



# The evolution of mating preferences for genetic attractiveness and quality in the presence of sensory bias

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Edited by Marcus Feldman, Stanford University, Stanford, CA; received April 9, 2022; accepted July 19, 2022

The aesthetic preferences of potential mates have driven the evolution of a baffling diversity of elaborate ornaments. Which fitness benefit—if any—choosers gain from expressing such preferences is controversial, however. Here, we simulate the evolution of preferences for multiple ornament types (e.g., “Fisherian,” “handicap,” and “indicator” ornaments) that differ in their associations with genes for attractiveness and other components of fitness. We model the costs of preference expression in a biologically plausible way, which decouples costly mate search from cost-free preferences. Ornaments of all types evolved in our model, but their occurrence was far from random. Females typically preferred ornaments that carried information about a male’s quality, defined here as his ability to acquire and metabolize resources. Highly salient ornaments, which key into preexisting perceptual biases, were also more likely to evolve. When males expressed quality-dependent ornaments, females invested readily in costly mate search to locate preferred males. In contrast, the genetic benefits associated with purely arbitrary ornaments were insufficient to sustain highly costly mate search. Arbitrary ornaments could nonetheless “piggyback” on mate-search effort favored by other, quality-dependent ornaments. We further show that the potential to produce attractive male offspring (“sexy sons”) can be as important as producing offspring of high general quality (“good genes”) in shaping female preferences, even when preferred ornaments are quality dependent. Our model highlights the importance of mate-search effort as a driver of aesthetic coevolution.

sexual selection | mate choice | ornament | handicap | causal inference

Many of life’s most striking and extravagant traits—from the dances of peacock spiders to the elaborate sculptures of bowerbirds—evolved to satisfy the aesthetic preferences of potential mating partners (1–3). The causal mechanisms by which such preferences evolve remain highly contentious, however. Multiple models provide plausible accounts of the coevolution of preferences and preferred traits (reviewed in ref. (4)), but there is no consensus as to which subset of these mechanisms dominates in the natural world (1–3, 5–8).

Models of aesthetic coevolution differ principally in the mechanisms by which preferences evolve. The simplest and least controversial of these are direct-benefits models, in which the expression of preferences leads to an increase in the survival or reproductive success of the chooser that is unrelated to the genotypes of their offspring (4, 9–11). Direct benefits may include access to resources—e.g., parental care, a territory, or a high-fecundity mate—or avoidance of harms, such as pathogens or harassment. A genetic basis for the relationship between preferred traits and direct benefits is not required for strong preferences to evolve, although there must be some causal mechanism maintaining such a relationship (4).

Direct benefits are not necessary for strong mating preferences to evolve, however. In the Fisher process, ornaments become genetically correlated with preferences due to nonrandom mating (12). A modest initial preference can generate selection for greater ornamentation, which in turn indirectly selects for stronger preferences. This can lead to a self-reinforcing process of ever-elaborating ornaments and preferences (13–16). In Fisherian models, the only adaptive benefit of mating preferences is the potential to produce attractive offspring (e.g., “sexy sons”). In other words, selection on preferences arises due to the causal effect of ornaments on attractiveness and the genetic correlation between preferences and ornaments. In contrast, “good genes” models posit that ornament expression is correlated with other aspects of genetic quality, such as fecundity, viability, or survival (10, 17–22). Such correlations can be generated by condition-dependent life-history strategies, but there is some debate over whether correlations are strong enough in practice to drive evolution (23–26). All of the above models assume that mating preferences are largely adaptive. In contrast, sensory exploitation models generally posit that preferences are initially selectively neutral in the context of mate choice, although they may evolve as by-products of selection in other contexts, such as

## Significance

Charles Darwin proposed that extravagant traits with no obvious function—like the famous peacock’s tail—are often explained by equally extravagant preferences in the opposite sex. Exactly why such preferences evolved has proved a much thornier question. One hypothesis is that female preferences evolved to ensure that offspring carry the genes of preferred males. These may include genes for attractiveness per se and for other, more general aspects of quality, like the ability to acquire resources. We show that preferences are more likely to evolve when ornaments are quality dependent and that females will invest significant resources to locate high-quality males. Flashiness matters, however: ornaments that are particularly striking with respect to females’ perceptual systems also evolve more frequently.

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Author contributions: J.M.H., L.F., and A.G.J. designed research; J.M.H. performed research; J.M.H. analyzed data; and J.M.H., L.F., and A.G.J. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at <http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2206262119/-DCSupplemental>.

Published August 8, 2022.

foraging (7, 8, 27). These preferences may even become maladaptive once sufficiently attractive ornaments evolve in the opposite sex (28). This can lead to rapid turnover in both ornaments and preferences over evolutionary time.

Importantly, the above mechanisms of sexual selection are not mutually exclusive. Most likely, each plays some role in the coevolution of ornaments and preferences, with their relative significance differing among species and even within species over time (28–30). For instance, the Fisher process arises naturally in any model in which genetic correlations between ornaments and preferences are permitted, even those described by their authors in terms of “direct benefits,” “good genes”, or “sensory exploitation.” There have been few attempts to evaluate the relative importance of these mechanisms, however, whether in theoretical or empirical settings (but see refs. (11, 23)).

Here, we compare the plausibility of indirect-benefits mechanisms of sexual selection—including sexy sons and good genes models—by simulating the coevolution of quality-dependent and purely Fisherian ornaments side by side (Fig. 1). Using causal inference (31), we also quantify how different selection pathways contribute to the evolution of ornaments and preferences, allowing a more nuanced, quantitative analysis of the continuum between sexy sons and good genes models (29). Although female ornamentation is widespread in animals (32, 33), our model focuses on the empirically most common scenario, in which male

ornaments coevolve with female preferences and where males’ material contributions to their offspring or mates are negligible.

