Perspective: Chase-Away Sexual Selection: Antagonistic Seduction Versus Resistance

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PERSPECTIVE:
CHASE-AWAY SEXUAL SELECTION:
ANTAGONISTIC SEDUCTION VERSUS RESISTANCE

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Abstract.—A model of sexual selection that leads to the evolution of exaggerated male display characters that is based on antagonistic coevolution between the sexes is described. The model is motivated by three lines of research: intersexual conflict with respect to mating, sensory exploitation, and the evolution of female resistance, as opposed to preference, for male display traits. The model generates unique predictions that permit its operation to be distinguished from other established models of sexual selection. One striking prediction is that females will frequently win the coevolutionary arms race with males, leaving them encumbered with costly ornaments that have little value except that their absence understimulates females. Examples from the literature suggest that the model may have broad application in nature. The chase-away model is a special case of the more general phenomenon of Interlocus Contest Evolution (ICE).

Key words.—Female preference, interlocus contest evolution (ICE), intersexual conflict, mate choice, sensory exploitation, sexual selection.

Female choice is the cornerstone for theory concerning the evolution of elaborate male traits via intersexual selection (Darwin 1871; Andersson 1994). Extant models make two alternative predictions concerning the joint evolution of male display traits and female attraction to these traits: (1) that concurrent increase in both male display trait and female attraction to the trait results from positive coevolutionary feedback between them (Fisher's run-away, good-genes, and direct-benefits models, for review see Kirkpatrick and Ryan [1991]; Andersson [1994]); or (2) that male display traits evolve in response to preexisting, static female attraction that developed as an incidental byproduct of viability selection on the female sensory system (West-Eberhard 1984; Kirkpatrick 1987; Endler and McLellan 1988; Basolo 1990; Ryan 1990; Kirkpatrick and Ryan 1991; Ryan and Rand 1993).

There is a growing body of data that is consistent with neither of these predictions (e.g., Andersson 1982; Ligon and Zwartjes 1995a,b; Morris et al. 1996; McClintock and Uetz 1996). These data, in combination with other recent studies, motivate a new model of intersexual selection that is based on antagonistic coevolution between the sexes.

In this model, preexisting sensory bias of females selects males to evolve an initial, rudimentary display trait that en-

hances their attractiveness to females, for example, a moderately longer tail. These overly attractive males induce females to mate in a suboptimal manner (e.g., too often, less-than-ideal time or place). This counter-selects females to evolve resistance to (i.e., decreased attraction), rather than preference for, the male display trait, for example, a higher requisite stimulatory threshold to induce her mating response (see below). Males are now selected to evolve a more extreme display trait to overcome the increased receiver threshold (by receiver we mean the signal receptor(s) and all associated neurological processing of the display signal), and cyclic antagonistic coevolution ensues.

A chase-away process between male signals and female receivers develops between the sexes, and this leads to exaggerated male display traits and discriminating females. Because advance of the male display trait is eventually checked by viability selection and because no such check (or weaker) may apply to female attraction, females will sometimes win such an evolutionary arms race. This will select males to recurrently evolve new display traits. In addition, males will sometimes be constrained to retain older ineffectual ornaments when these are needed to achieve threshold levels of stimulation in females.

