

# 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  $\alpha$  of females that mate with the former type (note that  $\alpha$  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  $\mu_0$ , the son of a nonornamented male is ornamented, and with probability  $\mu_1$ , 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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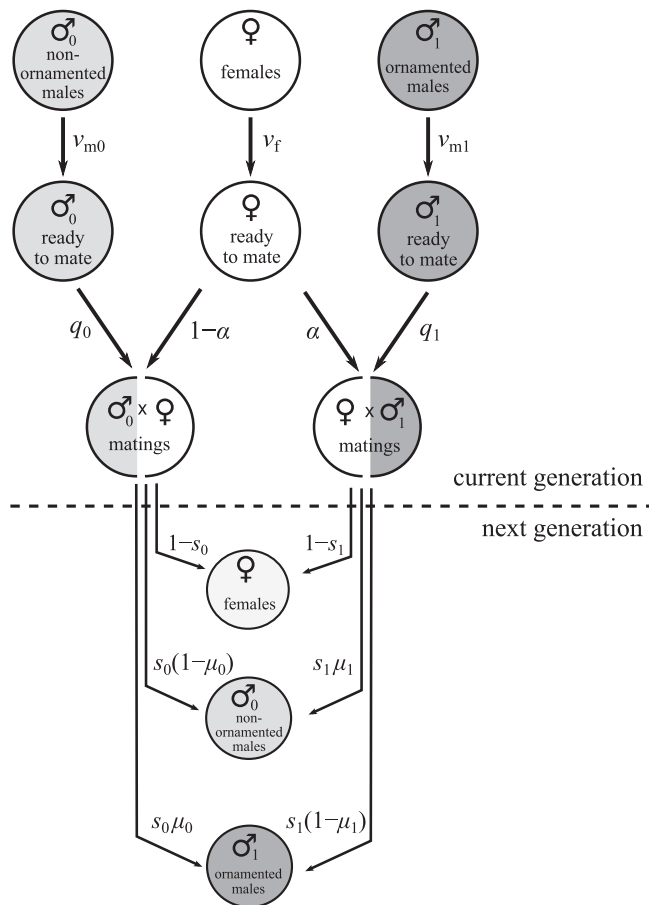
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**Fig. 1.** Summary of the sequence of events in each generation of our model. The survival of females ( $v_f$ ) and ornamented males ( $v_{m1}$ ) to reproduction is reduced by the cost of their preference and ornament, respectively (nonornamented males do not pay a cost;  $v_{m0} = 1$ ). Reproducing females give a proportion  $\alpha$  of their matings to ornamented males, resulting in an average number of mates  $q_1$  for ornamented males compared with  $q_0$  mates for nonornamented males ( $q_1 \geq q_0$ ). For each offspring produced, the probability that it is a son is  $s_0$  for females with nonornamented partners and  $s_1$  for those with ornamented partners. With mutation probability  $\mu_0$ , the son of a nonornamented male is ornamented, whereas with mutation probability  $\mu_1$ , the son of an ornamented male is nonornamented ( $\mu_1 > \mu_0$ , i.e., mutations are biased toward the loss of ornamentation).

**Overview of the Method.** Given this setup, we can use a reproductive value approach (16–18) to obtain selection differentials for male ornamentation, female preference, and conditional sex allocation, which together describe how the system evolves. This

**Table 1. Variables and parameters used in the model**

Symbol	Meaning
$y_f$	Relative frequency of females
$y_{mi}$	Relative frequency of type- $i$ males ( $i = 0, 1$ )
$Z_f$	Class-specific individual reproductive value of females
$Z_{mi}$	Class-specific individual reproductive value of type- $i$ males
$v_f$	Viability of females
$v_{mi}$	Viability of type- $i$ males
$\alpha$	Probability that a female mates with a type-1 male
$q_i$	Average number of mates per type- $i$ male
$s_i$	Proportion of sons produced when mated to a type- $i$ male
$\mu_i$	Probability that the son of a type- $i$ male mutates into the alternative type

approach involves three basic steps: (i) Determine the dynamics of a resident population with trait value  $x$  for a given trait of interest; (ii) determine the invasion fitness of a rare mutant with alternative trait value  $\hat{x}$  within this resident population; and (iii) determine how mutant fitness  $w$  depends on  $x$  and  $\hat{x}$ . Below we outline these steps in detail.

