

Sex-ratio control erodes sexual selection, revealing evolutionary feedback from adaptive plasticity

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Female choice is a powerful selective force, driving the elaboration of conspicuous male ornaments. This process of sexual selection has profound implications for many life-history decisions, including sex allocation. For example, females with attractive partners should produce more sons, because these sons will inherit their father's attractiveness and enjoy high mating success, thereby yielding greater fitness returns than daughters. However, previous research has overlooked the fact that there is a reciprocal feedback from life-history strategies to sexual selection. Here, using a simple mathematical model, we show that if mothers adaptively control offspring sex in relation to their partner's attractiveness, sexual selection is weakened and male ornamentation declines. This weakening occurs because the ability to determine offspring sex reduces the fitness difference between females with attractive and unattractive partners. We use individual-based, evolutionary simulations to show that this result holds under more biologically realistic conditions. Sexual selection and sex allocation thus interact in a dynamic fashion: The evolution of conspicuous male ornaments favors sex-ratio adjustment, but this conditional strategy then undermines the very same process that generated it, eroding sexual selection. We predict that, all else being equal, the most elaborate sexual displays should be seen in species with little or no control over offspring sex. The feedback process we have described points to a more general evolutionary principle, in which a conditional strategy weakens directional selection on another trait by reducing fitness differences.

evolutionary equilibrium | Fisher process | good genes | phenotypic plasticity | sex-ratio bias

Conspicuous male ornaments such as brightly colored or elongated feathers, loud vocalizations, and complex courtship dances are the hallmark of sexual selection, maintained despite their obvious costs because females find them attractive (1). This evolutionary force has profound implications for many life-history decisions, including which sex of offspring to produce and how to invest in them (2–4). Provided the heritable benefits of ornamentation are to some degree sex-limited, selection favors a conditional strategy of sex allocation: Females mated to attractive, highly ornamented males should overproduce sons, whereas those mated to unattractive males should overproduce daughters (3). This pattern of sex allocation has been supported by a number of theoretical (5–7) and empirical (8–10) studies, but no one has considered how it might feed back to alter sexual selection. Here, we investigate the dynamic interplay between sexual selection and sex-ratio adjustment. We first develop a simple mathematical model in which male ornamentation, female preference, and the sex-allocation strategy can coevolve and use this model to determine the direction of selection acting on all of these traits. We then extend our analysis to more biologically realistic conditions by using a series of individual-based, evolutionary simulations, incorporating continuous variation in ornamentation and preference, a finite population size, and stochastic factors such as genetic drift. This dual approach allows us to uncover the evolutionary forces linking sexual selection and sex allocation. After analyzing this coevolutionary feedback process in depth, we show how the same

principle extends to a wide range of other contexts in which selection favors phenotypic plasticity in response to a directionally selected trait.

Model

Basic Scenario. For the sake of tractability, we consider just two types of males, which differ in their ornamentation (5, 11, 12): those of type 0 lack ornamentation, whereas those of type 1 are ornamented to a degree given by the evolvable trait t ($t \geq 0$). Ornamentation is costly in that it reduces survival to adulthood, with the relative survival of type-1 (compared with type-0) males given by v_{m1} ($v_{m1} \leq 1$). This cost reflects the energy or resources invested in the development of secondary sexual traits or an associated predation risk of being conspicuous (1).

Females are of one type only and have an evolvable preference p ($p \geq 0$), which is costly and lowers their survival to v_f ($v_f \leq 1$). This cost may arise because the female has to invest in sensory apparatus for assessing males, or because she incurs a higher predation risk while choosing a mate (13). Her preference makes her more inclined to mate with an ornamented than a non-ornamented male, resulting in a proportion α of females that mate with the former type (note that α is not fixed but depends on p , t , and the relative frequencies of type-0 and type-1 males). Consequently, the expected number of mates is q_1 for an ornamented male and q_0 for a nonornamented male, with $q_1 \geq q_0$.

Crucially, females can adjust offspring sex ratios in relation to their partner's ornamentation: Sex allocation is determined by the evolvable traits s_0 and s_1 , where s_0 is the proportion of sons produced when mated to a nonornamented male and s_1 the proportion when mated to an ornamented male. Ornamentation is heritable from father to son, except when mutations occur: With probability μ_0 , the son of a nonornamented male is ornamented, and with probability μ_1 , the son of an ornamented male is nonornamented. In common with standard models of sexual selection (14, 15), we assume that mutations are biased toward the loss of ornamentation, i.e., that $\mu_1 > \mu_0$. This bias prevents fixation of the male ornament and thereby preserves the benefit of female choice (15). Individuals are assumed to die before their offspring become reproductively mature, so that generations are nonoverlapping. Fig. 1 summarizes the sequence of events in our model. Table 1 lists the variables and parameters with their associated symbols.

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ornamentation altogether, their viability v_{m0} and per-capita number of mates q_0 are the same as for resident type-0 males and so are left without a hat. The sex-allocation traits s_0 and s_1 receive hats in the first column, representing the reproductive output of mutant females, but not in the second and third columns because mutant males are assumed to mate with resident females only (due to the rarity of mutant females). Note that when the mutant's trait values are the same as those of the resident ($x = \hat{x}$), matrices **A** and **B** are identical.

The ability of mutant individuals to invade the resident population is given by their fitness w , which is the dominant eigenvalue of matrix **B**. Assuming mutations of small effect, the selection differential $\partial w / \partial \hat{x}$ expresses how w depends on \hat{x} , the mutant value for the trait of interest. According to a standard result (20) from evolutionary invasion analysis, this is

$$\frac{\partial w}{\partial \hat{x}} = \mathbf{z}^T \frac{\partial \mathbf{B}}{\partial \hat{x}} \mathbf{y} / \mathbf{z}^T \mathbf{y}, \quad [3]$$

where \mathbf{y} represents the relative frequencies of females, type-0 males, and type-1 males in the resident population (technically, a dominant right eigenvector of **A**), $\mathbf{z} = (z_f, z_{m0}, z_{m1})^T$ represents their reproductive values (technically, a dominant left eigenvector of **A**) and the derivatives are evaluated at the resident trait values.