Individual quality is operationalized in our model as the ability to acquire resources and convert them into offspring or ornaments (34). We assume that quality cannot be observed directly by potential mates, rather only indirectly via quality-dependent ornaments (cf. ref. (22)). We distinguish between two types of quality-dependent ornament (35–37) (Fig. 1). “Handicap” ornaments exaggerate steadily with increasing investment, with the result that even low-quality individuals can potentially produce large ornaments. However, the survival cost of producing a larger ornament is greater for low-quality individuals, leading to a correlation between ornament size and genetic quality (17, 34, 38). In contrast, “indicator” ornaments require only a small investment by their bearers to achieve their full size, at which point they provide a reliable (“honest”) signal of the bearer’s underlying quality (35–37). In addition to quality, we also consider how ornament evolution is shaped by the salience of individual ornaments (i.e., the extent to which they “stand out” to potential mates due to details of receiver perception and cognition).

We assume that male ornaments carry viability costs, which increase with the bearer’s total investment in all ornaments. In contrast to previous influential models of sexual selection (14, 18), we assume that preferences per se are not costly. Rather, females must pay a fecundity cost to sample additional potential mates. Costly mate search is thus necessary for females to translate their preferences into realized mate choice (8).

## Results

We simulated the coevolution of four types of traits: male investment in  $n$  distinct ornaments, female preferences for these ornaments, female mate-search effort, and individual quality (for details, see *Materials and Methods*). Ornaments were assigned to predetermined types—e.g., Fisherian, handicap, or indicator—based on the assumed relationship between ornament size, ornament investment, and male quality. Ornaments could provide reliable information about a male’s genes for attractiveness or quality but were assumed to be uncorrelated with direct fitness benefits to potential mates. A male’s viability was assumed to decrease with his total investment in ornaments. Females chose their mates from among a set of “suitors,” with the no. of suitors increasing with a female’s mate-search effort. A female’s fecundity increased with her individual quality but decreased with her mate-search effort. Females could evolve preferences for larger or smaller ornaments or be indifferent to ornament size; in all cases, the preferences themselves were assumed to be cost-free.

When ornaments of all three types—Fisherian, handicap, and indicator—coevolved in a single simulation, positive investment in all three types frequently evolved and persisted for hundreds of thousands of generations (Fig. 2). However, the frequency and extent of ornament exaggeration differed between types (see *Females Prefer Both Quality-Dependent and Salient Ornaments*).

**From Perceptual Biases to Adaptive Preferences.** Preferences for ornaments that were not currently expressed in the population evolved due to drift alone, with the consequence that strong preferences could emerge by chance alone in the absence of the target ornament (see, e.g., the ornament  $T_{14}$  and preference  $p_{14}$  in Fig. 2). Once an ornament arose, previously latent preferences were expressed as realized mate choice (7, 8). Selection then favored ornament exaggeration if existing preferences were strong enough to outweigh the viability costs of investing in the new ornament (see *Even Good Genes Models Come with a Fair Dose of*

**Fig. 1.** The relationship between male ornament investment  $x$ , male quality  $q$ , and ornament size  $T$  for Fisherian (A), handicap (B), and indicator ornaments (C). Shown with  $q - \bar{q} = -0.5, 0, 0.5$  for low, medium, and high quality, respectively. Values of  $c_j$  and  $b_j$  are as in Table 1.

**Table 1. Summary of parameters and trait variables**

Parameter	Meaning	Default value
$N$	Population size	1,000
$n$	No. of ornaments	
$c_j$	Extent of quality-dependence for the $j$ th ornament	0 (Fisherian traits) 1 (indicator and handicap traits) 1 (Fisherian and handicap traits) 10 (indicator traits)
$b_j$	Shape of investment-size curve for the $j$ th ornament	
$k$	Cost of female mate search	
$s_j$	Saliency coefficient of the $j$ th ornament	5
$\bar{x}_0, \bar{p}_0, \bar{m}_0, \bar{q}_0$	Initial mean allelic values for each trait type	$\bar{x}_0 = \bar{p}_0 = 0$ $\bar{m}_0 = 5, \bar{q}_0 = 1$
$d_x, d_p, d_m, d_q$	Initial SDs of allelic values for each trait type	$d_x = 0.1, d_p = 1,$ $d_m = 1, d_q = 0.1$
$\pi_x, \pi_p, \pi_m, \pi_q$	Per-generation probabilities of mutation for alleles affecting each trait type	$\pi_x = \pi_p = \pi_m = 0.01, \pi_q = 0.1$
$\mu_x, \mu_p, \mu_m, \mu_q$	Mean mutational effects for each trait type	$\mu_x = \mu_p = \mu_m = 0,$ $\mu_q = -0.5$
$\sigma_x, \sigma_p, \sigma_m, \sigma_q$	SDs of mutational effects for each trait type	$\sigma_x = \sigma_p = 0.1,$ $\sigma_m = 1, \sigma_q = 0.1$
Trait variable	Meaning	
$x = (x_1, \dots, x_n)$	Male investment in each ornament	
$p = (p_1, \dots, p_n)$	Female preferences for each ornament	
$m$	Female mate-search effort	
$q$	Male or female quality	

*Sexy Sons*). Mate choice further led to correlations between genes for preference, ornament investment, and (potentially) quality, which generated indirect selection on the preferences themselves.