**Dynamics of the Resident Population.** We first consider the dynamics of a resident population with ornamentation level  $t$ , preference  $p$ , and sex-allocation traits  $s_0$  and  $s_1$ . The numbers of females, type-0 males, and type-1 males change from one generation to the next according to the transition matrix

$$\mathbf{A} = \frac{1}{2} k \begin{bmatrix} [(1-\alpha)(1-s_0) + \alpha(1-s_1)]v_f & q_0(1-s_0)v_f & q_1(1-s_1)v_f \\ [(1-\alpha)s_0(1-\mu_0) + \alpha s_1\mu_1]v_{m0} & q_0s_0(1-\mu_0)v_{m0} & q_1s_1\mu_1v_{m0} \\ [(1-\alpha)s_0\mu_0 + \alpha s_1(1-\mu_1)]v_{m1} & q_0s_0\mu_0v_{m1} & q_1s_1(1-\mu_1)v_{m1} \end{bmatrix} \quad [1]$$

The factor 1/2 is a formality to prevent offspring being counted twice (once via its mother and once via its father), whereas the constant  $k$  is a scaling factor (equivalent to the average clutch size) to ensure that the population is stable (in technical terms, to ensure that the dominant eigenvalue is 1; see refs. 18 and 19). The leftmost column of  $\mathbf{A}$  represents the per-capita reproductive output of females, the center column that of type-0 males, and the rightmost column 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.

The entries in the matrix are derived from the basic assumptions of our model. To give an example, take the leftmost entry in the center row, which represents the reproductive contribution of mothers to type-0 males in the next adult generation. There are two scenarios in which a female gives birth to a type-0 son: either she mates with a type-0 male (probability  $1 - \alpha$ ) and produces a son (probability  $s_0$ ) who is unaffected by mutation (probability  $1 - \mu_0$ ), or she mates with a type-1 male (probability  $\alpha$ ) and produces a son (probability  $s_1$ ) who mutates to a non-ornamented state (probability  $\mu_1$ ). In either case, the survival of that son to reproductive age is  $v_{m0}$ . The other entries in matrix  $\mathbf{A}$  are derived by using similar logic, detailed in *SI Model*.

The relative frequencies of females ( $y_f$ ), type-0 males ( $y_{m0}$ ), and type-1 males ( $y_{m1}$ ) change from one generation to the next according to the dynamic equation  $\mathbf{y}_{t+1} = \mathbf{A}\mathbf{y}_t$ , where  $\mathbf{y}$  is the column vector  $(y_f, y_{m0}, y_{m1})^T$  representing the relative frequencies in the current generation ( $\mathbf{y}_t$ ) and the next generation ( $\mathbf{y}_{t+1}$ ), respectively (note that the superscript T indicates transposition). Explicit equations for  $y_f$  and  $y_{m1}$  are given in *SI Model*.

**Invasion Fitness of a Rare Mutant.** Now we ask whether rare mutants with different values for the traits of interest can invade the resident population. The dynamics of mutants are governed by a matrix similar to  $\mathbf{A}$ , with the appropriate parameters replaced by their mutant counterparts:

$$\mathbf{B} = \frac{1}{2} k \begin{bmatrix} [(1-\hat{\alpha})(1-\hat{s}_0) + \hat{\alpha}(1-\hat{s}_1)]\hat{v}_f & \hat{q}_0(1-\hat{s}_0)\hat{v}_f & \hat{q}_1(1-\hat{s}_1)\hat{v}_f \\ [(1-\hat{\alpha})\hat{s}_0(1-\hat{\mu}_0) + \hat{\alpha}\hat{s}_1\hat{\mu}_1]\hat{v}_{m0} & \hat{q}_0\hat{s}_0(1-\hat{\mu}_0)\hat{v}_{m0} & \hat{q}_1\hat{s}_1\hat{\mu}_1\hat{v}_{m0} \\ [(1-\hat{\alpha})\hat{s}_0\hat{\mu}_0 + \hat{\alpha}\hat{s}_1(1-\hat{\mu}_1)]\hat{v}_{m1} & \hat{q}_0\hat{s}_0\hat{\mu}_0\hat{v}_{m1} & \hat{q}_1\hat{s}_1(1-\hat{\mu}_1)\hat{v}_{m1} \end{bmatrix} \quad [2]$$