Results

Analytical Results. Using the approach (5, 21) outlined in *SI Model*, we can use Eq. 3 to obtain the following selection differentials (16) for the traits p , t , s_0 , and s_1 , evaluated at the resident trait values (i.e., where $\hat{p} = p$, $\hat{t} = t$, $\hat{s}_0 = s_0$, and $\hat{s}_1 = s_1$):

$$\frac{\partial w}{\partial \hat{p}} = \alpha' \left[\frac{z_{m1}}{q_1} - \frac{z_{m0}}{q_0} \right] y_f + \frac{v'_f}{v_f} z_f y_f \quad [4]$$

$$\frac{\partial w}{\partial \hat{t}} = \frac{q'_1}{q_1} z_{m1} y_{m1} + \frac{v'_{m1}}{v_{m1}} z_{m1} y_{m1} \quad [5]$$

$$\frac{\partial w}{\partial \hat{s}_0} = \frac{1 - \alpha}{s_0} \left[\frac{z_{m0}}{q_0} - \frac{1}{2(1 - \bar{s})} \right] y_f \quad [6]$$

$$\frac{\partial w}{\partial \hat{s}_1} = \frac{\alpha}{s_1} \left[\frac{z_{m1}}{q_1} - \frac{1}{2(1 - \bar{s})} \right] y_f, \quad [7]$$

where $\bar{s} = (1 - \alpha)s_0 + \alpha s_1$ is the average offspring sex ratio. Primes (') denote differentiation with respect to the trait under consideration.

At the equilibrium for the sex-allocation traits s_0 and s_1 , the selection differentials given by Eqs. 6 and 7 must be zero (20), and so $z_{m0}/q_0 = 1/[2(1 - \bar{s})]$ and $z_{m1}/q_1 = 1/[2(1 - \bar{s})]$. Thus, we have $z_{m0}/q_0 = z_{m1}/q_1$, which implies that the first term on the right of Eq. 4 vanishes as well. Assuming that $v'_f = dv_f/dp$ is negative, i.e., that female choice is costly (13), it follows that the selection differential for p is negative. Hence, at the sex-allocation equilibrium, selection cannot sustain a costly female preference. Sex-ratio adjustment dependent on male ornamentation erodes the female preference to zero, and as a result, male ornamentation will evolve to zero as well.

Numerical Results. A numerical implementation of this analytical model, illustrated in Fig. 2, shows how conditional sex-ratio adjustment erodes sexual selection (see *SI Model* for full details of the calculation). Initially, we fix the sex-allocation traits at $s_0 = s_1 = 0.5$, such that offspring sex ratios are unbiased (Fig. 2, left of the vertical dashed lines). Under these conditions, male orna-

mentation and female preference evolve away from their survival optima (at zero elaboration and zero preference, respectively) to a stable, exaggerated level (Fig. 2A), following predictions from standard models of sexual selection (14, 15, 22, 23). Then, from the point indicated by the dashed lines, we allow the sex-allocation traits s_0 and s_1 to evolve. Conditional sex-ratio adjustment evolves as predicted by theory (5, 6): Females mated to highly ornamented males have more sons than those mated to less-ornamented males (Fig. 2B, to the right of the dashed line). [Note that s_1 is prevented from deviating too far from 0.5 because of counterselection to restore an even population sex ratio, because type-1 males vastly outnumber type-0 males (6).] As biased sex allocation develops, however, this strategy weakens sexual selection, leading to a gradual decline in male ornamentation and female preference (Fig. 2A, right of the dashed line).

Thus, sexual selection favors conditional sex allocation, but this plasticity then erodes sexual selection. Two main processes are responsible for this erosion. First, sex-ratio adjustment allows females with unattractive partners to mitigate the fitness disadvantage of low male ornamentation. In simple terms, ending up with an unattractive male is not so disastrous if a female can skew offspring production toward daughters. This plasticity reduces the fitness benefit of female choosiness, which is selected against because of its costs. Second, because choosier females tend to mate with more ornamented males and, therefore, produce mainly sons, their strong preference genes will rarely be expressed by their offspring. This masking lowers the average female preference in subsequent generations and, thereby, reduces

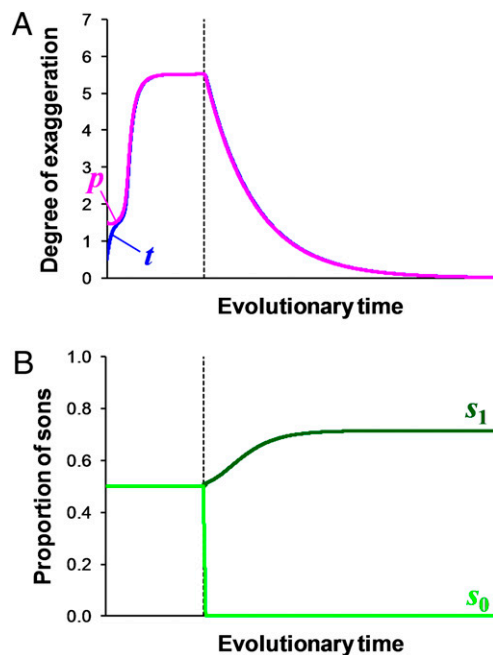


Fig. 2. Sex-ratio adjustment erodes sexual selection (numerical results). **A** shows the level of male ornamentation (t , blue) and female preference (p , pink; note that this partly obscures the blue line), whereas **B** shows the proportion of sons produced by females mated to nonornamented (s_0 , light green) and ornamented (s_1 , dark green) males. Offspring sex ratios are initially unbiased ($s_0 = s_1 = 0.5$), but they are allowed to evolve from the point indicated by the vertical dashed lines. Male ornamentation and female preference reach a stable level of exaggeration in the absence of sex-ratio bias, then decline to zero as conditional sex allocation develops (subject to counterselection on s_1 to restore an even population sex ratio; ref. 6) and s_0 and s_1 reach their optima. For the example shown, $c_p = 0.2$, $c_f = 0.001$, $c_m = 0.1$, $\mu_0 = 0.02$, and $\mu_1 = 0.3$; the starting values for ornamentation and preference were $t = 0.5$ and $P = 1.5$.

the fitness benefit of male ornamentation. In effect, the conditional strategy of sex allocation reduces the heritability of both low attractiveness and strong preferences, undermining selection to invest in costly ornamentation.

