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# Sexual Selection, Receiver Biases, and the Evolution of Sex Differences

Michael J. Ryan

## REVIEW

Recent approaches to analyzing the evolution of female mating preferences emphasize how historical influences on female receiver systems can bias the evolution of male traits that females find attractive. These studies combine animal behavior, sensory biology, phylogenetics, and artificial neural network models. They attempt to understand why specific phenotypes involved in sexual selection have evolved, rather than merely determining whether such traits and preferences are adaptive. It is now clear that traits and preferences often do not coevolve via genetic correlations, that female mating preferences for a given male trait are influenced by adaptations and constraints outside of the context of female responses to that particular trait, and that receiver biases can explain much of the diversity in male signaling phenotypes. It also appears that an understanding of historical effects will prove valuable in investigating why neural and cognitive systems respond to sensory stimuli as they do.

Many mating systems are characterized by males with striking morphologies and behaviors used to court females, and a preference by females to mate with such males. How is it that such male traits and female preferences come to coexist in a species? Sexual selection by female choice can explain why males evolve such elaborate traits. These males have increased mating success because of their enhanced attractiveness, which more than compensates for decreased survivorship associated with trait elaboration (1). But why do preferences for these traits evolve?

Female preferences are favored by natural selection if the preference influences the female's immediate reproductive success. Male display traits may correlate with immediate and direct effects on female fecundity. More elaborate males, for example, might fertilize more eggs, provide superior resources to females, prove to be better fathers, or have less risk of transmitting parasites and venereal diseases.

Females also exhibit mate preferences if preferences do not influence their immediate reproductive success, and understanding the evolution of these preferences has been a challenge (1). In this review, I consider the suggestion that past influences of evolution on how females generally perceive their world can bias the types of male traits that they now find attractive (2). I also discuss how this concept complements other approaches to understanding the evolution of female mating preferences.

### Preference Evolution, Genetic Correlations, and Animal Communication

Much of the research in sexual selection in the last two decades has examined how a female's preference that does not influence her immediate reproductive success can still evolve if it is genetically correlated with another character under direct selection (1). Two hypotheses for female preference evolution—runaway sexual selection and good genes selection—state that preferences evolve indirectly because they are genetically correlated with male traits that are

under direct selection; that is, the preferences themselves are not under direct selection. Thus, female preferences and male traits coevolve through genetic correlation. A more recent hypothesis, sensory exploitation, suggests that instead of preferences and traits coevolving through a genetic correlation, biases in the female's response to stimuli (receiver biases) favor the evolution of certain male traits. Thus receiver biases result in "preexisting preferences," and males that evolve traits that exploit these preexisting preferences are favored by sexual selection (2).

In runaway sexual selection, the female preference is genetically correlated with the male display trait. Female preference generates direct selection on the male trait, and the preference evolves as a correlated response to evolution of the display trait. Trait-preference evolution is driven by the greater mating success of attractive or "sexy" males. These males are "sexy" but are not necessarily superior in other components of fitness, such as survivorship. In good genes selection, however, the elaborate male display trait indicates a genotype that is superior for survival. The female preference is now correlated with the male's superior heritable survivorship. The good genes evolve under direct natural selection (because they enhance survivorship), and the preferences evolve under indirect selection as a correlated response to good genes evolution (1).

The sensory exploitation hypothesis suggests that, contrary to coevolution through genetic correlation, a trait and a preference in sexual selection—or, more generally, a signal and a receiver in animal communication—can evolve out of concert, with the evolution of one component lagging behind that of the other (Fig. 1A). If a receiver has a bias toward responding to certain signal parameters, such as louder sounds or brighter colors because they are easier to detect, we would expect the evolution of louder or brighter signals without assuming the need for genetic correlations between trait and preference, as required by indirect selection. Such a receiver-bias process is probably also responsible for the evolution of interactions between flowers and their insect pollinators, in which correlations between genes determining the plant's signal and the insect's response to that signal are not possible.