1

MATING RATE ————————— ♀ ♂ —————

FEMALE
STIMULATION
THRESHOLD ♂ ♀ —————
TO MATE

FEMALE ♂ (non-mate) ♀ ♂ (mate)
FIDELITY

SEMINAL FLUID ♀ ♂ —————————
TOXICITY

FEMALE
PROXIMATE ————————— ♀ ♂ —————
FECUNDITY

PROXIMATE
MATERNAL ————————— ♀ ♂ —————
INVESTMENT

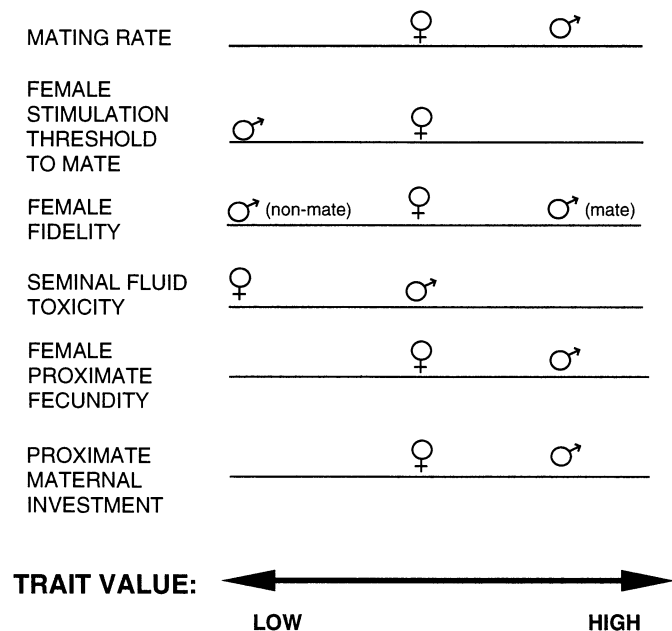**TRAIT VALUE:** ◄———————————————►
LOW **HIGH**

FIG. 1. Male versus female optima in reproductive traits. In the absence of monogamy, males and females can differ in their optima for many reproductive characters.

This "antagonistic seduction" model is motivated by recent research concerning three phenomena: intersexual conflict, sensory exploitation, and female resistance (as opposed to attraction) to sensory stimulation. For brevity, we first develop the rationale for the new model in the context of a promiscuous mating system with intersexual conflict over mating rate, and then generalize to other forms of conflict and mating systems.

INTERSEXUAL CONFLICT

A fundamental discord occurs in nonmonogamous, bisexual organisms because one sex, hereafter assumed to be females, invests primarily in offspring while the other sex invests primarily in fertilization opportunities (Bateman 1948; Trivers 1972). This central discord may lead to many forms of intersexual conflict (Parker 1979; Eberhard 1996; Gowaty 1996a,b,c; Smuts and Smuts 1993; Rice 1996; Rowe et al. 1994; Rice and Holland 1997; Fig. 1).

For example, in species with internal fertilization, seminal fluid proteins accompany sperm, and many of these find their way into the female's blood stream and act as hormones (allocrines or pheromones; reviewed in Eberhard 1996; Wolfner 1997). Experiments with insects demonstrate that male seminal fluid proteins can harm females by reducing their survival. These proteins benefit males, however, by migrating to the brain and other tissues of females, thereby suppressing their propensity to remate (reviewed in Eberhard 1996; Wolfner 1997).

Conflict over mating rate may be particularly relevant to the evolution of male courtship displays. Recent experiments demonstrate that mating is costly to both male and female *Drosophila*, even under the benign conditions of laboratory culture (Partridge and Farquhar 1981; Fowler and Partridge

1989; Chapman et al. 1995). Although mating is costly to both sexes, males are expected to have a higher optimal mating rate owing to its larger contribution to male fitness (Bateman 1948).

Mating costs to females have many potential causes (Daly 1978; Rowe et al. 1994; Stockley 1997). Physiological costs include seminal fluid toxicity (Chapman et al. 1995) and pheromonal alteration of the female's endocrine system. Behavioral and ecological costs include increased predation and energy expenditure (Parker 1979; Arnqvist 1989; Rowe 1994) and exposure to parasites (Kirkpatrick and Ryan 1991).

Direct experimental evidence for male-female conflict over mating rate comes from recent work with *Drosophila* (Rice 1996). In these experiments females were artificially prevented from coevolving while males were free to evolve. Males evolved increased fitness at the expense of their mates. A major part of the gain in male fitness was an increased capacity of experimental males to induce previously mated females to remate. Owing to the toxicity of seminal fluid in *Drosophila*, the increased mating rate of the experimental males reduced female survival. In addition, in one replicate the seminal fluid of experimental males became more toxic to females. Obviously males are not selected to harm the females who are producing their offspring. The reduction in female fitness appears to be an incidental byproduct of the benefits to males associated with seminal fluid proteins and increased mating rate.