Individual-Based Simulations. Using individual-based computer simulations, we can extend this analysis to a more realistic situation where male ornamentation and female preference vary continuously and the evolutionary dynamics are subject to stochastic demographic factors. We simulated a finite population in which a costly male ornament and a costly female preference could change over time through selection and mutation (see *Materials and Methods* for full details). As in the earlier numerical results, evolutionary change in the male ornament and female preference follows predictions from standard analytical models of sexual selection (14, 15, 22, 23), with both traits quickly evolving to a stable, exaggerated level (Fig. 3A, left of the dashed line). Similar patterns are seen regardless of whether male ornamentation is an arbitrary Fisherian trait (Fig. 3) or is a condition-dependent indicator of “good genes” (see additional simulation results in *SI Results* and Fig. S1).

We then allowed a conditional strategy of sex-ratio adjustment to evolve by incorporating two additional traits, s_- and s_+ (6). These traits determine a female’s sex-allocation strategy, with s_- ($0 \leq s_- \leq 1$) being the chance of producing a son when mated to a male with below-average ornamentation and s_+ ($0 \leq s_+ \leq 1$) that when mated to a male with above-average ornamentation. Starting from a situation in which offspring sex ratios are unbiased ($s_- = s_+ = 0.5$), conditional sex-ratio adjustment gradually develops as predicted by theory (5, 6): Females mated to highly ornamented males overproduce sons, whereas those mated to less-ornamented males overproduce daughters (Fig. 3B). [Note that with continuous variation in male ornamentation, s_- and s_+ become biased to a similar extent (6).] This strategy then weakens sexual selection, leading to a gradual decline in male ornamentation and female preference (Fig. 3A, right of the dashed line).

When male ornamentation is a condition-dependent indicator of good genes (23), sexual selection is weakened to a lesser extent than when it is a purely Fisherian trait (*SI Results*). In the former case, the heritable benefits for a female who mates with an attractive male are not entirely sex-limited; although only her sons can profit from their father’s ornamentation genes, both her daughters and her sons will inherit his genes for viability. Thus, even when females exert a great degree of control over the sex of their offspring, it still pays to mate with more ornamented males. This difference notwithstanding, for both Fisherian and good genes models of sexual selection, ornamentation and preference are substantially reduced as conditional sex allocation develops.

To check that sex-ratio adjustment is directly responsible for this decline, we ran another set of simulations in which strategies with varying degrees of sex-ratio bias were introduced partway through (Fig. 4). Initially, with the sex ratio fixed at 0.5, the male ornament and female preference quickly evolve to a stable, exaggerated level as before. We then introduced a biased sex-allocation strategy for all females, causing them to produce more sons when mated to an attractive partner and more daughters when mated to an unattractive partner. The effect on sexual selection is dramatic. For a moderate degree of bias, $s_+ = 0.7$ and $s_- = 0.3$, very rapidly the ornament and preference drop to approximately one-half of their original level of expression. Adjustment strategies involving weaker biases result in a smaller drop, whereas with stronger biases the decline in ornamentation is even sharper (Fig. 4).

Our simulation results confirm that the equilibrium levels of female preference and male ornamentation are substantially lower when sex-ratio adjustment is possible. In effect, sexual

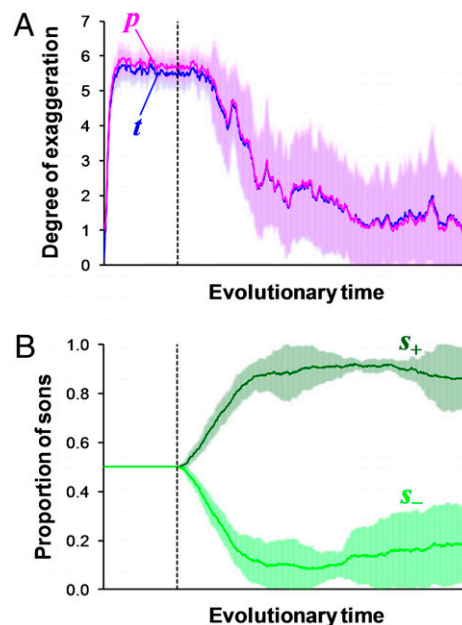


Fig. 3. Coevolutionary dynamics of sexual selection and sex allocation (individual-based simulations). *A* shows the level of male ornamentation (t , blue) and female preference (p , pink) under Fisherian sexual selection, whereas *B* shows the female sex-allocation strategy in the same set of simulations based on traits s_+ and s_- , where s_+ (dark green) is the probability of producing a son when her partner has above-average ornamentation and s_- (light green) is the probability of producing a son when he has below-average ornamentation. Offspring sex ratios are initially unbiased ($s_- = s_+ = 0.5$), but they are allowed to evolve from the point indicated by the vertical dashed lines. All values are shown as the mean (solid line) \pm SD (stippling) from 20 replicate simulation runs. For parameter values, see *Materials and Methods*.

selection undermines itself by favoring a conditional strategy of sex-ratio adjustment based on male attractiveness.

