensory bias (with no necessarily negative effects on female fitness if the A population is phylogenetically older or if B is derived from A; Appendix).

Inherent population differences may influence the outcome of a population matrix independently from sexual conflict

CA suggests that sexually antagonistic coevolution will take allopatric populations along diverging evolutionary routes. As discussed above, it is precisely this variation between populations that weakens the ability to test CA using a population matrix approach.

Variation due to isolation presents further problems. The key assumption that populations are "sufficiently" diverged, may be invalid. When using a population matrix approach to detect sexually antagonistic coevolution the populations being compared must have sufficiently diverged to allow one to detect differential fitness outcomes through interpopulation matings but not diverged enough to be incipient species that may be reproductively incompatible. If the period of reproductive isolation is too short, evolution may have not generated enough divergence to detect using a population matrix approach. If reproductive isolation has been too long, so that incipient spe-

TABLE 3. Assumptions of a single male trait, ejaculate display, on the outcome and interpretation of a between-population experiment. The experimental mating scheme and predicted and observed results for mating speed, assuming that only female response to male ejaculate manipulation was assayed, are shown. The results compare female mating speed between different mating combinations (as in Table 2). The rationale describes the reasoning for the differences between predicted and observed and their associated conclusions.

Mating (female \times male \times male)	Results		
	Predicted	Observed	Rationale
(1) A \times A \times A (2) A \times B \times A	$2 < 1$	$2 = 1$	A females are not resistant to B males' ejaculate display but they are resistant to A males' courtship display so the observed results are a combination of conflict on different traits and could not be distinguished from one another. Erroneous conclusions: no sexual conflict.
(3) B \times B \times B (4) B \times A \times B	$4 < 3$	$4 = 3$	B females are resistant to homopopulation males' ejaculate manipulation and A males do not use ejaculate manipulation so no difference in subsequent remating speeds between these crosses will be found. Erroneous conclusion: no sexual conflict.

ciation occurs between the populations, speciation and hybridization may confound or account for differential female response (and fitness payoffs) to sympatric and allopatric partners (e.g., conspecific sperm precedence; Howard 1999). Determining what constitutes a sufficiently intermediate period of reproductive isolation is difficult and depends on inherent properties of the study system (e.g. mutation rate, population size, degree of isolation). Mechanisms that can explain differential female response to sympatric and allopatric males and are not necessarily linked to sexually antagonistic coevolution have been recently considered by several studies (e.g., Veen et al. 2001; Smadja and Ganem 2002).

MISCONCEPTIONS AND MISMEASURES OF SEXUALLY ANTAGONISTIC COEVOLUTION

In addition to problems specific to between-population comparisons, two main misconceptions about sexual conflict may weaken current tests of CA. These are: (1) sexual conflict is an alternative to intra- and intersexual selection, and (2) behavioral observations are sufficient to demonstrate sexually antagonistic coevolution.

(1) Sexual conflict is sometimes considered a different episode of sexual selection, an alternative to intra- and intersexual selection (e.g., Smuts and Smuts 1993; Brown et al. 1997; McLain and Pratt 1999). This is erroneous and confuses the selective advantage of a trait with the differential fitness payoff to males and females generated by such a trait. Selection favors genes conferring an overall fitness advantage that compensates for costs associated with such genes. Sexually selected traits that increase the ability to compete with other phenotypes of the same sex (intrasexual selection episodes) and that influence the reproductive decisions of members of the opposite sex (intersexual selection episodes) will be promoted. The fitness outcome of the spread of a sexually selected trait may either be beneficial to both sexes and consistent with traditional models, or sexually antagonistic and consistent with CA. Thus, sexual conflict is not an episode of sexual selection or an alternative to intra- and intersexual selection, but a (negative) intersexual fitness relationship that may generate sexually antagonistic coevolution when mediated by interlocus conflict. Sexually antagonistic selection (as predicted by CA) is in turn simply another model of sexual selection, like good genes.