### Receiver Biases and Historical Patterns

The receiver in a communication dyad decodes information using some combination of peripheral end organs, central nervous system circuitry, and cognitive processes. Receiver biases are responses to stimuli that were not involved in shaping the evolution of the receiver's responses in a given context; they are incidental consequences rather than evolved functions (3). Such receiver biases can evolve in contexts unrelated to a specific task, as a result either of selection in other contexts or of general operating principles of neural and cognitive systems. Some male insects, for example, pollinate orchids that have flower parts resembling female insects. The male's attraction to the flower is not favored by selection, but is a receiver bias that results from the selective advantage of responding to real conspecific females. Similarly, a species that evolved retinal sensitivity to certain colors to enhance foraging efficiency might be more likely to locate males sporting those same colors when searching for mates. Sensory exploitation is a theory that males evolve traits to exploit preexisting receiver biases, rather than preferences and traits coevolving via a genetic correlation.

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Sensory exploitation can be contrasted to the coevolution hypotheses if historical patterns of signal-receiver evolution can be reconstructed. Several examples support the sensory exploitation hypothesis. Platyfish and swordtails are both in the genus *Xiphophorus*, but only swordtails have swords (Fig. 1B). Females of two platyfish and a species in the closely related and swordless genus *Priapella* prefer their own males to which swords have been appended over normal unadorned males (4). Hence, the preference for swords appears to have predated the evolution of *Xiphophorus* and thus predated the evolution of swords. A similar example of sensory exploitation involves the addition of call suffixes to advertisement calls in frogs of the *Physalaemus pustulosus* species group (5). Male *P. pustulosus* and a closely related species exhibit the derived trait of facultatively adding a suffix to the species-specific component of the advertisement call; none of the other ~40 species in the genus do this. *Physalaemus coloradensis* females, however, prefer the call of their own males with the *P. pustulosus* suffix added rather than the normal, simpler conspecific call (Fig. 1C). Additional studies of auklets (Fig. 1D), wolf spiders (Fig. 1E), manakins, and water mites support the hypothesis of sensory exploitation (6).

Females of other species show preferences for traits occurring in closely related species that are absent in their own, but either the phylogenetic information necessary to determine the pattern of trait-

preference evolution is lacking, or the phylogenetic information suggests that the preferred male trait has been lost (7). These studies do not support the simple pattern of male traits exploiting preexisting preferences. They do, however, suggest that trait evolution and preference evolution are often decoupled in sexual selection, that they need not evolve through genetic correlation, nor are the response properties of the receiver tightly matched to the properties of the signal, as a lock and key would be matched. Analogies between animal communication systems and human-engineered systems often stress the necessity of tightly matched signals and receivers. Studies of receiver biases suggest that such analogies might not be broadly applicable. The receiver's past history might bias neural processing strategies toward those that are merely sufficient to enhance the receiver's evolutionary fitness but are not optimal engineering solutions. Furthermore, tightly matched signal-receiver systems might have a selective disadvantage if they constrain the receiver's ability to accommodate meaningful population variation.