Discussion

Previous theory (5, 6) has confirmed the empirical suggestion (3) that variation in male sexual displays favors conditional sex allocation by females. Here, we have shown an unexpected consequence of this process: that by reducing the fitness difference between females with attractive and unattractive partners, this sex-allocation strategy undermines the same selective force that created it, causing male ornamentation to decline. Moreover, because choosier females tend to mate with more highly ornamented males and, therefore, produce sons, their stronger preference genes are likely to be masked in the next generation, weakening sexual selection still further. Our evolutionary simulations predict a lower level of sexual display than in cases where facultative sex-ratio adjustment is not possible. This finding implies that, all else being equal, the most exaggerated secondary sexual traits should be seen in species with little or no control over offspring sex. For instance, we might expect that species with genotypic sex determination will have more exaggerated sexual ornamentation than closely related species with temperature-dependent sex determination, assuming that the latter mechanism affords parents greater control over the sex of their offspring.

It is known that the evolution of phenotypic plasticity in a quantitative trait can alter the evolution of the average phenotype for that trait (24–27). Here, we have shown a related effect: that plasticity in one trait (sex-ratio bias) can alter the evolution of another trait (ornamentation) on which it is conditional. We propose that this phenomenon is not restricted to sex allocation, but is an example of a more general principle. Whenever heritable variation in fitness is maintained for a given trait, selection

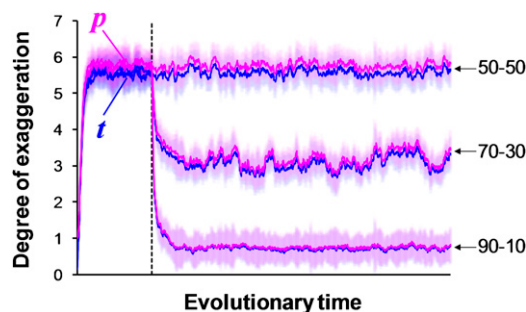


Fig. 4. Stronger degrees of sex-ratio bias have stronger eroding effects on sexual selection. The plots show the level of male ornamentation (t , blue) and female preference (p , pink). Offspring sex ratios are initially unbiased ($s_+ = s_- = 0.5$), but from the point indicated by the vertical dashed line, females use a fixed sex-allocation strategy conditional on the male's ornamentation. Three different degrees of sex-ratio bias are shown: $s_+ = s_- = 0.5$ (50–50, i.e., no bias); $s_+ = 0.7, s_- = 0.3$ (70–30); and $s_+ = 0.9, s_- = 0.1$ (90–10). All values are shown as the mean (solid line) \pm SD (stippling) from 20 replicate simulation runs. For parameter values, see *Materials and Methods*.

should favor any conditional strategy that improves the fitness prospects of the least successful phenotypes, but in doing so, it erodes selection on the trait.

To illustrate the general nature of our argument, we give examples from a range of contexts that do not involve sex allocation. The first concerns kleptoparasitism (28), in which one animal steals food that a conspecific has caught before the latter can eat it. Selection for good hunting skills is expected to be strong in any predatory species, but there may still be substantial variation in hunting success because of mutations in polygenic traits affecting the development of motor skills. If poor hunters adopt kleptoparasitic behavior, however, this conditional strategy will reduce fitness differences based on hunting success and, thereby, weaken selection on hunting ability. Combined with the costs incurred by parasitized hunters, the weakened selection may lead to a decline in hunting skills that, in turn, will reduce the benefits of stealing. Thus, selection on hunting ability and kleptoparasitism interact in a highly dynamic fashion.

The second example involves polygynous mating systems in which access to females is determined by male dominance relations. In such systems, there will be strong selection for male characteristics related to dominance, such as large body size. Slight differences between males in these characteristics early in life may largely determine their relative positions in the dominance hierarchy, leading to substantial differences in lifetime reproductive success. If small males adopt a “sneaker” tactic (29), however, allowing them to achieve significant reproductive success by subversive means, this conditional strategy will reduce fitness differences between males of high and low dominance rank and, thereby, weaken selection on body size. This weakening of selection, in turn, will alter the selection–mutation balance, allowing greater levels of genetic variation for body size to persist in the population.

Our final example deals with costly dispersal. In many plant and animal species, dispersal away from the natal habitat may be favored despite the energetic cost or mortality risk associated with this movement. The benefits of dispersal will typically be frequency-dependent, with the greatest pressure to disperse occurring when most individuals stay at home. However, if individuals that forgo dispersal can adapt better to overcrowding, for

example, through niche construction, then the strength of selection on dispersal will be weakened. Selection favors a strategy that mitigates the fitness disadvantage of staying in the natal habitat, and this plasticity erodes directional selection on the ability to disperse away from that habitat.

These diverse examples show that our model applies to a broad range of contexts. The evolutionary feedback process we have described is likely to be a widespread and important force maintaining phenotypic variation in the face of directional selection.

Materials and Methods

Details of the Individual-Based Simulations. The individual-based simulations were similar to those described in an earlier paper (6). In the main text, we focus on Fisherian sexual selection, whereas the simulations for good genes sexual selection are presented in *SI Results*. We modeled a population of 5,000 individuals, each with diploid, autosomal genetic values for the following traits: p , coding for preference (expressed only by females); t , coding for ornamentation (expressed only by males); and two sex-allocation traits, s_- and s_+ (expressed only by females). The value for p can take any real number, whereas t is limited to positive values and s_- and s_+ are limited between 0 and 1. We chose to restrict t to positive values because this range might better represent certain forms of male display (30), for example, the height of a plumage crest, but we obtain similar results when male ornamentation can also take negative values (see additional simulation results in *SI Results* and Fig. S2). Female preference and male ornamentation are both assumed to be costly; survival to maturity is maximized for $p = 0$ and $t = 0$ and declines away from these optima as specified by the functions $\exp(-c_f p^2)$ and $\exp(-c_m t^2)$, where c_f and c_m are positive constants.