#### Females Prefer Both Quality-Dependent and Salient Ornaments.

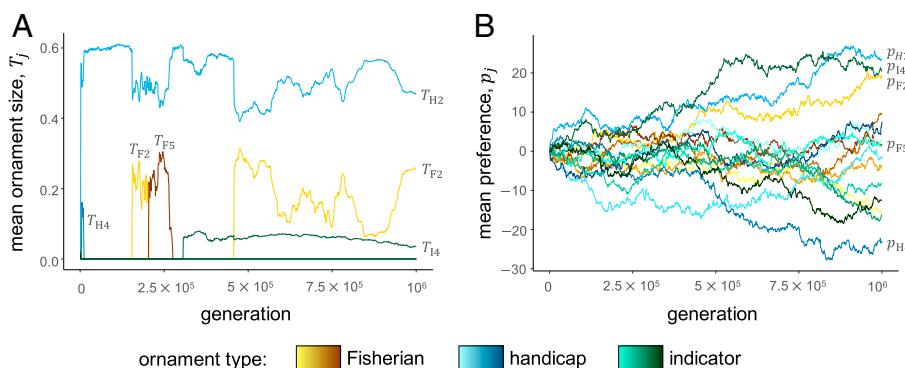
Although all ornament types could evolve, some evolved more frequently than others. We next simulated sets of ornaments that differed only in their quality dependence, representing a gradient between Fisherian and handicap types. Highly quality-dependent ornaments were more likely to become the target of strong female preferences and were consequently overrepresented among those ornaments with exaggerated expression (Fig. 3). Similarly, when ornaments differed only in their saliency coefficients, highly salient ornaments were more likely to become exaggerated (Fig. 4). Higher saliency was preferred in both Fisherian (Fig. 4 A and B) and handicap (Fig. 4 C and D) ornaments.

#### No Clear Winner between Handicap and Indicator Ornaments.

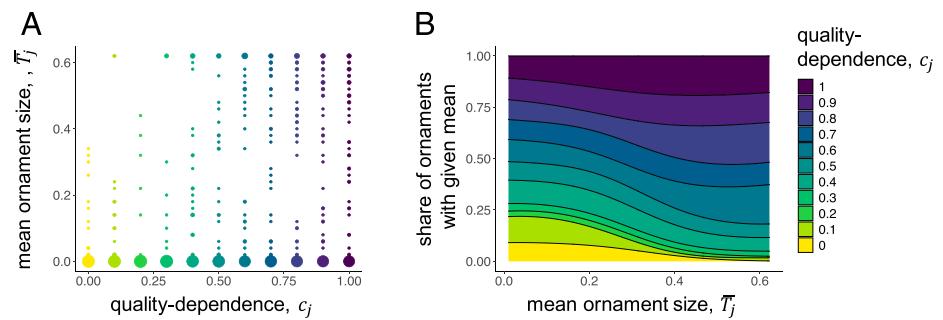
Differences between handicap and indicator ornaments were more nuanced. We defined the relationship between ornament investment and ornament size (Eq. 3 in Materials and Methods)

such that, when male investment is small, all ornament types grow equally steeply with increasing investment. If the saliency coefficients  $s$  of all ornaments are equal, this means that handicap and indicator ornaments are equally salient to females when they first evolve. However, since the relationship between investment and size quickly levels off for indicator ornaments, this also implies that indicator ornaments reach a smaller maximum size than handicap ornaments (Fig. 1). Indicator ornaments are consequently less noticeable to females when male investment is large. Under these assumptions, females preferred handicap to indicator ornaments due to their higher salience (Fig. 5A) and handicap ornaments were consequently more frequently exaggerated (Fig. 5B).

Rather than standardizing the initial saliency of ornaments, one could alternatively standardize their maximum saliency under large male investment (i.e., for  $x_j \approx 1$ ). We achieved this by elevating the salience coefficient of indicator ornaments ( $s_I = 30$ ) relative to Fisherian and handicap ornaments ( $s_F = s_H = 5$ ). Under this assumption, indicator ornaments are initially more salient than the other types, but salience equalizes



**Fig. 2.** Exemplary simulation results for the coevolution of five ornaments (A) and preferences (B) of each type ( $n = 15$  ornaments in total) over  $10^6$  generations. Ornament types are Fisherian (F subscripts, yellow/brown), handicap (H subscripts, blue), and indicator (I subscripts, green). Shown with cost of mate search  $k = 10^{-4}$  (all other parameters as in Table 1).



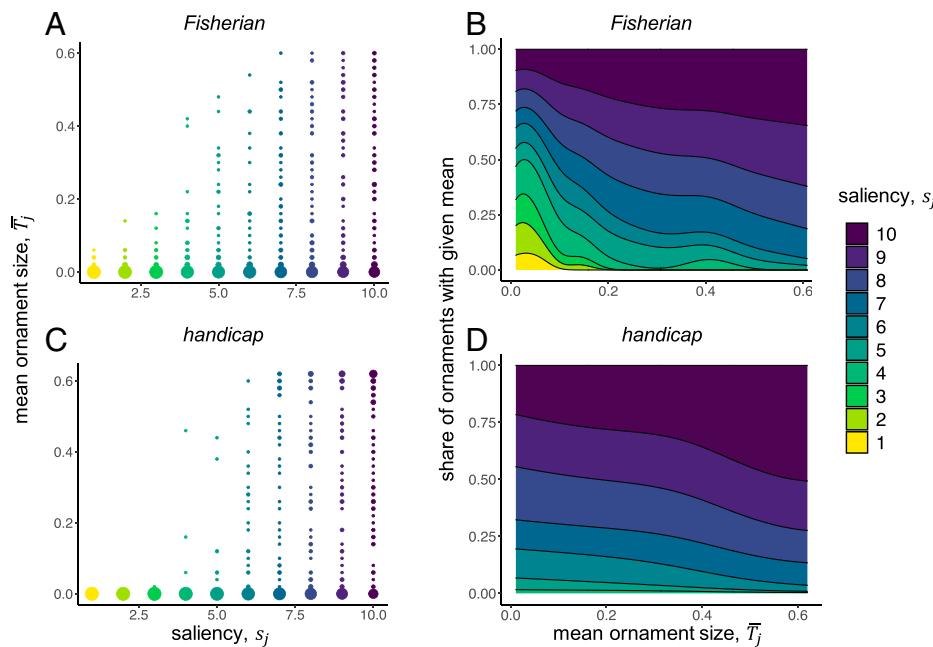
**Fig. 3.** Sizes of 11 ornaments that differ only in their quality dependence, shown as (A) area-weighted scatter plot of mean ornament sizes  $\bar{T}_j$  and (B) kernel densities of the proportional share of ornaments with a given mean size. Results are based on 200 simulation runs, where each run followed the evolution of 11 traits with quality dependence  $c = (0, 0.1, \dots, 1)$  over  $10^6$  generations. Means  $\bar{T}_j$  were calculated across all individuals over all generations within each simulation run. The scatter plot (A) represents means from all simulation runs, which were rounded to the nearest 0.02 for ease of presentation. The area of each disk is proportional to the no. of simulation runs with rounded mean trait size given by the center of that disk. Kernel densities (B) were based only on means  $\bar{T}_j > 0.01$  (sample size = 330). Smoothed kernel densities were estimated using “geom\_density()” in the R package “ggplot2” with the smoothing parameter “adjust = 2” (55) (note that some noise is present in both the scatter plots and the kernel density estimates). Both panels are shown with  $b_j = 1$  for all traits and cost of mate search  $k = 10^{-4}$  (all other parameter values as in Table 1).