(2) Intersexual behavioral interactions are important indicators of reproductive strategies. However, the assumption that certain interactions, such as aggression, are symptomatic of or even synonymous with a negative fitness relationship between the sexes, and thus of sexually antagonistic coevolution, is unjustified for two reasons. First, behavioral aggression may or may not reflect a conflict between individual partners. Males are selected to manipulate females to bias their decisions, but this manipulation does not imply fitness consequences for the females. On one extreme, there are male traits that influence female decisions through positive feedback, by generating sensory stimuli that are attractive to females. Potential examples of these "seductive" traits may be male ornamentation, courtship displays, and male courtship feeding. At the other extreme, there are "coercive" male traits that manipulate female decisions through negative feed-

back by generating traumatic stimuli and thereby discouraging a female from ignoring males. Potential examples may be forced copulation, sexual punishment, and traumatic insemination. Intersexual aggression is more likely to occur at this end of the gradient. We cannot, however, infer fitness payoffs from seduction or coercion. The probability that a female will copulate with a male with a seductive display does not indicate whether the female's decision to copulate with that male is beneficial or costly to her. Likewise, female resistance against aggressive males may be a result of sexual conflict but could also be a strategy to select more persistent and thus better quality partners who provide either direct and/or indirect benefits to the female. Moreover, male effects that are more cryptic, such as the effect of male seminal fluids in *D. melanogaster* (Chapman et al. 1995; Chapman 2001), may be ignored if precopulatory behavioral interactions between the sexes are a primary focus of sexual conflict studies. Second, behavioral conflict between individual partners over a reproductive decision may or may not translate into a negative relationship between the *average* male and female net fitness of the population on the whole. Thus, we cannot assume intersexual fitness relationship of a population based on aggression between individual partners over a single reproductive decision.

Therefore, although behavioral observations are crucial in the study of reproductive strategies and individual variation in such strategies (e.g., Shuker and Day 2001), they do not indicate whether these strategies are symptomatic of sexually antagonistic or mutualistic coevolution. The problem of choosing arbitrary behavioral traits as a measure of sexual conflict becomes even more problematic in between-population comparisons as illustrated below.

Using three allopatric populations of houseflies, "D," "S," and "M," Andres and Arnqvist (2001) found a significant male x female interaction effect on oviposition rate as predicted (CA prediction 3). Optimal oviposition rate may differ between females and their partners and be a source of sexual conflict leading to sexually antagonistic coevolution. Females from population D mated to allopatric males had significantly ($P = 0.001$) increased oviposition "rates" (rate was assayed as the presence or absence of eggs for a 24-hour period after the first mating). In population S, female oviposition rates were marginally but nonsignificantly elevated ($P = 0.069$) with allopatric males, and in population M there was no difference in female response to sympatric and allopatric males. In no case did females respond significantly more strongly to males of their own population. Because of the significant response by D females (and including the nonsignificant result from the S population) to allopatric males, and the nonsignificant response in all populations to sympatric males, the authors interpreted oviposition response being sexually antagonistic and rejected traditional models. The elevated response in oviposition of D and S females with allopatric males revealed the footprint of sexual conflict (i.e., they were resistant to sympatric, but not to allopatric, male manipulation) and the authors concluded that genetic divergence in the seminal fluid signal and receptor system had occurred (Andres and Arnqvist 2001).

There are three difficulties with this conclusion. First, only one population showed a statistically significant response to

allopatric males. Second, there was no assessment of whether variance in oviposition rate was associated with a net fitness cost in females and a fitness advantage in males, so concluding that lack of oviposition when mating with sympatric males is a footprint of sexual conflict may not necessarily be true. Third, the experimental design may be insufficient to uncover sexual conflict. Andres and Arnqvist (2001) interrupted initial pairs after 30 minutes. Transfer of seminal fluids is complete after 40 minutes (Leopold et al. 1971) and the effects of this fluid on female physiology is dose dependent (Riemann and Thorson 1969). Given that allopatry promotes reproductive divergence, the populations may have diverged in the order, timing of transfer, and/or the dosage of components and thus the effects of these chemicals on female physiology may be different. The sensitivity of females to those signals and their influence on oviposition rate may then be subject to this confounding factor when using interrupted matings. For example, if M males transfer a complete amount of an ejaculatory chemical that induces oviposition but D and S males do not completely transfer this component during an interrupted copulation, females of any population mated to M males will have relatively high oviposition rates, irrespective of sexual conflict. The observed difference in female response to D and S males may then be caused, for example, by the sensitivity of the D, S, and M female receptors to receiving an incomplete chemical cocktail. The fact that mating order, timing of transfer, and/or the dosage of components changed does not indicate whether such change harms females in any way.