For reproduction, females are drawn from the population with a chance proportional to their survival probability. Each surviving female then samples 10 males, again weighted by survival probability, and chooses one of them on the basis of his ornamentation. The chance that she picks a given male is proportional to $\exp(c_p p t)$, where c_p is a positive constant scaling the importance of ornamentation to female choice. Thus, females with a positive preference ($p > 0$) prefer more ornamented males, those females with a negative preference ($p < 0$) prefer less ornamented males and those females with $p = 0$ mate randomly. To facilitate sexual selection, we started the simulations with a positive preference (22, 30); the same process occurs when starting from a situation of random choice, but it takes longer.

Each mating produces a single offspring, whose genetic values are determined by standard Mendelian inheritance. We assume that there is no genetic dominance and that the loci are unlinked. Offspring sex is determined by the father's ornamentation and the mother's sex-allocation strategy: the probability of producing a son is s_+ when the father's ornamentation level is above average and s_- when it is below average. For each trait, we assume that mutations occur in a small fraction of offspring (with probability μ_p for p , μ_t for t , and μ_s for s_- and s_+), causing the genetic value to change upward or downward by an amount drawn from a uniform probability distribution (up to a certain maximum amount). Upward and downward mutations are equally likely except in the ornamentation trait t , for which we assume that a downward mutation bias reduces ornamentation by an average amount g (6, 15). Reproduction continues until a total of 5,000 offspring have been produced, at which point all of the adults die and are replaced by the offspring generation. The same cycle of events was repeated for 100,000 generations, which is the timespan depicted in our figures. Computer code for the simulations is available from the authors upon request.

For the results shown in the main text, the parameter values were $c_p = 1.0$, $c_f = 0.001$, $c_m = 0.5$, $\mu_p = \mu_t = \mu_s = 0.05$ and $g = 0.02$, with the average genetic values in the initial population set at $\bar{p} = 1$, $\bar{t} = 0$, and $\bar{s}_+ = \bar{s}_- = 0.5$. However, the eroding effect of sex-ratio adjustment is seen for a wide range of parameter values, whenever sexual selection leads to exaggerated male ornamentation.

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Supporting Information

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SI Model

Full Derivation of the Resident Transition Matrix \mathbf{A} . Here, we explain how we derived the entries of the transition matrix \mathbf{A} (Eq. 1), which governs the dynamics of a resident population with ornamentation level t , preference p , and sex-allocation traits s_0 and s_1 . We reproduce the matrix here for clarity:

$$\mathbf{A} = \frac{1}{2} k \begin{bmatrix} [(1-\alpha)(1-s_0) + \alpha(1-s_1)]v_f & q_0(1-s_0)v_f & q_1(1-s_1)v_f \\ [(1-\alpha)s_0(1-\mu_0) + \alpha s_1 \mu_1]v_{m0} & q_0 s_0(1-\mu_0)v_{m0} & q_1 s_1 \mu_1 v_{m0} \\ [(1-\alpha)s_0 \mu_0 + \alpha s_1(1-\mu_1)]v_{m1} & q_0 s_0 \mu_0 v_{m1} & q_1 s_1(1-\mu_1)v_{m1} \end{bmatrix}. \quad [\text{S1}]$$

To recap: The first column of \mathbf{A} (\mathbf{a}_1) represents the per-capita reproductive output of females, the second column (\mathbf{a}_2) that of type-0 males, and the third (\mathbf{a}_3) that of type-1 males. The three rows represent, from top to bottom, the result of this reproductive output in terms of surviving females, type-0 males, and type-1 males in the next generation. We will use the notation a_{nm} to represent the element occupying the n th row and m th column of matrix \mathbf{A} .

The top-left entry (a_{11}) represents the per-capita reproductive contribution of mothers in the current generation to mothers in the next generation. A proportion $1 - \alpha$ of their matings are with nonornamented males, with whom a proportion $1 - s_0$ of the offspring they produce are daughters. The remaining α matings are with ornamented males, with whom a proportion $1 - s_1$ of the offspring they produce are daughters. In both cases, these daughters survive to reproduce with probability v_f .

The middle-left entry (a_{21}) represents the per-capita reproductive contribution of mothers in the current generation to nonornamented fathers in the next generation. A proportion $1 - \alpha$ of these mothers' matings are with nonornamented males, with whom a proportion s_0 of the offspring they produce are sons; with probability $1 - \mu_0$, these sons are unaffected by mutation and, therefore, inherit their father's lack of ornamentation. The remaining α matings are with ornamented males, with whom a proportion s_1 of the offspring they produce are sons; with probability μ_1 , these sons lose their father's ornamentation through mutation. In both cases, these nonornamented sons survive to reproduce with probability v_{m0} .

The bottom-left entry (a_{31}) represents the per-capita reproductive contribution of mothers in the current generation to ornamented fathers in the next generation. A proportion $1 - \alpha$ of these mothers' matings are with nonornamented males, with whom a proportion s_0 of the offspring they produce are sons; with probability μ_0 , these sons mutate into the ornamented state. The remaining α matings are with ornamented males, with whom a proportion s_1 of the offspring they produce are sons; with probability $1 - \mu_1$, these sons are unaffected by mutation and, therefore, inherit their father's ornamentation. In both cases, these ornamented sons survive to reproduce with probability v_{m1} .

The top-center entry (a_{12}) represents the per-capita reproductive contribution of nonornamented fathers in the current generation to mothers in the next generation. The expected number of mates for these fathers is q_0 . A proportion $1 - s_0$ of their offspring are daughters, who survive to reproduce with probability v_f .

The middle-center entry (a_{22}) represents the per-capita reproductive contribution of nonornamented fathers in the current generation to nonornamented fathers in the next generation. The expected number of mates for these fathers is q_0 . A proportion s_0 of their offspring are sons, who inherit their father's

lack of ornamentation with probability $1 - \mu_0$ and then survive to reproduce with probability v_{m0} .

The bottom-center entry (a_{32}) represents the per-capita reproductive contribution of nonornamented fathers in the current generation to ornamented fathers in the next generation. The expected number of mates for nonornamented fathers is q_0 . A proportion s_0 of their offspring are sons, who mutate into the ornamented state with probability μ_0 and then survive to reproduce with probability v_{m1} .