with increasing investment. In this case, females preferred indicator ornaments (Fig. 5C), and this led to indicator ornaments being the dominant type of exaggerated ornament (Fig. 5D). Investment in indicator ornaments remained modest in comparison with exaggerated Fisherian or handicap ornaments, even when female preferences were strong (Fig. 5B and D). This is because the investment-size curve for indicator ornaments shows strongly diminishing returns on increased investment (Fig. 1). Indicator ornaments were consequently less costly to males, even in the presence of strong female preferences.

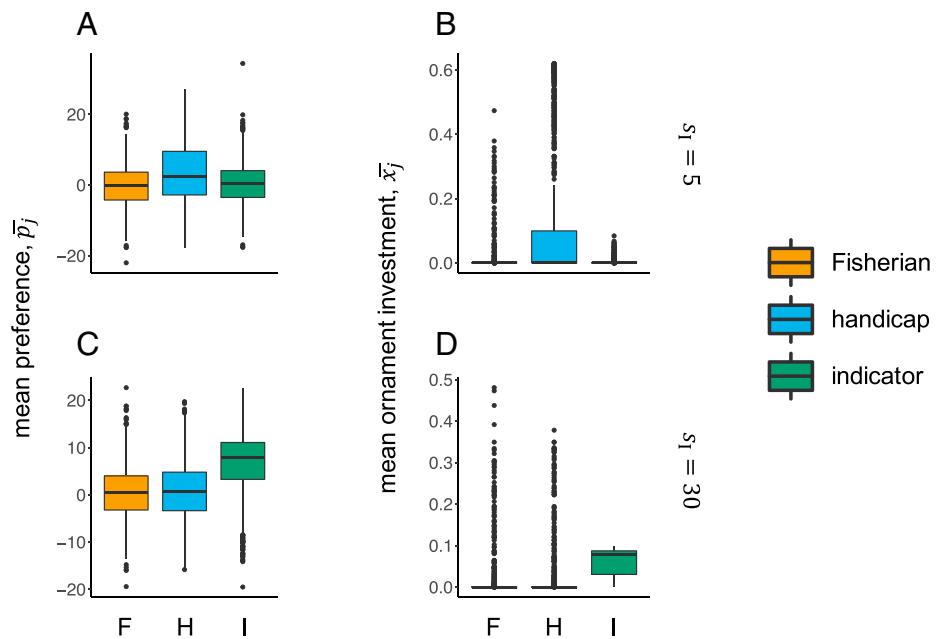
#### Quality-Dependent Ornaments Are Necessary for Costly Mate Search, but Fisherian Ornaments Can Come Along for the Ride.

Females who sample from a larger no. of suitors are more likely

to find a mate that they rate highly, potentially leading to higher-quality offspring of both sexes (good genes) or more attractive male offspring (sexy sons). Good genes benefits are, however, only accessible to females if males express quality-dependent ornaments. All else being equal, females reduced their investment in mate search as the fecundity cost of mate search  $k$  increased (Fig. 6). When all potential ornaments were Fisherian, females invested in mate search as long as the costs were very small (Fig. 6A). This contrasts with models in which preferences per se are costly, which predict that costly preferences can only persist when mutations on ornament size are negatively biased [refs. 14, 15, 39, 40 but see also (41)] (note that mutations affecting ornament investment are unbiased in our model). Nonetheless, females largely ceased investing in mate



**Fig. 4.** Sizes of ten ornaments that differ only in their saliency, shown as (A and C) area-weighted scatter plots of mean ornament sizes  $\bar{T}_j$  and (B and D) kernel densities of the proportional share of ornaments with a given mean size. All ornaments are either of Fisherian (A and B) or handicap (C and D) type. Results are based on 200 simulation runs, where each run followed the evolution of ten traits with saliences  $s = (1, 2, \dots, 10)$  over  $10^6$  generations. Means  $\bar{T}_j$  were calculated across all individuals over all generations within each simulation run. Scatter plots (A and C) represent means from all simulation runs, which were rounded to the nearest 0.02 for ease of presentation. The area of each disk is proportional to the no. of simulation runs with rounded mean trait size given by the center of that disk. Kernel densities (B and D) were based only on means  $\bar{T}_j > 0.01$  (sample sizes of 419 and 327 for B and D, respectively). Smoothed kernel densities were estimated using geom\_density() in the R package ggplot2 with the smoothing parameter adjust = 2 (55) (note that some noise is present in both the scatter plots and the kernel density estimates). Shown with costs of mate search  $k = 10^{-5}$  and  $k = 10^{-3}$  for simulations of Fisherian and handicap ornaments, respectively (all other parameter values as in Table 1).