### The Origin of Receiver Biases

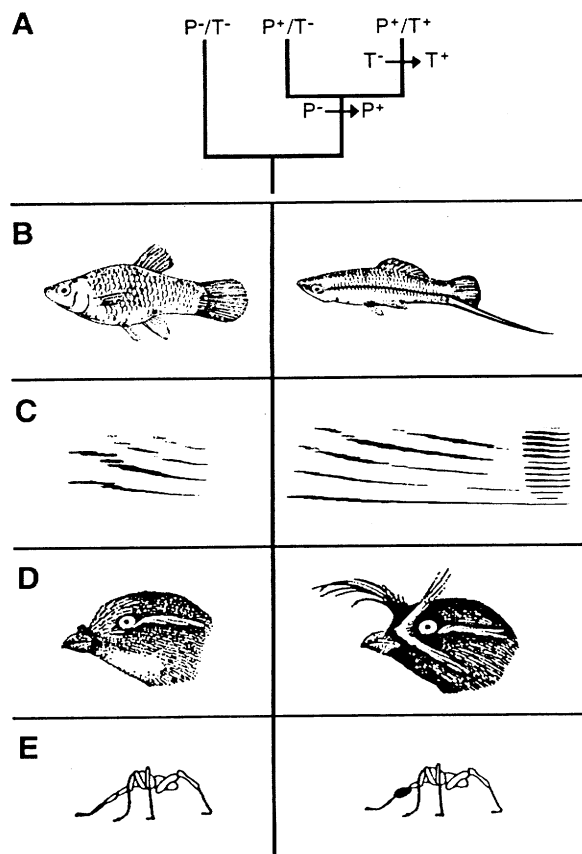
The sensory exploitation hypothesis does not specify the origin of preexisting receiver biases. Receiver biases can result from several causes: They may reflect incidental effects from other mate choice preferences, responses that have evolved to locate prey or avoid predators, and limitations imposed by the more general operating principles of neural and cognitive systems. Artificial neural networks, for example, have shown that biases for exaggerated traits and symmetric traits, which are often found in real animals, incidentally emerge without any training or selection to respond to such stimuli; receiver biases might be a necessary outcome of sensory processing (8).

**Receiver biases and mate choice.** The preexisting bias for males with swords in fishes of the genera *Xiphophorus* and *Priapella* might result from a more general preference for body size, a preference that is widespread among these types of fishes. Rosenthal and Evans (9) used playbacks of video animations to show that females did not exhibit a preference between a swordless male and a sworded male if the total body length of the two were equal. They suggested that males might have evolved a sword to exploit a preexisting preference for large body size. It is not clear in this case what, if any, benefits females derive by mating with larger males. Transference of preferences to other parts of the phenotype has also been shown in zebra finches; females prefer males with red beaks as well as with artificial red leg bands. Burley (10) argued that the preference for red beaks is adaptive because it indicates male health, and this preference is then transferred to leg-band color.

Preexisting biases that result from other types of mate preferences need not be maintained by sexual selection. An all-female species of poeciliid fish, the Amazon molly (*Poecilia formosa*), uses sperm from males of other species to reproduce successfully, but the male's genes are not incorporated in the offspring's genome. Individuals exhibit the same preferences for body size as females of their two sexual, parental species despite the lack of any direct benefits from mate choice and the impossibility of genetic correlations of male traits and preferences needed for runaway or good genes selection (11).

Receiver biases can also result from selection to choose males of the correct species. Females should be under strong selection to avoid mating with males of other species. If traits of conspecific and heterospecific males are similar, an incidental consequence of species-specific mate preference is a bias against conspecific males that are more similar to heterospecific males. Character displacement of female preferences in zones of sympatry (12) could lead to such an effect.

**Receiver biases, finding prey, and avoiding predators.** There are only a limited number of sensory modalities an organism can use to assess its environment, and receiver biases might originate from



**Fig. 1.** (A) A hypothetical phylogenetic tree showing the distribution of absence (-) and presence (+) of female preferences (P) and male traits (T) consistent with the sensory exploitation hypothesis. The most parsimonious explanation is that the preference existed before the trait evolved. (B to E) Studies supporting the sensory exploitation hypothesis show that females prefer traits absent in their own males (left panels) but present in males of other species (right panels), and also offer phylogenetic evidence that supports the scenario shown in (A). These include preferences for sword in poeciliid fish (B) (4), call suffixes in *Physalaemus* frogs (C) [sonogram, frequency versus time (5)], feather ornaments in auklets (D) (6), and hair tufts in wolf spiders (E) (6).

noncommunication functions of these sensory modalities. Selection for finding prey and for avoiding predators are two examples of how selection in contexts outside of mate choice have pleiotropic effects on female mating preferences.

Water mites feed on copepods and locate them by sensing their prey's water-borne vibrations (8). Males of one species of water mite mimic copepod vibrations as part of their mating display. Females are more likely to be seduced by this stimulus when they are hungry than when they are satiated. Phylogenetic reconstruction shows that this form of male courtship evolved after mites used vibrations to locate prey. Thus, selection to find food can generate pleiotropic effects on mate choice.