DEMONSTRATING SEXUAL CONFLICT: THE SELECTION DIFFERENTIAL APPROACH

In the previous sections we have illustrated some problems associated with current approaches to test CA. Despite much focus on antagonistic coevolution driven by sexual conflict, and the ability of several studies to successfully demonstrate that males can harm females (e.g., Chapman et al. 1995; Gems and Riddle 1996; Civetta and Clark 2000; Crudgington and Siva-Jothy 2000; Stutt and Siva-Jothy 2001; Blackenhorn et al. 2002), no agreement has been reached on how to measure sexually antagonistic selection. Crucially, the primary prediction of antagonistic coevolution—a negative intersexual fitness relationship—has not been adequately tested. Arnold and Wade (1984a,b) have demonstrated how selection on polygenic traits can be quantified through careful studies of individuals within a population. Here we adopt a similar argument to measure sexually antagonistic selection within a population, based on the covariance of male and female fitness and taking advantage of phenotypic variance in a population.

The intensity of sex specific directional selection (Δ_s) in a population can be measured as:

$$\Delta_s \equiv \frac{\left(\frac{\partial W_m}{\sigma_{W_m}}\right)}{\left(\frac{\partial W_f}{\sigma_{W_f}}\right)},$$

where ∂W is the difference in the mean fitness of males (m) and females (f) between two consecutive generations (e.g.,

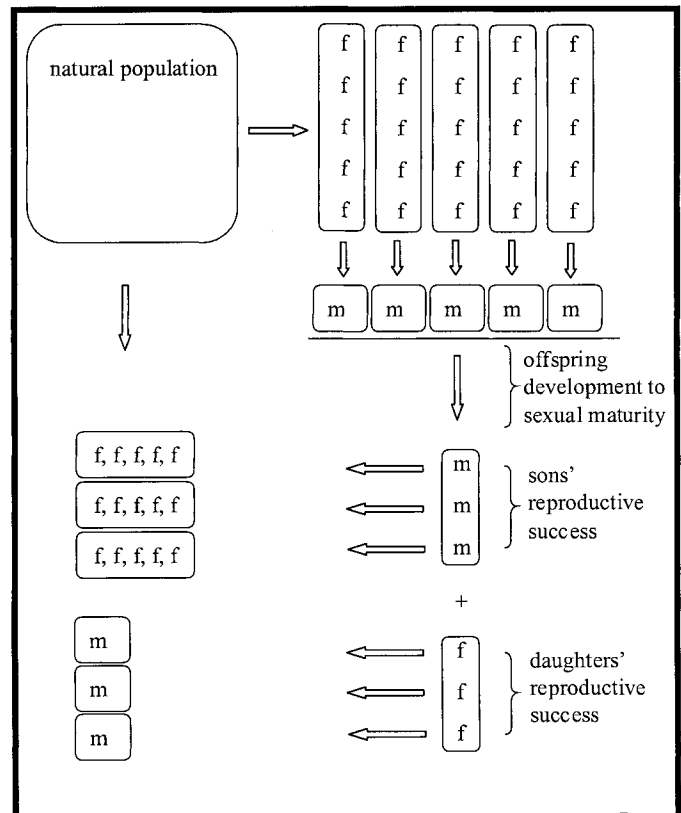


FIG. 4. Experimental design to measure sexually antagonistic selection in a population. From a natural population, a series of males (m) and females (f) are selected to obtain representative samples of male and female phenotypic distributions. Ideally, environmental variation can be reduced by selecting males and females of similar age and raising them under similar controlled conditions. The range in male reproductive fitness is obtained by allowing individual males to copulate with a higher than average number of females, and female fitness is averaged over all the copulation partners for each individual male (each male ends up with a mean female fitness associated with his reproductive performance). In addition, offspring reproductive performance is measured in a standardized way by exposing individual sons to females from the natural population and by exposing daughters to individual males from the natural population.