In general, intersexual conflict over mating rate will continually select for new, or more elaborate, traits in males that cause females to mate at a rate beyond their optimum, and for females to evolve counter-adaptations. Sexual coercion of females by males (Parker 1979; Clutton-Brock and Parker 1995; Rowe et al. 1994) is one evolutionary outcome, but we have found little evidence that this is the predominant mating system in most species that have been studied to date.

Alternatively, males can evolve to persuade females to mate at a rate beyond their optimum via seduction. The two major consequences of sexual selection via intersexual conflict in mating rate are: (1) males are continually screened by sexual selection for new traits that induce females to mate beyond their optimum, and (2) females are continually selected for resistance, rather than attraction, to male traits that stimulate mating.

SENSORY EXPLOITATION

There is recent experimental evidence that female attraction to male display traits can evolve as an incidental byproduct of viability selection on the female's sensory system, and that males can exploit this affinity. For example, Ryan (1990) demonstrated that the frog *Physalaemus pustulosus* includes "chucks" in its male mating calls, and that conspecific females are attracted to these chucks. Remarkably, this same attraction exists in females from a different clade in which the males lack the chuck element in their vocalization (Kirkpatrick and Ryan 1991). Phylogenetic analysis indicates that the female attraction predates the male trait (Ryan and Rand 1993).

Fish provide another recent example of sensory exploitation. In one group of swordtails, including *Xiphophorus hel-*

leri, males possess colored extensions of the caudal fin (swords) which attract females (Basolo 1990). In a sister group, including *Priapella olmaceae*, swords are absent. When Basolo surgically attached artificial swords to males of the swordless species, their conspecific females were strongly attracted to them (Basolo 1995). As with the frogs, phylogenetic analysis indicates that the female attraction predates the male trait (Sinervo and Basolo 1996).

Females attraction for traits that are absent in conspecific males has also been sought and found in several other species (reviewed in Sinervo and Basolo 1996, see also McClintock and Uetz 1996). Collectively, these studies suggests that the opportunity for males to exploit preexisting female attraction may be widespread.

FEMALE RESISTANCE

Sexual conflict predicts that females may evolve reduced attraction for traits that stimulate them to mate. Several recent experiments support this prediction.

Pigmy Fish

Prior to 1988, all known populations of the pygmy swordtail fish, *X. pygmaeus,* contained only small males (Ryan and Wagner 1987; Morris et al. 1996). By using larger, heterospecific males in choice tests, Ryan and Wagner (1987) demonstrated strong sexual selection for large male size by female pigmy swordtail fish. At that time large body size was not known to occur in any natural pygmy populations.

In 1988, large males were discovered in three tandemly located, natural populations of the pygmy swordtail (Morris and Ryan 1995). The frequency of large males graded from common to rare along a distance gradient, apparently reflecting the spread of large males from a tributary population to two down-stream populations. In 1988, female preference for large body size was found only in the population where large males were rare. This pattern was also observed in 1993, but the degree of preference for large male body size had diminished in the population where large males were rare. Both the absence of female preference in the two populations where large males were common, and the diminishing preference in the population where large males were rare, suggest that female resistance, rather than preference, was evolving for large body size.

Wolf Spiders

Additional evidence for the evolution of female resistance to a male display trait comes from the work of McClintock and Uetz (1996) on two species of wolf spiders. One species has evolved large tufts of bristles on the forelegs which are absent in the other. Phylogenetic analysis indicates that the tufts are a derived character, that is, they have not yet evolved in the lineage leading to the tuftless species.