There is selection not only to find food, but to avoid becoming food. Toward this end, many moths have evolved the ability to detect ultrasonic echolocation calls of bats, and fewer moth species also have evolved the ability to produce ultrasonics in this same frequency band to deter further bat predation. This sensory channel has become secondarily adapted for communication between the sexes in some moths. Male acoustic courtship increases mating success in both ctenuchid and wax moths, and in some ctenuchids the males and females conduct an ultrasonic dialog (13). Bat predation was the selection force responsible for opening the ultrasonic world to moths; its relaxation has allowed this sensory channel to be used for communication (13).

**Receiver biases and neural system function.** The most interesting cases of receiver biases are derivative of more general operating principles of neural and cognitive systems. Two interesting possibilities relate to how stimulus organization and presentation influence the receiver's attention, and how processes of stimulus generalization and categorization can lead to receiver biases.

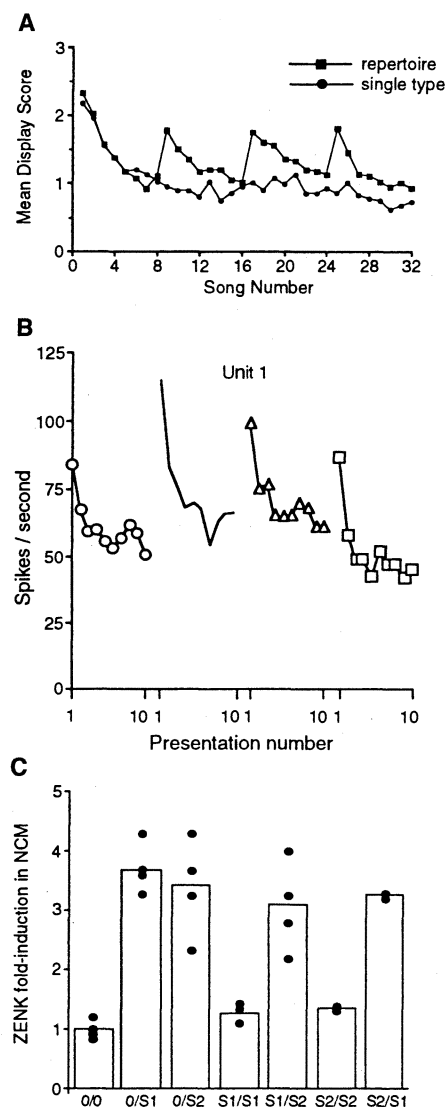
**Habituation and the precedence effect.** According to the anti-monotony hypothesis, habituation plays an important role in the evolution of complex vocalizations in songbirds: Increased song complexity reduces habituation of neighboring males and courting females (14, 15). Females often are attracted preferentially to more complex songs. Grackles do not have complex song repertoires. But female grackles are nonetheless more attracted to an artificially constructed song with different syllables repeated in groups rather than an alternative song that contained the same number of syllables but of only one type. Interestingly, the females' responses decrease during repetition of the same syllable, but responsiveness increases during the transition between syllable types in the more attractive song (Fig. 2A) (14). Thus, grackles have a preference for a complex repertoire despite its absence in the song of conspecific males. The physiological cause of this phenomenon might be the general phenomenon of habituation. Studies of zebra finches and canaries show that both electrophysiological response (Fig. 2B) and gene expression (Fig. 2C) habituate to repeated song stimuli (16–18). Both neurophysiology and molecular genetics may be useful tools to investigate the mating preference in favor of signal complexity (Fig. 2).