$W_1 - W_2$), measured as the lifetime number of offspring reaching sexual maturity, and σ_w is the standard deviation in fitness at generation 1. Antagonistic selection is demonstrated when: $\Delta_s < 0$. At any generation, males will be winning if male mean relative fitness exceeds female mean relative fitness. To test whether such antagonism is generated by CA we must reveal the causal relationship between the fitness of males and their reproductive partners.

One way to study how fitness varies in relation to partner fitness is to generate a male \times female fitness matrix in which each phenotypically variable male of a large, random sample of males from a population is provided with the opportunity to mate with a large number of phenotypically variable females, n (i.e., $n >$ maximum number of females inseminated by an individual male in the population), randomly sampled from the same population (as illustrated in Fig. 4). The reproductive fitness of each male in the experimental male \times female matrix is:

$$Wm_x = \sum_{i=1}^n N_i,$$

where N is the number of offspring produced by the i th female mated to the x th male. The mean fitness of the females mated to the x th male in the experiment is:

$$\bar{W}_{f_x} = \frac{Wm_x}{(n - q)},$$

where q is the number of females that were exposed to, but failed to reproduce with the x th male. Similarly, we can measure mean N for the z offspring surviving to sexual maturity produced by each of the $n - q$ females mated to the x th male (as in Fig. 4):

$$\bar{W}_{o_x} = \frac{\sum_{i=1}^n \sum_{j=1}^{z_j} N_j}{(n - q)}.$$

By standardizing fitness payoffs (Arnold and Wade 1984a), we can measure the average relative fitness response of a phenotypic range of females to a range of males of the same population. This allows us to quantify both the direction and magnitude of direct and indirect selection on male and female fitness (see Fig. 4) as the regression of the product of W_f (direct selection) and W_o (indirect selection) on W_m (Fig. 5). By doing so, we can study the female reaction norm against a male fitness gradient indicating whether females are directly and/or indirectly selected to resist or respond to the manipulation by male phenotypes with progressively higher reproductive fitness (Fig. 5). The sign and the shape of the intersexual fitness relationship will reveal the extent of sexual conflict in the population (Fig. 5). The slope of this regression, α , measures the intensity of direct antagonistic selection in a population. Sexual conflict will be demonstrated by a significantly negative relationship between male and female fitness: $\alpha < 0$ (Fig. 5). In this case, selection will favor male manipulation, and natural selection will directly favor female resistance. The current opportunity for selection promoting male manipulation, I_m , is given by the variance in relative male fitness and the current opportunity for female resistance, I_{fo} , is the variance in the female \times offspring relative female fitness product. Crucially, considering the fitness of one sex as the phenotypic trait determining fitness variation in the other sex, we can measure the overall differential of sexually antagonistic selection, β (i.e., selection promoting male manipulation and female resistance) as the covariance between female and male relative fitness: $\beta = \text{Cov}(W_m, \bar{W}_f \bar{W}_o)$. The potential for sexual conflict to generate sexually antagonistic selection in a population depends on all these factors. Sexually antagonistic selection is most intense when sexual conflict is intense ($\alpha \ll 0$), and I_m , I_{fo} , and β are high.

The selection differential approach has three advantages. First, it allows the measure of sexually antagonistic selection without a priori information on the traits causing sexual conflict (Fig. 5a). Second, it allows us to identify the phenotypic traits that confer a fitness advantage through sexually antagonistic effects, a posteriori, once we obtain evidence that sexually antagonistic selection occurs. This identification can be done by multiple regressions of male phenotypic traits