The top-right entry (a_{13}) represents the per-capita reproductive contribution of ornamented fathers in the current generation to mothers in the next generation. The expected number of mates for these fathers is q_1 . A proportion $1 - s_1$ of their offspring are daughters, who survive to reproduce with probability v_f .

The middle-right entry (a_{23}) represents the per-capita reproductive contribution of ornamented fathers in the current generation to nonornamented fathers in the next generation. The expected number of mates for ornamented fathers is q_1 . A proportion s_1 of their offspring are sons, who mutate into the nonornamented state with probability μ_1 and then survive to reproduce with probability v_{m0} .

Finally, the bottom-right entry (a_{33}) represents the per-capita reproductive contribution of ornamented fathers in the current generation to ornamented fathers in the next generation. The expected number of mates for these fathers is q_1 . A proportion s_1 of their offspring are sons, who inherit their father's ornamentation with probability $1 - \mu_1$ and then survive to reproduce with probability v_{m1} .

Finding the Relative Frequencies. For consistency, it is required that all females (relative frequency y_f) have the same reproductive output as all males ($y_{m0} + y_{m1}$), in other words that

$$\mathbf{a}_1 y_f = \mathbf{a}_2 y_{m0} + \mathbf{a}_3 y_{m1}. \quad [\text{S2}]$$

This equation is helpful in finding the dominant eigenvalue λ of \mathbf{A} , which is the long-term growth rate of the resident population. Let $\mathbf{y} = (y_f, y_{m0}, y_{m1})^T$ be the dominant right eigenvector of \mathbf{A} , containing the stable relative class frequencies; this eigenvector is given by $\mathbf{A}\mathbf{y} = \lambda\mathbf{y}$, or, in terms of the columns of \mathbf{A} , $\mathbf{a}_1 y_f + \mathbf{a}_2 y_{m0} + \mathbf{a}_3 y_{m1} = \lambda\mathbf{y}$. Substituting S2 into this equation, we get $\lambda\mathbf{y} = 2\mathbf{a}_1 y_f \Rightarrow \lambda = 2a_{11} = k(1 - \bar{s})v_f$, where $\bar{s} = (1 - \alpha)s_0 + \alpha s_1$ is the average offspring sex ratio. The long-term growth rate is therefore equal to the per-capita number of surviving daughters. Note that k gets rescaled by density dependence so that in a stable population $\lambda = 1$, i.e., $k = 1/(1 - \bar{s})v_f$ (see refs. 1 and 2). For the rest of our analysis, we do not need an explicit solution for the stable class distribution, but it will prove useful to have explicit equations for y_f and y_{m1} :

$$2\lambda y_f = (1 - \bar{s})v_f y_f + q_0(1 - s_0)v_f y_{m0} + q_1(1 - s_1)v_f y_{m1}, \quad [\text{S3a}]$$

$$2\lambda y_{m1} = [(1 - \alpha)s_0 \mu_0 + \alpha s_1(1 - \mu_1)]v_{m1} y_f + q_0 s_0 \mu_0 v_{m1} y_{m0} + q_1 s_1(1 - \mu_1)v_{m1} y_{m1}. \quad [\text{S3b}]$$

Calculating the Selection Differentials for a Rare Mutant. The transition matrix \mathbf{B} , as given in Eq. 2, is as follows:

$$\mathbf{B} = \frac{1}{2}k \begin{bmatrix} [(1-\hat{\alpha})(1-\hat{s}_0) + \hat{\alpha}(1-\hat{s}_1)]\hat{v}_f & q_0(1-s_0)\hat{v}_f & \hat{q}_1(1-s_1)\hat{v}_f \\ [(1-\hat{\alpha})\hat{s}_0(1-\mu_0) + \hat{\alpha}\hat{s}_1\mu_1]v_{m0} & q_0s_0(1-\mu_0)v_{m0} & \hat{q}_1s_1\mu_1v_{m0} \\ [(1-\hat{\alpha})\hat{s}_0\mu_0 + \hat{\alpha}\hat{s}_1(1-\mu_1)]\hat{v}_{m1} & q_0s_0\mu_0\hat{v}_{m1} & \hat{q}_1s_1(1-\mu_1)\hat{v}_{m1} \end{bmatrix}, \quad [\text{S4}]$$

where mutant phenotypes have hats ($\hat{}$) to distinguish them from resident phenotypes. This matrix describes the dynamics of rare mutant individuals in the resident population.

To quantify the invasion prospects of mutants, we investigate the sensitivity of \mathbf{B} 's dominant eigenvalue w with respect to small changes in the mutant trait values. If \mathbf{z} and \mathbf{y} are left and right eigenvectors of \mathbf{A} , then according to a standard result (3),

$$\frac{\partial w}{\partial \hat{x}} = \mathbf{z}^T \frac{\partial \mathbf{B}}{\partial \hat{x}} \mathbf{y} / \mathbf{z}^T \mathbf{y}, \quad [\text{S5}]$$

where \hat{x} is the mutant value for the trait of interest and the derivatives are evaluated at the resident trait values. Because we are mainly interested in the direction of selection, we will ignore the denominator of the right-hand side (which is always positive). The vectors \mathbf{y} and \mathbf{z} correspond to the stable class distribution and class reproductive values for the resident population (3). As with \mathbf{y} , it is not necessary to calculate the reproductive values \mathbf{z} explicitly, but we do need the following equations for the reproductive values of type-0 and type-1 males:

$$2\lambda z_{m0} = q_0[(1-s_0)v_f z_f + s_0(1-\mu_0)v_{m0}z_{m0} + s_0\mu_0v_{m1}z_{m1}] \quad [\text{S6a}]$$

$$2\lambda z_{m1} = q_1[(1-s_0)v_f z_f + s_1\mu_1v_{m0}z_{m0} + s_1(1-\mu_1)v_{m1}z_{m1}]. \quad [\text{S6b}]$$