**Fig. 5.** Box-and-whisker plots of mean investment  $\bar{x}_j$  in Fisherian (F) (brown), handicap (H) (blue), and indicator (I) (green) ornaments (panels B and D) and mean preferences  $\bar{p}_j$  for these ornaments (panels A and C). The saliency coefficient  $s_I$  for indicator traits was chosen so that all trait types are equally salient either when investment  $x \approx 0$  ( $s_F = s_H = s_I = 5$ , panels A and B) or when  $x \approx 1$  ( $s_F = s_H = 5$ ,  $s_I = 30$ , panels C and D). Each simulation run followed the evolution of 15 traits (five of each type) over  $10^6$  generations (200 simulation runs per panel). Means  $\bar{x}_j$  and  $\bar{p}_j$  were taken across all individuals over all generations and all traits of the same type within each simulation run. Shown with cost of mate search  $k = 10^{-4}$  (all other parameter values as in Table 1).

search for Fisherian ornaments when  $k > 10^{-4}$  (Fig. 6A), resulting in a negligible exaggeration of ornaments (Fig. 6B). In contrast, when all ornaments were of the handicap type, females continued to search for additional mates even given search costs as high as  $k = 10^{-2}$  (Fig. 6A), which in turn selected for exaggerated ornaments (Fig. 6B).

Quality-dependent ornaments are consequently essential for the evolution of highly costly mate search. However, only some ornaments need be quality dependent. When handicap and Fisherian ornaments evolved side by side, costly mate search was maintained by the handicap ornaments (Fig. 6C). Females were consequently free to exercise their preferences for all ornament types, leading to the exaggeration of both Fisherian and handicap ornaments (Fig. 6D). Fisherian ornaments could thus “piggyback” on female mate-search investment that evolved due to quality-dependent ornaments.

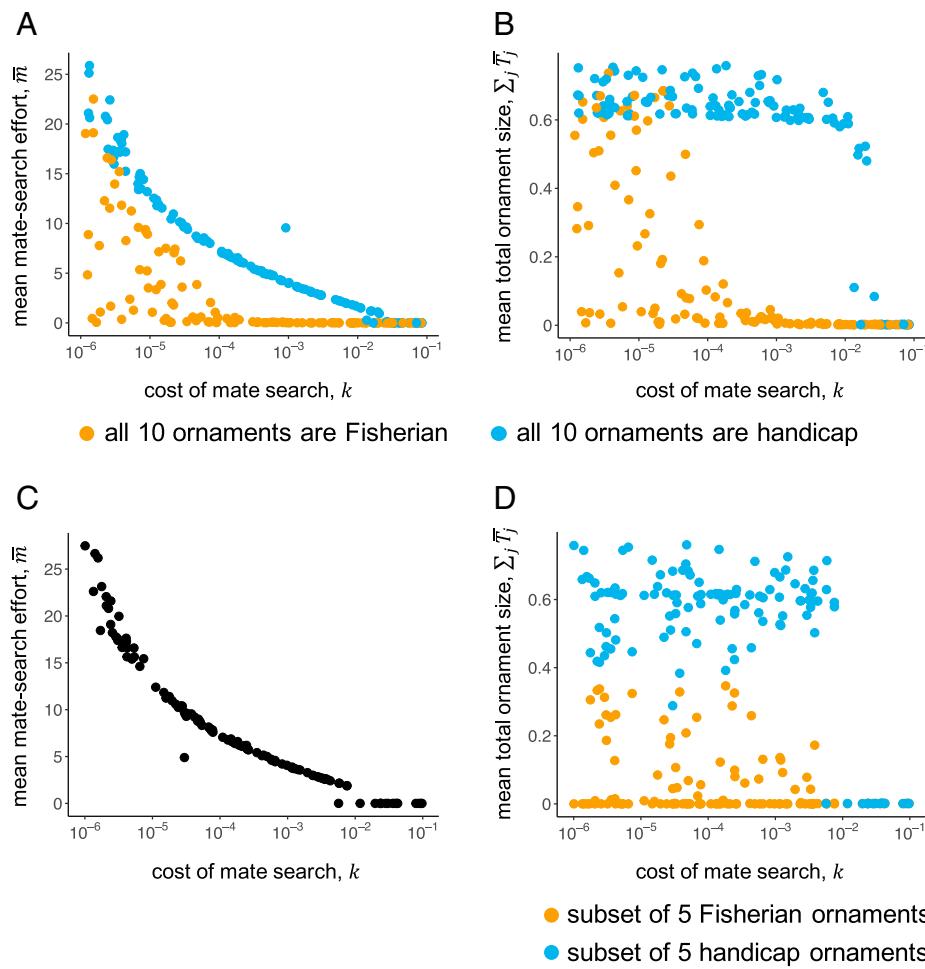
**Even Good Genes Models Come with a Fair Dose of Sexy Sons.** To better understand the causes of selection acting on individual traits, we simulated the coevolution of a single handicap ornament and a preference for this ornament over 1,000 generations. We then analyzed the output of this simulation using nonparametric causal inference (see qualitative causal diagram in Fig. 7). The evolution of investment in the ornament was shaped mainly by selection in males (Fig. 8A). Female preferences for exaggerated ornaments led to sexual selection for greater ornament investment (via the pathway  $x \rightarrow T \rightarrow MS \rightarrow w_m$ : Fig. 7), which was opposed by viability selection for reduced investment (via the pathway  $x \rightarrow V \rightarrow MS \rightarrow w_m$ : Fig. 7). The size of the ornament stabilized when these two selection pressures were approximately balanced (Fig. 8B). In contrast, selection acting on preferences for the handicap ornament was comparable in strength in males and females (Fig. 8C). Preferences were selected for in females due to genetic correlations between preference strength and quality (good genes). In males, preference genes were favored due to their correlations with

ornament investment and/or quality, which jointly determine a male’s mating success (sexy sons). Thus, even for highly quality-dependent ornaments, a substantial proportion of selection on preferences arose via the increased mating success of male offspring (Fig. 8C).