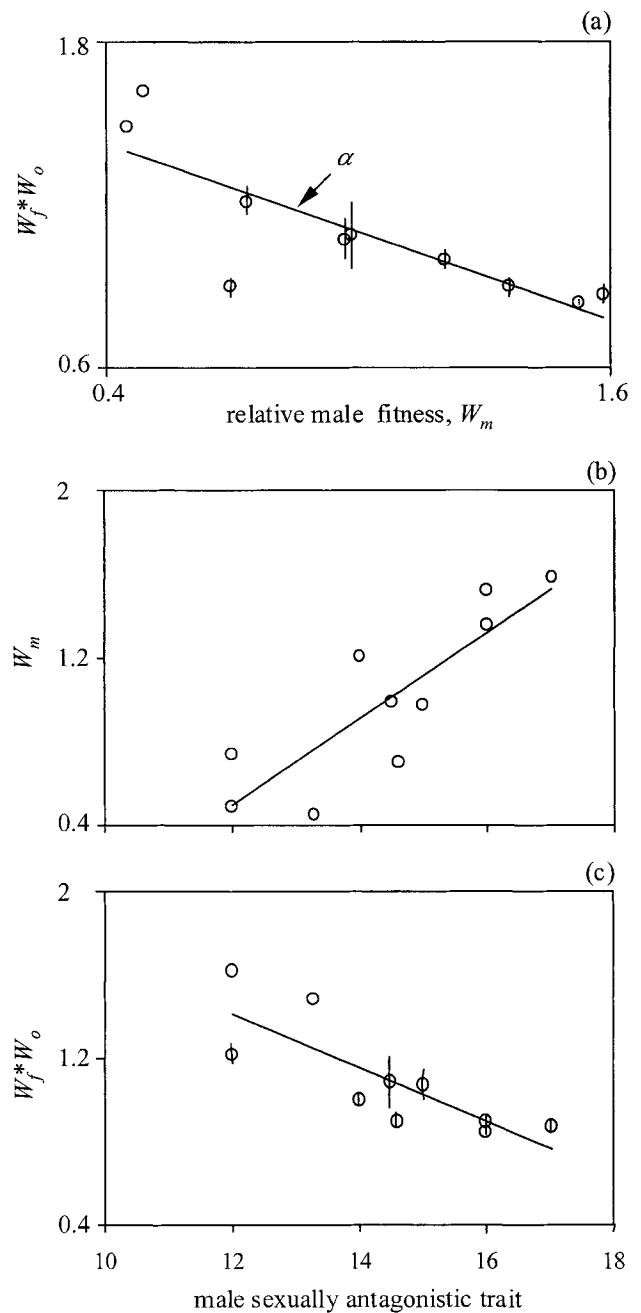


FIG. 5. Relationship between the relative reproductive fitness of a male and the relative mean fitness of his partners and their offspring. (a) A negative relationship reveals the presence of sexual conflict in a population and the slope of the intersexual relationship, α , measures the intensity of sexual conflict. (b, c) A sexually antagonistic trait is a trait whose expression is positively associated with the fitness of the carriers (in b) and negatively with the fitness of their reproductive partners and their offspring (in c).

(e.g., weapons and body mass, sexual ornaments, and fertility traits) and female phenotypic traits (e.g., anti-clasping devices, behavioral resistance) on average male reproductive fitness and average female fitness (Fig. 5b,c). The expression of these traits will be sexually antagonistic if they increase the fitness of the carrier (Fig. 5b) and reduce the product of