Now we can work out the selection differential for p , using the numerator of the right-hand side of Eq. S5. Writing $v'_f = dv_f/dp$ and $\alpha' = d\alpha/dp$, we get

$$\frac{\partial w}{\partial p} = \frac{\mathbf{z}^T}{2\lambda} \begin{bmatrix} \alpha'(s_0 - s_1)v_f + v'_f(1-\bar{s}) & q_0(1-s_0)v'_f & q_1(1-s_1)v'_f \\ \alpha'[s_1\mu_1 - s_0(1-\mu_0)] & 0 & 0 \\ \alpha'[s_1(1-\mu_1) - s_0\mu_0] & 0 & 0 \end{bmatrix} \mathbf{y} \quad [\text{S7a}]$$

$$= \frac{\mathbf{z}^T}{2\lambda} \begin{bmatrix} \alpha'(s_0 - s_1)v_f + v'_f/v_f[(1-\bar{s})v_f y_f + q_0(1-s_0)v_f y_{m0} + q_1(1-s_1)v_f y_{m1}] \\ \alpha'[s_1\mu_1 - s_0(1-\mu_0)] y_f \\ \alpha'[s_1(1-\mu_1) - s_0\mu_0] y_f \end{bmatrix} \quad [\text{S7b}]$$

$$\stackrel{[\text{S3a}]}{=} \frac{\mathbf{z}^T}{2\lambda} \begin{bmatrix} \alpha'(s_0 - s_1)v_f + (v'_f/v_f)2\lambda y_f \\ \alpha'[s_1\mu_1 - s_0(1-\mu_0)] y_f \\ \alpha'[s_1(1-\mu_1) - s_0\mu_0] y_f \end{bmatrix} \quad [\text{S7c}]$$

$$\stackrel{[\text{S6a,b}]}{=} \alpha' \left[\frac{z_{m1}}{q_1} - \frac{z_{m0}}{q_0} \right] y_f + \frac{v'_f}{v_f} z_f y_f. \quad [\text{S7d}]$$

Likewise, the selection differential for t , with primes denoting differentiation with respect to t , is

$$\frac{\partial w}{\partial \hat{t}} = \frac{\mathbf{z}^T}{2\lambda} \begin{bmatrix} 0 & 0 & a_{13}q'_1/q_1 \\ 0 & 0 & a_{23}q'_1/q_1 \\ a_{31}v'_{m1}/v_{m1} & a_{32}v'_{m1}/v_{m1} & a_{33}(v'_{m1}/v_{m1} + q'_1/q_1) \end{bmatrix} \mathbf{y} \quad [\text{S8a}]$$

$$= \frac{\mathbf{z}^T}{2\lambda} \begin{bmatrix} a_{13}(q'_1/q_1)y_{m1} \\ a_{23}(q'_1/q_1)y_{m1} \\ (a_{31}y_f + a_{32}y_{m0} + a_{33}y_{m1})v'_{m1}/v_{m1} + a_{33}(q'_1/q_1)y_{m1} \end{bmatrix} \quad [\text{S8b}]$$

$$\stackrel{[\text{S3b}]}{=} \frac{\mathbf{z}^T}{2\lambda} \begin{bmatrix} a_{13}(q'_1/q_1)y_{m1} \\ a_{23}(q'_1/q_1)y_{m1} \\ 2\lambda(v'_{m1}/v_{m1})y_{m1} + a_{33}(q'_1/q_1)y_{m1} \end{bmatrix} \quad [\text{S8c}]$$

$$= \frac{1}{2\lambda}(q'_1/q_1)(a_{13}z_f + a_{23}z_{m0} + a_{33}z_{m1})y_{m1} + (v'_{m1}/v_{m1})z_{m1}y_{m1} \quad [\text{S8d}]$$

$$\stackrel{[\text{S6b}]}{=} (q'_1/q_1)z_{m1}y_{m1} + (v'_{m1}/v_{m1})z_{m1}y_{m1}. \quad [\text{S8e}]$$

Next we turn to the sex-allocation traits. The selection differential for s_0 is

$$\frac{\partial w}{\partial \hat{s}_0} = \frac{1-\alpha}{2(1-\bar{s})v_f} [-v_f + (1-\mu_0)v_{m0}z_{m0} + \mu_0v_{m1}z_{m1}] y_f \quad [\text{S9a}]$$

$$= \frac{1-\alpha}{2(1-\bar{s})v_f} \left[-\frac{v_f z_f}{s_0} + \frac{1-s_0}{s_0} v_f z_f + (1-\mu_0)v_{m0}z_{m0} + \mu_0v_{m1}z_{m1} \right] y_f \quad [\text{S9b}]$$

$$= \frac{1-\alpha}{2(1-\bar{s})v_f} \left[-\frac{v_f z_f}{s_0} + \frac{2(1-\bar{s})v_f}{q_0s_0} z_{m0} \right] y_f \quad [\text{S9c}]$$

$$= \frac{1-\alpha}{s_0} \left[\frac{z_{m0}}{q_0} - \frac{1}{2(1-\bar{s})} \right] y_f, \quad [\text{S9d}]$$

whereas that for s_1 , calculated in a similar way, is

$$\frac{\partial w}{\partial \hat{s}_1} = \frac{\alpha}{s_1} \left[\frac{z_{m1}}{q_1} - \frac{1}{2(1-\bar{s})} \right] y_f. \quad [\text{S10}]$$

The selection differentials S7d, S8e, S9d, and S10 form Eqs. 4–7.