Females were exposed to videos of courting males and then assayed for the presence or absence of behaviors demonstrating sexual receptivity. Manipulation of the video image was used to add, remove, or enlarge the tufts on males. In the tufted species (*Schizocosa ocreata*), the propensity of females to accept a male (i.e., display one or more stereotyped

receptivity displays) was unaffected, or so small as to be statistically indiscernible, by the presence, absence, or enlargement of tufts. But in the tuftless species (*S. rovneri*), the addition of tufts more than doubled the acceptance rate of females to their own, naturally tuftless males.

The fact that females were strongly stimulated to mate with tufted males in the species where they had not evolved, while females disregarded the tufts (or were far less attracted) in the species where they had previously evolved, indicates that females from the tufted species had evolved resistance to, rather than preference for, this sexual stimulant.

Sword Tail Fish

Unpublished experimental work by Alexandra Basolo (pers. com.) also provides support for the evolution of female resistance. She measured the strength of female preference for swords in the naturally sworded *X. helleri* and the artificially sworded *P. olmaceae* (see above). Female preference is substantially stronger in the genus that has not evolved swords. Assuming the level of attraction to swords in the swordless species is representative of the primitive state in the sworded species, then the degree of female attraction to swords has declined in the sworded species.

Jungle Fowl

Ligon and Zwartjes (1995a) genetically manipulated the multifarious, striking plumage of male red jungle fowl (*Gallus gallus*). Manipulated males were hormonally, behaviorally, and structurally normal except that they developed henfeathered plumage. When females were give a choice between normal males and those with feminized plumage, there was no measurable preference for the males with normal plumage. Although we do not know for certain that the elaborate male plumage of the red jungle fowl evolved to attract females, it is nonetheless remarkable that no aspect of this complex phenotype presently is attractive to females, or has such a small effect that it was not statistically discernible.

Widow Birds

In his classic study of widow birds, Andersson (1982) found that male widow birds with artificially extended (reduced) tails secured more (fewer) mates per territory compared with unmanipulated control males. Interestingly, however, he also observed no significant correlation between male mating success and tail length within the natural range of tail lengths. Andersson (1982) suggested that this was due to low statistical power ($n = 36$), but an alternative explanation is that females have evolved resistance within the natural range of tail lengths.

In summary, while the evidence for the evolution of female resistance to male displays is still modest, the number of published studies may substantially underrepresent the frequency of the phenomenon. If one finds a significant association between a male trait and mating success, it is consistent with current models, it is interesting, and easy to publish. Negative results, however, are less exciting and potentially attributable to low statistical power, so they are far less likely to be submitted, let alone accepted for publication.

Viability selection on female sensory system

↓

Female attraction for a male trait that is absent
(Preexisting bias)   Initial
                                                          Sensory
↓   Exploitation

Mutation produces a rudimentary male display trait
(Exploitation)

↓

Female fitness declines

Antagonistic Seduction   Female Resistance
Exaggeration of male   Female mating
display   threshold increases

Male attraction declines
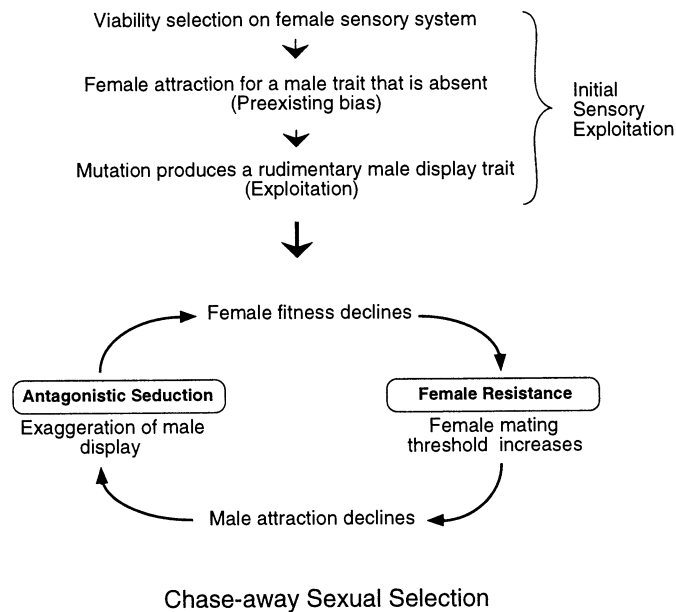
Chase-away Sexual Selection

FIG. 2. The chase-away sexual selection model for the evolution of elaborate male display traits. A male display trait is defined as any phenotype trait that attracts females, and thereby increases the probability of mating.