Mutant phenotypes are equipped with a hat ( $\hat{\phantom{x}}$ ) to distinguish them from resident phenotypes. Note that the probability  $\hat{\alpha}$  that a mutant female mates with a type-1 male is distinct from the corresponding resident probability  $\alpha$ , because it is determined by the female's mutated preference  $\hat{p}$ . Her viability  $\hat{v}_f$  also depends on  $\hat{p}$ , whereas that of mutant males  $\hat{v}_{m1}$  depends on their mutant level of ornamentation  $\hat{t}$ . In contrast, because type-0 males lack

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  $\hat{s}_1 = s_1$ ):

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

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

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

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

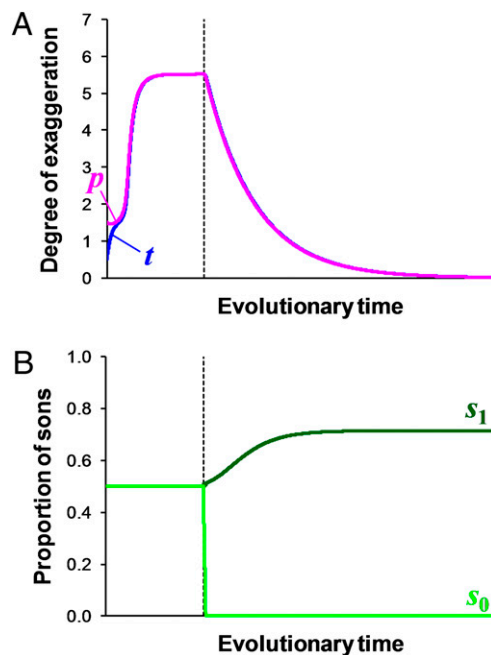
where  $\bar{s} = (1 - \alpha)s_0 + \alpha s_1$  is the average offspring sex ratio. Primes (') denote differentiation with respect to the trait under consideration.

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.

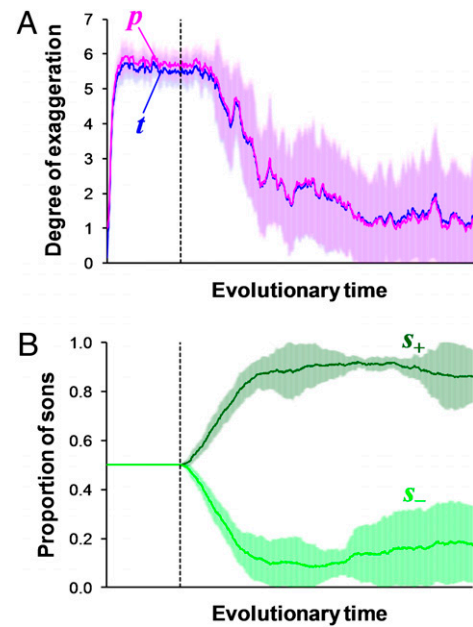
**Individual-Based Simulations.** Using individual-based computer simulations, we can extend this analysis to a more realistic situation where male ornamentation and female preference vary continuously and the evolutionary dynamics are subject to stochastic demographic factors. We simulated a finite 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



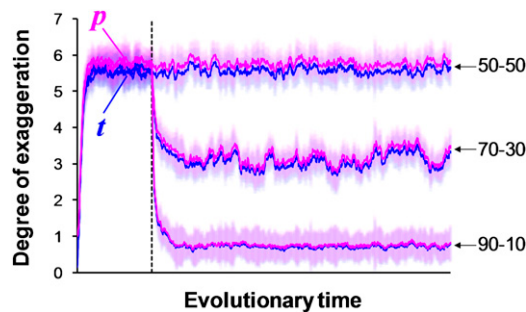
**Fig. 3.** Coevolutionary dynamics of sexual selection and sex allocation (individual-based simulations). A shows the level of male ornamentation ( $t$ , blue) and female preference ( $p$ , pink) under Fisherian sexual selection, whereas B shows the female sex-allocation strategy in the same set of 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  $\mu_p$  for  $p$ ,  $\mu_t$  for  $t$ , and  $\mu_s$  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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