Numerical Simulations. For numerical simulations, we need to make some additional specific assumptions. Let $r = \exp(c_p p t)$ be the odds that a resident female with preference p chooses a type-1 male with ornamentation level t over a type-0 (non-ornamented) male, where c_p is a positive constant. Then the probability α that such a female will mate with a type-1 male is given by

$$\alpha = \frac{r y_{m1}}{y_{m0} + r y_{m1}}. \quad [\text{S11}]$$

Eq. S11 is actually an implicit equation for α , because the class frequencies y_{mi} will depend on α . However, for a mutant female, the class frequencies are constant, giving $\alpha' = \alpha(1-\alpha)(dr/dp)/r$. The odds that a type-1 male with mutant ornamentation level \hat{t} is chosen by a resident female is $\hat{r} = \exp(c_p p \hat{t})$, which makes his expected number of mates

$$\hat{q}_1 = y_f \frac{\hat{r}}{y_{m0} + r y_{m1}}, \quad [\text{S12}]$$

and, therefore, $q'_1/q_1 = (dr/dt)/r$. Likewise, $\hat{q}_0 = y_f/(y_{m0} + r y_{m1}) = q_0$ (the expected mating success of mutant and resident type-0 males is identical because neither expresses an ornament). Finally, we assume (as in the individual-based simulations) that viability decreases according to a Gaussian function with p and t :

$$v_f = \exp(-c_f p^2) \quad [\text{S13a}]$$

$$v_{m1} = \exp(-c_m t^2) \quad [\text{S13b}]$$

and $v_{m0} = 1$.

Evolutionary dynamics can be modeled by using the dynamic equation $\dot{x} = \partial w / \partial x|_{x=\bar{x}}$ for the traits p , t , s_0 , and s_1 . An example is shown in Fig. 2.

SI Results

Good Genes Sexual Selection. For the good genes simulations, we included an extra trait, v , to model genetic variation in viability, which affects survival to adulthood. Female survival now depends on her viability and her expressed preference, as specified by the function $v \cdot \exp(-c_f p^2)$, whereas male survival is proportional to $v \cdot \exp(-c_m t^2)$, where γ denotes his expressed ornamentation. This ornamentation is assumed to be condition-dependent, with $\gamma = tv$, which means that males of higher viability are more ornamented for a given value of t . Thus, male ornamentation acts as a conditional indicator of genetic viability (4). Females choose on the basis of this condition-dependent ornamentation; so now the chance that a given male is picked from the sample of 10 males is proportional to $\exp(c_p p \gamma)$. Likewise, sex-ratio adjustment by females is based on the expressed ornamentation of her chosen partner, so it depends on γ rather than t . Mutations occur in both t (with probability μ_t) and v (with probability μ_v), but in contrast to the Fisherian

simulations, those mutations in t are unbiased ($g = 0$). Instead, biased mutations are assumed to affect the viability trait v , reducing its value by an average amount h ($h > 0$) and, thereby, maintaining genetic variation between males (4, 5).

Fig. S1 shows the results of these good genes simulations with parameter values $c_p = 1.0$, $c_f = 0.0025$, $c_m = 0.5$, $\mu_p = \mu_t = \mu_v = 0.05$, and $h = 0.02$ and average genetic values starting at $\bar{p} = 1$, $\bar{t} = 0$, $\bar{v} = 0.01$, and $\bar{s}_+ = \bar{s}_- = 0.5$. As in the Fisherian simulations, male ornamentation and female preference coevolve to exaggerated levels under sexual selection, but then decline as sex-ratio adjustment develops.

When Ornamentation Can Take Negative Values. We ran additional simulations in which the genetic value for ornamentation could take any real number, as in some previous models of sexual selection (4, 6). Otherwise, the details of the simulations were kept the same, with male survival maximized for $t = 0$ and declining away from this optimum according to the function $\exp(-c_m t^2)$, where c_m is a positive constant.

Fig. S2 shows the results of these simulations for Fisherian sexual selection with parameter values $c_p = 1.0$, $c_f = 0.001$, $c_m = 0.5$, $\mu_p = \mu_t = \mu_s = 0.05$, and $g = 0.02$ and average genetic values starting at $\bar{p} = 1$ and $\bar{t} = 0$. The sex-allocation traits were initially fixed at $s_+ = s_- = 0.5$, but partway through the simulations, we allowed these traits to evolve. As before, male ornamentation and female preference coevolve to exaggerated levels under sexual selection, but then decline as sex-ratio adjustment develops.

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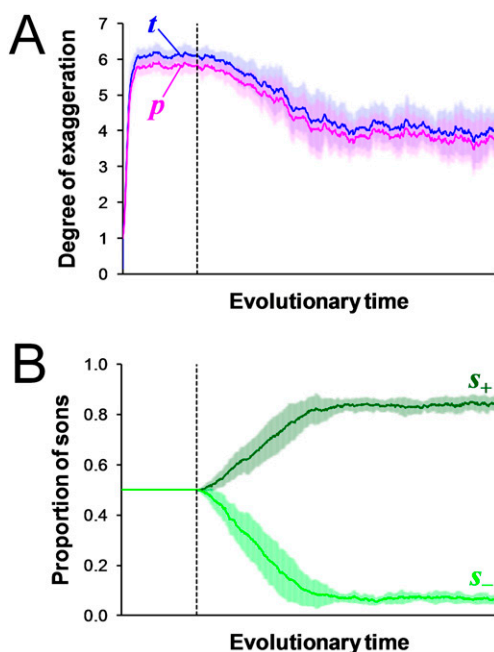


Fig. S1. Coevolutionary dynamics of good genes sexual selection and sex allocation (individual-based simulations). *A* shows the level of male ornamentation (t , blue) and female preference (p , pink) under good genes sexual selection, whereas *B* shows the female sex-allocation strategy in the same set of simulations based on traits s_+ and s_- , where s_+ (dark green) is the probability of producing a son when her partner has above-average ornamentation and s_- (light green) is the probability of producing a son when he has below-average ornamentation. Offspring sex ratios are initially unbiased ($s_+ = s_- = 0.5$) but are allowed to evolve from the point indicated by the vertical dashed lines. All values are shown as the mean (solid line) \pm SD (stippling) from 20 replicate simulation runs.