Socially dependent signal interactions can also perturb signal perception. Humans presented with identical signals in quick succession do not perceive the second signal. Other animals, as well, respond only to the leading signal. Such a perceptual bias, termed a precedence effect or forward masking, can influence how signaling males interact in nature when advertising to females (19, 20). Previous studies of acoustic and bioluminescent interactions had emphasized potential advantages to group-signaling organization, such as minimizing predation, preserving species-specific signal characters, or increasing the attractiveness of the group. Alternatively, Greenfield *et al.* (19) argued that a precedence effect results in males evolving a resettable oscillator that controls male calling as an evolutionarily stable strategy, and that striking patterns of collective signaling thus emerge as incidental consequences. Other context-dependent phenomena that mediate the attraction of the male's phenotype include how the color of a male and the

light in the surrounding environment influence when and where a male displays (21), and how females' perceptions of male attractiveness can be altered by preferences of other females (22).

**Generalization and receiver biases.** Recognition parameters of a receiver need not be mapped precisely onto properties of the target signal for sufficiently effective recognition to occur, and it might be assumed that overly precise mapping between signal and receiver is costly, both because it would involve detailed neural computation and because it risks failing to perceive signals slightly variant from the ideal.

As mentioned above, artificial neural networks have shown that receivers trained to recognize simple, arbitrary visual patterns show incidental biases for exaggerated and symmetric patterns (8). These computer models can also provide more direct insights into receiver biases in real communication systems. Phelps and Ryan used artificial neural networks to study historical effects on receiver biases in túngara frogs (23). Networks were trained to recognize túngara frog calls. They were then tested with a variety of heterospecific and ancestral calls that had been tested with female túngara frogs (24). The response biases of the artificial neural networks and the frogs were significantly correlated with one another. The historical effects were explored by training networks under a "mimetic history" training regime to recognize the ancestral call at the root of the phylogenetic tree (Fig. 3). Once trained



**Fig. 2.** (A) Female courtship displays in response to complex song in grackles show higher levels in response to multiple-song repertoires than to single song types. There is habituation to repeated songs within octets in the repertoire (1–8, 9–16, and so forth) and release from habituation at transition between octets (14). (B) Electrophysiological responses of units in the zebra finch's caudomedial neostriatum, which borders the song control nucleus, show decreased spike rates in response to repeated presentation of the same song (circles, solid line, triangles, squares) and enhanced spike rates in response to new song (16). (C) Expression of an immediate early gene, *zenk*, is higher during transitions from no song to song (0/S1) or from one song to another song (S1/S2, S2/S1) than during absence of song (0/0) or repeated stimulation of the same song (S1/S1, S2/S2) (17).

to the recognition criterion, the networks were trained to the next ancestral call on the evolutionary pathway to the túngara frog call; eventually, they were trained to a sequence of three ancestral calls before they were finally trained to recognize the túngara frog call. These networks traversed signal landscape mimicking that of the receivers of túngara frog ancestors. In the "mirror history," the three ancestral calls used in the mimetic history were rotated in multivariate space and synthesized (Fig. 3). These calls were as different from the túngara frog call as the ancestral calls, but they did not resemble calls made by these kinds of frogs. In "random histories," the three ancestral calls were chosen randomly from the assortment of heterospecific and ancestral calls (Fig. 3). Networks evolved to recognize the túngara frog call in all three historical regimes: mimetic, random, and mirror. Only networks trained with the mimetic history, however, predicted the response biases of tungara frogs. In the cyberspace of artificial neural networks, and possibly in the brains of túngara frogs, history has left a footprint that can be seen in receiver biases.

### Receiver Biases in Other Contexts

The importance of receiver biases has been appreciated in fields besides sexual selection. For example, the common cuckoo is a brood parasite that produces a begging call quite unlike that of its reed

warbler host. Cuckoo begging, however, mimics the sound of an entire brood of reed warbler chicks and apparently serves as a supernormal stimulus in promoting feeding behavior from the parasitized parents (25).

Perceptual biases abound in humans and might form the basis for what we view as sexually attractive. Does the attractiveness of symmetrical features in humans have a basis in the Gestalt law of a more general preference for symmetry (26)? Is there a perceptual bias that results in attractiveness for average faces in some contexts but caricatures in others (27)? This approach also could be applied to the extended phenotype of humans. Studies of musicology, for example, are beginning to concentrate on the physiological bases of pleasing sound. Helmholtz suggested that the organization of the inner ear makes harmonic rather than discordant music more pleasing to humans, a prediction recently borne out by studies of infants (28). A useful guideline might be to consider what commercial product advertisers have hit upon as attractive stimuli. These are probably caricatures or supernormal stimuli. The attraction of these stimuli might be currently maintained by selection, they might be totally based in learning and cultural influence, or they might be ghosts of selection past; but they surely have a mechanistic basis, and knowing that mechanism can only contribute to understanding its evolution.