## Discussion

Our results demonstrate that strong preferences for ornamental traits can evolve due to the indirect genetic benefits of mating with ornamented partners. Two types of indirect benefit were potentially available to choosy females in our model, depending on the targets of their preferences: genes for attractive male offspring (sexy sons) and for general quality (good genes). Preferences for purely arbitrary “Fisherian” ornaments can provide only the former type of benefit, whereas preferences for quality-dependent (handicap or indicator) ornaments can provide both. Both quality-dependent and Fisherian ornaments frequently became the targets of strong preferences in our simulations, even when both types of ornament evolved side by side (Figs. 2, 3, 5, and 6). We should consequently expect to encounter both quality-dependent and purely arbitrary sexual ornaments in nature. Nonetheless, females more frequently preferred quality-dependent than Fisherian ornaments (Figs. 3, 5, and 6), with highly salient ornaments also typically being favored (Figs. 4 and 5).

These results confirm the important role of stochasticity in the evolution of mating preferences (42) while simultaneously showing that the targets of mating preferences are far from wholly random. Preexisting sensory and cognitive biases, which affect the salience of ornaments to receivers, should result in some types of ornaments emerging and persisting more frequently than others (7, 27). For instance, Ryan and colleagues showed that the pitch structure of male advertisement calls in túngara frogs closely matches the peak sensitivities of the female auditory system (27, 43). Selection in other contexts (e.g., foraging) might also determine the direction of preexisting preferences



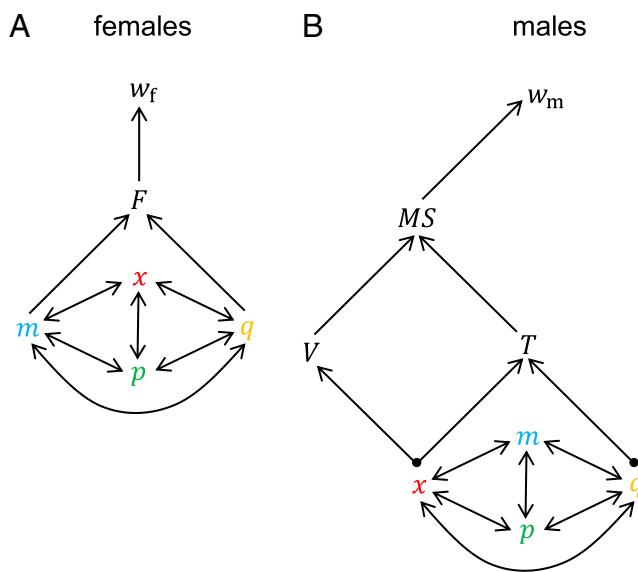
**Fig. 6.** Mean mate-search effort  $\bar{m}$  (A and C) and total ornament size  $\sum_j \bar{T}_j$  (B and D) in simulation runs over 10<sup>6</sup> generations with randomly chosen costs of mate search  $k$ . The upper panels (A and B) represent simulations in which all ten coevolving ornaments are of the same type (Fisherian in brown; handicap in blue). The lower panels (C and D) represent simulations in which five Fisherian and five handicap ornaments coevolve. All other parameters are as in Table 1.

or even contribute to preference evolution after the corresponding ornament arises, but we do not consider this possibility in our model. Our results additionally support the notion of a continuum between sexy sons and good genes models of sexual selection (29). The attractiveness of male offspring always played an important role in selecting for female preferences in our simulations, even when the preferred ornaments were quality dependent (Fig. 8). Similar analyses of the causal mechanisms of sexual selection could also be applied to empirical data to obtain a more nuanced picture of the mechanisms of sexual selection (31).

In contrast to many previous models of sexual selection (e.g., refs. 14, 15, 18), we assumed that female preferences are not costly in themselves but that sampling multiple potential mates reduces female fecundity. This is consistent with the viewpoint that mating preferences often co-opt existing sensory and cognitive machinery rather than requiring additional investment in costly structures (7, 8). When the fecundity costs of mate search were low—as we might expect, for example, in lekking species—females sampled additional mates, regardless of which type of indirect benefit was available. In contrast, highly costly mate search was only possible when at least some ornaments provided information about mate quality. Our results consequently suggest that, in species where females invest strongly in mate search (e.g., by traveling great distances to sample multiple males), we should expect to see either direct benefits or quality-dependent male ornaments. Intriguingly, however, elaborate Fisherian ornaments could still evolve when mate search

was costly, as long as quality-dependent ornaments were also present to offset the costs of search. Fisherian ornaments could thus piggyback on the mate-search effort that evolved in response to unrelated male ornaments. The same kind of piggybacking by Fisherian ornaments might also be possible when costly mate search is maintained by variation in direct benefits; however, we did not model this possibility here.

Two key assumptions of our model regarding the genetic basis of ornament expression are worth highlighting. First, we assume that ornament genes code for a fixed survival cost of ornament expression rather than a fixed material investment. In other words, two males carrying the same ornament investment genes will not necessarily produce ornaments of the same size, but rather such that their mortality cost due to ornament production is the same. This automatically leads to quality-dependent expression of handicap ornaments, because higher-quality males can produce larger ornaments for the same survival cost. Future studies could explicitly model the evolution of the reaction norm relating male quality to ornament investment (as in ref. (17)). Second, our model assumes that male ornamentation can evolve de novo without correlated expression in females. This is plausible if the genes underlying such ornaments are located on sex chromosomes or if new ornaments are linked to existing hormone pathways. However, the majority of novel ornaments are likely expressed in both sexes, often to similar degrees, at least until sex-linked expression has a chance to evolve secondarily (44). Any costs of monomorphic ornaments will also be carried by females,



**Fig. 7.** Causal diagram for relationships between traits, fitness components, and fitness in females (A) and in males (B). Single-headed arrows indicate causal effects, whereas double-headed arrows indicate spurious associations arising from genetic correlations. Phenotypic traits:  $w_f$  = female fitness;  $F$  = female fecundity;  $m$  = (genes for) female mate-search effort;  $x$  = (genes for) male ornament investment;  $p$  = (genes for) female preference strength;  $q$  = quality;  $w_m$  = male fitness;  $MS$  = male mating success;  $V$  = male viability;  $T$  = male ornament size.

potentially hindering the emergence of new ornaments. We expect that such barriers will disproportionately affect Fisherian ornaments, for which the modest indirect benefits may not be sufficient to offset costs of ornamentation in both sexes. Future models could take such genetic constraints into account.