CHASE-AWAY SEXUAL SELECTION HYPOTHESIS

The phenomena of intersexual conflict, sensory exploitation, and female resistance outlined above motivate a new hypothesis for the evolution of male display traits (Fig. 2). The major distinction between this chase-away model and previous models is that coevolution between the male trait and female attraction is antithetic rather than reinforcing. Such antagonistic coevolution has been demonstrated for the case of male coercion of females (Arnqvist and Rowe 1995; Gowaty 1996a,b,c; Smuts and Smuts 1993; Clutton-Brock and Parker 1995). The antagonistic seduction model replaces physical coercion with attractive stimulation.

For brevity, we have concentrated to this point on intersexual conflict in mating rate, in the context of a promiscuous mating system. Many other forms of intersexual conflict (Fig. 1), as well as other mating systems, can lead to the antagonistic seduction process.

True Monogamy

Consider the case of monogamy, with no extrapair fertilizations, in which males and females cooperate in rearing offspring. The suitability of potential mates is determined by their "net worth" as an ally in reproduction, that is, based on some combination of the material and genetic benefits that they will provide. If mate selection were optimal by both sexes, then there would be a high correlation between the rank order in net worth of paired males and females.

But consider a display mutation that, based on preexisting sensory bias, overstimulated a potential mate and thereby made the displaying individual more attractive than its rank order in net worth. Carriers of such a mutation would, on average, secure mates exceeding their own rank order in net worth, and the display mutation should spread to fixation.

This counterselects the receiver system to disregard the display trait, and such a receiver allele should subsequently spread to fixation. Assuming the attraction to the stimulating display trait was built-up as an incidental byproduct of viability selection, counter-selection in the context of viability may make it difficult to ignore the display trait.

One way to counter a overly stimulating display signal would be to increase the requisite stimulatory threshold for the display trait to induce pairing. Such an evolutionary outcome would counterselect for increased amplitude of the display signal. A resulting chase-away process between genes magnifying the display signal and those dampening its reception would lead to exaggerated display characters in both sexes, which would ultimately be halted by viability selection.

Monogamy with Cheating

Socially monogamous mating systems frequently include extrapair copulations (EPC). Females, in the context of both social monogamy and polygyny, may be selected to mate with more than one male for a variety of reasons, the simplest of which is to guard against infertility of their mate (Westneat et al. 1990). A recent experiment supports this tendency of females to mate with multiple males. Ligon and Zwartjes (1995b) permitted female red jungle fowl to choose between two males over the course of laying an entire clutch. One male had a much larger comb than the other and, when allowed to choose only once, females strongly biased their mating toward the larger-combed male. But when given an opportunity to mate multiply, over the course of producing a full clutch, females typically mated with both males, despite their strong preference for larger-combed males.

Male display traits can influence female fidelity. An experimental study by Houtman (1992) began by measuring attractiveness scores of a set of male zebra finches (socially monogamous) and then paired them with females. Male attractiveness was strongly correlated with beak brightness and song rate. Males were next individually paired with females until a clutch was initiated. At this time the pair-bonded females, while hidden from their mate, were given an opportunity to extra-pair mate with a new male. The probability of an EPC was strongly correlated with the difference in the attractiveness score between the females mate and the introduced male. Thus, there is experimental evidence that male display phenotype strongly influences the probability of an EPC.