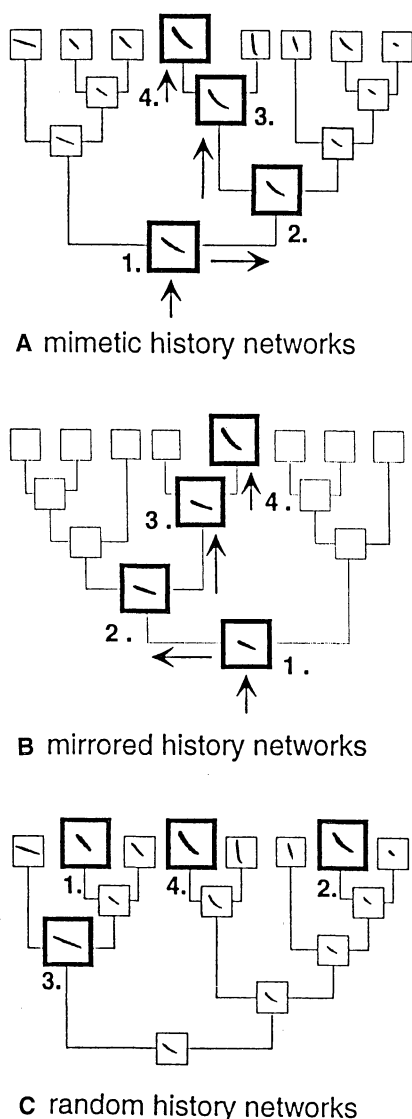
### Conclusions

Studies of receiver biases in sexual selection have shown that the evolution of traits and preferences can be decoupled and often do not coevolve because of genetic correlations. Thus, the continued emphasis on runaway sexual selection and good genes models of preference evolution to the exclusion of other factors is unwarranted. These studies also show that traits and preferences are not tightly matched; there is often a range of stimuli not encompassed by the signals of conspecific males that can elicit a receiver response. These unexploited biases should have some influence on the types of signal favored by selection, but documenting these biases requires a more creative experimental approach than is often applied in sexual selection studies. Receiver biases are not random but are determined in part by the history of receiver responses and the more general operating properties of neural and cognitive systems. Understanding these constraints, along with adaptive outcomes of mate choice, might contribute to our understanding of why certain kinds of traits are often favored by sexual selection. Finally, historical effects of receiver biases have implications for signal processing. Strategies used by receivers to decode signals might not be optimal in any engineering sense, but might exhibit response patterns indicative of how ancestral receivers decoded signals.

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**Fig. 3.** Phylogeny of the *Physalaemus pustulosus* species group and three closely related species used for outgroup analysis (24). The túngara frog, *P. pustulosus*, is number 4. The curves in each square are sonograms (frequency versus time) of synthetic advertisement calls for each species (tip of branches) and calls that are estimated at ancestral nodes (nodes of branches). The different histories used to train neural networks are shown (23). (A) Networks in the mimetic history were trained to calls on the direct evolutionary trajectory from the root to the túngara frog (1 to 4). (B) In mirrored histories, calls 1 to 3 in (A) were rotated in multivariate space to synthesize three novel calls 1 to 3 that retained the same magnitudes of acoustic similarity among themselves and to the túngara frog call. (C) Networks in random histories were trained to three calls chosen at random from the phylogeny and then trained to the túngara frog call. One of the 20 random histories is shown.