The causal mechanisms of sexual selection are complex and likely differ among species, between the sexes, among traits, and even for particular traits over time (7, 19–21). Our results additionally underscore that multiple mechanisms can act simultaneously on the same traits (29). All this complexity belies rich and fascinating patterns, many of which are yet to be fully uncovered. We believe that the time has come to develop a more nuanced theory of sexual selection that both quantifies and explains systematic variation in the relative importance of the underlying causal mechanisms. This should include pinning down the effects of key variables, including the mode of fertilization, the mating and parental care systems, ecological variables (e.g., population density and encounter rates), and primary sensory modalities. On the empirical side, ongoing technological advances (e.g., in next-generation sequencing and automated phenotyping) will facilitate the kind of large-scale data collection to which more nuanced causal analyses can be applied. In addition, the ability to genetically engineer novel ornaments into laboratory populations will shed light on the early stages of aesthetic coevolution, which are otherwise difficult to study in an empirical setting.

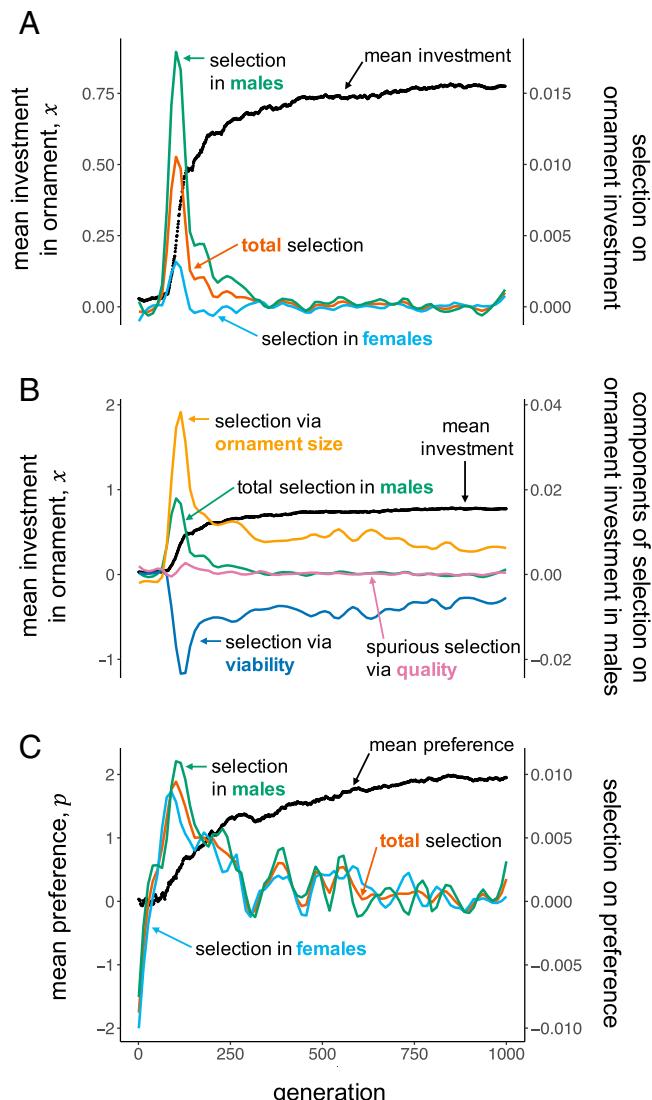
## Materials and Methods

We simulated a population of  $N$  individuals with equal nos. of males and females at maturity (see *SI Appendix* for simulation code written for Julia v1.6: (45); all simulated data used to generate figures is available on Dryad (46). Generations are nonoverlapping and there is a single breeding season per generation. We tracked the evolution of four types of trait:

- i. male investment  $x = [x_1, \dots, x_n]$  in each of  $n$  distinct ornaments,
- ii. female preferences  $p = [p_1, \dots, p_n]$  for these ornaments,
- iii. female mate-search effort  $m$ , and
- iv. male or female quality  $q$ .

The size of a male's  $j$ th ornament depends on his investment  $x_j$  in that ornament and may also depend on his quality. The nature of this relationship is ornament specific, allowing us to compare the evolution of Fisherian, handicap, and indicator ornaments. A male's viability decreases with his investment in ornaments. Each breeding female chooses her mate from a randomly chosen subset of viable males (suitors), where the no. of suitors increases with her mate-search effort. Her preferences determine how likely each suitor is to sire her offspring. Preferences may favor larger or smaller values of any given ornament or be indifferent to ornament size. We assume that mating is entirely under female control (i.e., males are unable to coerce matings or otherwise override female choice). A female's fecundity increases with her quality but decreases with her mate-search effort. This means that mate search is costly; on the other hand, preferences themselves are cost-free. We now consider each of these processes in more detail.