Socially monogamous males are selected to lower the rate of extrapair fertilizations by their mates, and to simultaneously seduce females mated to rival males. The optimum extra-pair copulation rate is expected to differ between a female, her mate, and other males (Fig. 1). This selects for attractive male displays for two reasons: (1) to lower the relative attraction of competitor males, and thereby enhance a female's fidelity to her mate; and (2) to overstimulate females to engage in extra-pair copulations at a rate beyond their optimum.

Given that extra-pair copulations take place, males are expected to evolve behavior and seminal fluid proteins that both reduce a female's propensity to mate with other males, and

mediate displacement of sperm from other males. In both fruit flies (*Drosophila*; Chapman et al. 1995) and nematodes (*C. elegans*; Gems and Riddle 1996), the only model systems where this phenomena has been experimentally sought, seminal fluid proteins are toxic to females, such that the more they receive the more harm that is done. Assuming that seminal fluid benefits the male via influencing the female's endocrine system and by displacing another male's sperm, males will be selected to inseminate their mates at a rate that exceeds the female optimum. This difference in optimal within-pair mating rate selects for seductive males and hard-to-please females, and can lead to a signal-receiver chase-away process.

Harem Polygyny

Consider a female who is deciding which male to select. Ideally the female should select the male based on his net worth, that is, based on a combination of his resources (discounting for already established females) and genes. If a mutation influencing a display character made a male more attractive than his actual net worth, then such a mutation would spread, as would counter mutations, causing females to resist the male display, and a signal-receiver chase-away process can ensue. The additional conflict over mating rate between a male and the females within his harem, analogous to that described above in the context of monogamy, will also apply to harem polygyny.

Lek Polygyny

In this case the opportunity for male-female conflict is lower since females control mating rate by how often they choose to enter the leking arena. Nonetheless, females potentially can be enticed by male displays to mate in suboptimal ways, such as mating on the periphery of the lek where the risk from predation or harassment by other males may be higher.

Although male-female antagonistic coevolution may play a lesser role in leking species, much of the ornamentation found on these males may be due to male-male signal-receiver antagonistic coevolution (Rice and Holland 1997). In many leking species such as sage grouse, black grouse, and ruff, there is intense competition among males for centrally located lek positions, where most mating takes place (reviewed in Welty 1975). Males will continually be screened by natural selection for genes, producing displays that, due to preexisting bias, intimidate their rivals. The spread of such a male-male display gene will counter-select the male receiver system to resist the display, and a signal-receiver chase-away process can ensue, paralleling that described above for male-female interactions.

Males Left Holding-the-Baggage

Antagonistic seduction predicts that males will evolve to be a mosaic of newer (more effective) and older (less effective) display traits. All models of sexual selection agree in predicting that continued exaggeration of a male display trait eventually will be arrested by opposing natural selection (Darwin 1871; Andersson 1994; Kirkpatrick and Ryan 1991).

At this point, antagonistic seduction further predicts that female resistance may frequently continue to evolve until the level of stimulation is optimal for females. Recent studies indicate that it may be common for females to show no preference for at least some putative male ornaments in highly ornamental bird species (Ligon and Zwartjes 1995a; Moller and Pomiankowski 1993). Thus, males may become a virtual graveyard of ineffectual display traits that have little utility except that their absence causes understimulation of females.

DISCUSSION

The foundation for the chase-away model of sexual selection is antagonistic coevolution among the loci coding for male display versus female receiver systems. This is only one example of the broader process of Interlocus Contest Evolution (ICE) in which intergenomic conflict leads to the evolution of counter-adapted gene complexes (Rice and Holland 1997). Just as species within a community can coevolve either mutualistically or antagonistically, so too can non-allelic, interacting genes within the genome of a single species. The functional interaction between genes coding for signal and receiver systems make these genes particularly susceptible to antagonistic coevolution, and hence chase-away coevolution.