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## Sex and Conflict

Linda Partridge and Laurence D. Hurst

### REVIEW

Evolutionary conflict occurs when the deterministic spread of an allele lowers the fitness either of its bearer or of other individuals in the population, leading to selection for suppressors. Sex promotes conflict because associations between alleles are temporary. Differing selection on males and females, sexual selection, and differences in transmission patterns between classes of nuclear and cytoplasmic genes can all give rise to conflict. Inert Y chromosomes, uniparental inheritance of cytoplasmic genes, mating strains and sexes, and many features of sexual behavior may have evolved in part as a result of evolutionary conflict. Estimates of its quantitative importance, however, are still needed.

Why do around 5 percent of species of flowering plant have a significant proportion of individuals that are male sterile (1)? Why does the Y chromosome of the fruit fly *Drosophila melanogaster* contain multiple copies of a gene whose sole function appears to be suppression of the effects of another multicopy gene on the X chromosome (2)? And why does mating sometimes kill female fruit flies (3, 4)? These failures in individual adaptation can be understood through the theory of evolutionary conflict. Conflict occurs when the spread of an allele at one locus in a population lowers the fitness either of the individuals in which it resides or of other members of the same population. The spread of this "harmful" allele therefore results in natural selection for suppressors at other gene loci, which reduce the phenotypic effects of the original allele (5).

One of the first people to document this situation was Östergren (6) [see also (7, 8)] who argued that the small B chromosomes in many plants could be "parasitic." B chromosomes can be costly to their host (9), and they themselves will be subject to the fitness reduction that they cause. However, as Östergren noticed, some B chromosomes have mechanisms by which they are transmitted at a greater than Mendelian rate. This "overrepresentation" can be sufficient to ensure their spread in the population, even if they are bad for the plant, or as Östergren concluded, "They need not be useful for the plants. They need only be useful to themselves" (6, p. 163) (10).

Let us assume that an organism with a B chromosome has

fitness  $1 - s$ , whereas an organism with none has fitness 1. If an organism with the B chromosome transmits this to a proportion,  $k$ , of its progeny, the spread of the element is possible if  $2k(1 - s) > 1$ . If the element can gain over-representation ( $0.5 < k \leq 1$ ) then  $s > 0$  can hold, that is, the chromosome can both be deleterious and spread. Related calculations can apply to other genetic elements such as transposable elements (11) and meiotic drive genes (12–14). The spread of a parasitic chromosome that reduces the fitness of its host creates the conditions for the spread of suppressors (15). There is then a potential conflict between the B chromosome and the genes of the host genome (16). For didactic purposes, we shall here present verbal evolutionary arguments. However, purely verbal arguments can mislead, and those we present have, in the main, been subject to extensive theoretical analysis. Where the arguments are on a less secure footing, we shall point it out.

Conflict can also be instigated as a result of interactions between individual organisms. Consider, for example, an allele that when present in a male bird causes him to prevent the female from mating with other males, to the point where he interferes with her feeding success (17). The reduced feeding success of the female may reduce her fertility or survival. However, the allele in the male may increase its own rate of transmission, despite reducing the fertility of his mate, because it will increase the proportion of her offspring that are sired by this particular male (18–20). There may now be selection on other gene loci to suppress the fertility reduction caused by the mate-guarding behavior. This outcome would increase the fitness not only of alleles present in females, but also of alleles in males, provided that it did not also reduce the effectiveness with which males other than the mate were denied access to the female. This type of evolutionary conflict has received less theoretical attention than has intragenomic conflict.

Sexual reproduction greatly increases the likelihood of evolutionary conflict. In an asexual, clonal species all the genes present in an individual are in permanent association and share their evolutionary fate. The fitness effects of one allele on the individual therefore affects its own transmission in the same way as that of all the other genes in the organism. In contrast, in a sexual population, associations among genes at different loci are temporary and are broken up through sex and recombination. Intragenomic conflict is therefore more likely with sex (21). Situations in which conflicts may occur can be deduced from Price's notion of fitness covariance (22). When two genes are in permanent association, a positive increment in the fitness of one is a positive increment in the fitness of the other: their fitness covariance is positive. The conditions permissive for negative fitness covariance are those permissive for

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