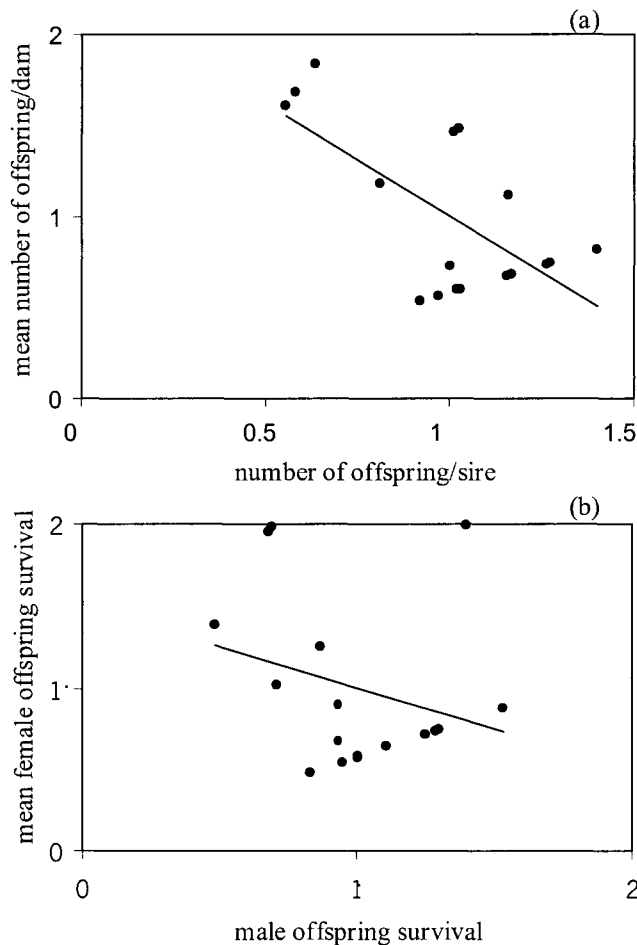


Fig. 6. Example of how intersexual fitness relationships can be partitioned into multiple fitness components corresponding to different selective episodes: (a) the number of offspring produced (direct selection), and (b) offspring survival to sexual maturity (indirect selection). The intersexual fitness relationship is negative in both fitness components; however, it is much stronger in (a) than in (b), suggesting that in this example most of the sexually antagonistic selection generated from sexual conflict arises during offspring production rather than during offspring growth.

the fitness of its reproductive partners \times their offspring (Fig. 5c). The selection differential for male manipulation is the covariance between male relative fitness and the sexually antagonistic trait(s) determining male reproductive fitness, whereas the selection differential for female resistance is the covariance between female fitness and the sexually antagonistic trait(s) protecting female fitness against male deleterious manipulation (Arnold and Wade 1984a). When the selection differential for male manipulation is higher than the selection differential for female resistance we expect antagonistic selection to be more intense on male manipulation than on female resistance. Third, the selection differential approach can partition reproduction into multiple selective episodes and measure sexually antagonistic selection arising from different episodes. This generates important a posteriori information on how different reproductive decisions acting at different selective episodes contribute to the overall differential of sexually antagonistic selection (Fig. 6a,b). There-

fore, the proposed approach first provides a general but precise measure of sexually antagonistic selection in a population, then it allows us to home in the traits and selective episodes that are causing such conflict, through successive experimental steps.

CONCLUSIONS

The early realization that sexual reproduction fosters evolutionary conflict between the sexes (Trivers 1972) and may be an important catalyst of evolutionary change in reproductive strategies (Parker 1979) has recently received theoretical (e.g. Rice and Holland 1997; Holland and Rice 1998; Partridge and Hurst 1998; Gavrillets et al. 2001) and experimental attention (Chapman et al. 1995; Rice 1996; Holland and Rice 1999; Arnqvist and Rowe 2002). Specifically, the CA provides an alternative hypothesis to traditional models of sexual selection by proposing that sexual traits have evolved as a response to sexually antagonistic, rather than mutualistic, selection. Both the appeal and novelty of this approach have generated a paradigm shift in the study of sexual selection. The risk potentially associated with this enthusiasm is that these novel and appealing ideas may be promoted without adequate testing.

Testing CA is difficult. The currency of CA predictions is ultimately sex-specific net fitness payoffs. Although proximate traits, such as variation in female behavioral resistance to males, paternity gained by second males in sperm competition, and oviposition rates are easy to quantify, they do not necessarily reflect or measure sexual conflict. Whether male and female reproductive decisions diverge cannot be assumed a priori or inferred from proximate mechanisms (e.g., sexual aggression). Because direct and indirect selection on female reproductive decisions may compensate for and counteract each other, fitness payoffs to females and their offspring must be measured to convincingly demonstrate sexual conflict.

Another problem is that some CA predictions (2, 3, and 4) are currently of limited use because they require detailed information that is either not available or is unclear how to measure. Moreover, predictions (3) and (4) rely on interpopulation comparisons, which are confounded by inherent genetic and ecological differences and incipient reproductive isolation between populations. The main limitation of the interpopulation approach is that the results are often consistent with so many different mechanisms that they ultimately have limited explanatory value. Predictions 1 and 2 have been tested through experiments based on artificial selection, and although this approach is powerful, it is limited to very few species with design and interpretation problems (Snook 2001; Pitnick and García-González 2002).