Empirical tests of the chase-away model are facilitated by the fact that it makes two predictions that are unique compared to other established models of sexual selection. First, it predicts the evolution of diminished female attraction to the male display trait. In contrast, the run-away, good-genes, and direct-benefits models predict increased attraction, while the sensory-exploitation model predicts a static level of attraction. Since this is a prediction of change over time, an appropriate test requires historical information. At an arbitrary point in time, all three of these models predict that females may be strongly attracted to the male display trait. Phylogenetic reconstruction (e.g., wolf spider example) is therefore critical in evaluating this prediction.

A second prediction of the chase-away model is that female attraction to the male display trait reduces her net fitness, whereas the good-genes and direct-benefits models predict that such attraction is adaptive. This prediction must be tested under conditions where the ecological, hormonal, and physiological costs of mating are manifest. It also must be tested in the currency of net fitness since many fitness components may not include some of these costs. Many studies (reviewed in Andersson 1994) have demonstrated that female choice increases some fitness components of the female, at least in some circumstances, and this would appear to militate against the chase-away model. But other studies, briefly reviewed here, demonstrate that mating can be costly to females, so that male display traits may also cause females to mate too often, at suboptimal places or times, etc. These costs of mating in combination with the conflict between the sexes in mating decisions makes it inescapable, at least to us, that at least some male display traits will evolve that increase male fitness at the expense of their mates.

Unfortunately, empirical estimates of the genetic cor-

relation between female attraction and male-display traits will not prove useful in testing for the operation of the chase-away model. This model, like many others, can predict a positive correlation (see Appendix). In fact we can think of no observation of natural populations, at a single point in time, that will prove that the chase-away model is operating: only historical information on the trajectory of female attraction versus male display trait will be definitive.

One context where the model might feasibly be tested is two allopatric populations (A and B) in which a specific male display trait has evolved in A but not B. The chase-away model would be strongly supported if introduction of genetic variation for the display trait into population B led to its accumulation due to increased male mating success, reduced female fitness owing to its expression in males, and the evolution of reduced female attraction to the trait.

We see no reason to conclude that the chase-away model, or any other model of sexual selection, is operating at the exclusion of others; although the models may differ in their relative importance. All models of sexual selection can be viewed as coevolution between signal and receiver phenotypes. Each of these phenotypes is multifarious and likely to be controlled by many genes. Different subsets of signal and receiver genes may be evolving via different sexual-selection processes. Here we suggest that antagonistic seduction is an important part of such a mosaic sexual selection process.

In summary, it is our evaluation that the available data are still too incomplete to conclude that antagonistic seduction is more or less important than other established models. Nonetheless, there is substantial evidence for the operation of the chase-away model and hence it appears to be an important alternative hypothesis that needs to be considered when evaluating data from studies of sexual selection.

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APPENDIX

Consider a simple, two locus genetic model of coevolution between a male display trait and female attraction to the display. The D locus codes for the display trait with $D_1D_1 > D_1D_0 > D_0D_0$, that is, the display trait is most extreme in the D_1 homozygote, intermediate in the heterozygote and least exaggerated in the D_0 homozygote. The T locus, unlinked to the D locus, codes for the female's stimulatory threshold to induce mating, with $T_1T_1 > T_1T_0 > T_0T_0$, i.e. the threshold is most stringent in the T_1 homozygote, intermediate in the heterozygote, and least in the T_0 homozygote.

In this simple model increasing numbers of D_1 alleles produce more extreme male displays and increasing numbers of T_1 alleles make females more discriminating. Next suppose that the stimulatory threshold of the female T_1 homozygotes is achieved only by males that are homozygous for D_1, that the female T_1T_0 heterozygotes requires expression of at least one T_1 allele in her mate, and that female T_0 homozygotes mate randomly, i.e.

Female Genotype	Acceptable Male Genotype
T_1T_1	D_1D_1
T_1T_0	D_1D_1, D_1D_0
T_0T_0	D_1D_1, D_1D_0, D_1D_0

The nonrandom mating produced by the T locus generates positive linkage disequilibrium between the T and D alleles (i.e. an excess of coupling T_1D_1 and T_0D_0 gametes and a deficit of T_1D_0 and T_0D_1