We suggest that prediction 1, a negative intersexual fitness relationship within a population, is the most promising approach to test whether sexual conflict occurs and generates sexually antagonistic coevolution. We provide an experimental approach to test prediction 1 by measuring the intensity of sexually antagonistic selection. In this methodology, the reaction norm of female fitness to male reproductive success within a population is analyzed taking into account indirect effects on male and female offspring. This design pro-

vides a testable, operational definition of sexually antagonistic coevolution that can be distinguished from traditional models.

Sexually antagonistic selection proposed by CA is likely to be a pervasive evolutionary force with critical repercussions on the coevolutionary trajectories of the sexes, sexual selection, and its role in life-history theory and speciation. Although this explains the recent interest in sexual conflict, it cannot justify the incipient paradigm shift. To critically test sexual conflict and its role in sexual selection, we must minimize confusion between sexual conflict, episodes of sexual selection, and traditional models of sexual selection; avoid assumptions about the extent to which sexual coevolution is driven by sexual mutualism or antagonism; and experimentally determine the fitness function between the sexes.

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APPENDIX

The main challenge in the study of sexual selection has been to establish the fitness consequences of female reproductive strategies and the consequent evolution of male traits directed to influence female reproductive decisions. Traditional models differ in the relationship between female choice, polyandry, and male trait evolution. A brief review of five traditional models and their predictions is provided below as supplementary information for comparisons with sexual conflict.

Direct benefits.—Females choose partners on the basis of male provision of fitness benefits (e.g., nutrients, paternal care or protection). Female choice is under positive direct selection and imposes directional selection on males. Unlike the other models below this model is mainly restricted to preinsemination selection episodes.

Good genes.—Females select males that carry genes conferring viability benefits (Zahavi 1977; Kirkpatrick and Ryan 1991; Andersson 1994). The good genes model predicts that female choice imposes directional selection on males, occurs during pre- and post-copulatory episodes, and is under indirect positive selection through the viability advantage conferred to the young.

Fisherian runaway.—Linkage disequilibrium between genes determining female arbitrary aesthetic criteria and genes underlying male traits that fulfill female criteria translates into female preference being indirectly positively selected through the production of more attractive sons and daughters that have a similar aesthetic preference, resulting in a mutualistic coevolutionary process (Fisher 1958; Andersson 1994). Under the Fisherian runaway model, female choice is adaptive, under indirect positive selection, and imposes directional selection on males.

Sexually selected sperm.—Linkage disequilibrium between female

promiscuity and male fertilizing efficiency translates into indirect positive selection on female polyandry and on direct selection for male fertilizing efficiency (Keller and Reeve 1995; Pizzari and Birkhead 2002), resulting in a mutualistic coevolutionary runaway (Keller and Reeve 1995).

Genetic compatibility.—Females gain fitness by reproducing with males that are genetically more complementary or more compatible due to such effects as MHC heterozygosity, inbreeding avoidance, and offspring genetic diversity (e.g., Zeh and Zeh 1996, 1997; Brown 1997; Tregenza and Wedell 2000, 2002). These different mechanisms share one important evolutionary implication: the effect of male genes on female reproductive fitness is not constant across females but crucially depends on the female genotype with which they interact. In other words, it is the combination of male

and female genomes, rather than the genes of the male per se, that affects female reproductive fitness. Therefore, this model proposes that female choice is directly and positively selected and generates nondirectional selection on males, both before (on the basis of some phenotypic predictors, e.g. Boughman 2001) and after insemination (on the basis of differential molecular sperm/female or egg responses; see Birkhead and Pizzari 2002).

The “sensory drive” or “sensory bias” model (West-Eberhard 1984; Ryan et al. 1990; Endler and Basolo 1998) is not reviewed here because it is more concerned with proximate (i.e., how females choose partners) rather than ultimate (i.e., the fitness consequences of that choice) evolutionary mechanisms and can be applied to both adaptive (Dawkins and Guilford 1996; Boughman 2001) and maladaptive female choice (Rice and Holland 1997; Holland and Rice 1998).