**Genetics and Inheritance.** We assume diploid inheritance. Genes for all traits are carried by both males and females, even where expression is sex limited. The value of each trait is determined by a single locus. There are thus  $n$  loci for ornament investment,  $n$  preference loci, one mate-search locus, and one quality locus ( $2n + 2$  loci in total). Each allele is represented by a real number,



**Fig. 8.** Exemplary causal analysis of selection on male investment  $x$  and female preference  $p$  for a single handicap ornament, based on a single simulation run over 1,000 generations. Total selection is given by the average of selection in each sex (A and C). Selection on investment in males can be partitioned into selection via ornament size, selection via viability, and spurious selection via quality (B). All selection estimates were smoothed via LOESS regression using the “geom\_smooth()” function in the R package ggplot2 with the smoothing parameter “span = 0.1” (55).

following a continuum-of-alleles model. Trait values are given by the arithmetic mean of the two allelic values at the corresponding locus. Negative values for ornament investment, mate-search effort, and quality (but not preference) are rounded up to zero. At the beginning of each simulation run, values for each allele are drawn from a normal distribution with trait-type-specific means ( $\bar{x}_0$ ,  $\bar{p}_0$ ,  $\bar{m}_0$ ,  $\bar{q}_0$ ) and SDs ( $d_x$ ,  $d_p$ ,  $d_m$ ,  $d_q$ ).

We assume fair meiosis and perfect recombination, such that a parent passes on either allele copy at a given locus with a probability of one-half, independently of inheritance at the other loci. All genes are subject to random mutation that adds a normally distributed random variable to the current allele value. Mutations occur with trait-type-specific probabilities  $\pi$  per allele per generation, and their effects are distributed with trait-type-specific means  $\mu$  and SDs  $\sigma$ . This results in 12 parameters:  $\pi_x$ ,  $\pi_p$ ,  $\pi_m$ ,  $\pi_q$ ,  $\mu_x$ ,  $\mu_p$ ,  $\mu_m$ ,  $\mu_q$ ,  $\sigma_x$ ,  $\sigma_p$ ,  $\sigma_m$ , and  $\sigma_q$ . Importantly, we assume that mutations affecting ornaments, preferences, and mate-search effort are unbiased (i.e.,  $\mu_x = \mu_p = \mu_m = 0$ ), whereas mutations in quality are negatively biased (i.e.,  $\mu_q < 0$ ). This reflects the viewpoint that most mutations in traits closely linked to fitness are deleterious. The quality locus in our model serves as a simplified stand-in for the presumably many loci at which mutations may affect an individual's overall quality (47).

**Ornament Size in Relation to Quality and Investment.** The size of a male's  $j$ th ornament depends on his investment  $x_j$  in that ornament and potentially also on his quality, according to ornament-specific functions. For a male of quality  $q$  in a population with average male quality  $\bar{q}$ , ornament size is given by

$$T_j(x_j, q, \bar{q}) = Q_j(q, \bar{q})l_j(x_j). \quad [1]$$

Negative ornament sizes are rounded up to zero. We write  $T$  for the vector of a male's ornament sizes, with elements given by  $T_j(x_j, q, \bar{q})$ .

The factor  $Q_j(q, \bar{q})$  determines how ornament size changes with individual quality and is given by

$$Q_j(q, \bar{q}) = 1 + c_j(q - \bar{q}). \quad [2]$$

The parameter  $c_j \geq 0$  is ornament specific. If  $c_j$  is large, then ornament expression is highly quality dependent, whereas  $c_j = 0$  implies that ornament expression is independent of quality. For quality-dependent ornaments ( $c_j > 0$ ), we assume that higher-quality males always express larger ornaments given fixed values of the investment trait  $x_j$ . This assumption is justified by the broad conditions favoring quality-dependent ornament expression (34) while avoiding the need to explicitly model the evolution of quality dependence here. Note that the dependence on  $\bar{q}$  in Eq. 2 ensures that a fixed investment by a male of average quality will produce an ornament of the same size, regardless of quality dependence  $c_j$ . This allows for a more informative comparison of ornaments with varying levels of quality dependence.

The factor  $l_j(x)$  determines how ornament size responds to investment and is given by

$$l_j(x_j) = \frac{1}{b_j} (1 - e^{-b_j x_j}). \quad [3]$$

If  $b_j$  is small, then ornament size increases roughly linearly with investment. If  $b_j$  is large, then increases in ornament size are strongly diminishing as investment increases. The function  $l_j(x)$  was chosen so that its slope at zero  $l'_j(0)$  does not depend on the choice of  $b_j$ . This means that, for low levels of male investment, all traits end up being equally salient to females, all else being equal. However, we also allow for ornament-specific salience biases (see Eq. 6 below).

We classify traits as Fisherian if they are independent of male quality ( $c_j = 0$ ) and continue to grow strongly with increasing investment ( $b_j$  is small). In contrast, handicap and indicator traits are both quality dependent ( $c_j > 0$ ). Handicap traits grow strongly with increasing investment ( $b_j$  is small), whereas indicator traits face strongly diminishing returns ( $b_j$  is large) (see Fig. 1 and default parameter values in Table 1) (35–37).

**Fecundity, Viability, and Mate Choice.** Each generation, we repeatedly sample breeding females from the population with replacement. Each chosen female produces a single offspring, and sampling continues until a total of  $N$  offspring have been produced. The probability that a female is chosen is proportional to her fecundity, which is given by

$$F(q, m) = q(1 - km^2). \quad [4]$$

Negative values of  $F(m)$  are rounded up to zero. Note that fecundity increases with a female's quality  $q$  but decreases with her mate-search effort  $m$ . The parameter  $k$  determines the cost of mate search.

Each breeding female chooses her mate from among a randomly chosen subset of suitors. The no. of suitors is given by  $1 + M$ , where  $M$  is a Poisson-distributed random variable with mean  $m$ . Thus, we assume that all females seek out a minimum of one suitor, regardless of the value of  $m$ . In particular, this means that there is no "wallflower effect" in our model (48). Suitors are sampled with replacement from the population in proportion to their viability.

We assumed that a male's viability depends on the sum of his investments  $\|x\| = \sum_{j=1}^n x_j$  in each ornament, according to

$$V(x) = \max[0, 1 - \|x\|^2]. \quad [5]$$

This assumption might hold, for instance, if ornament investments draw from a common resource pool that is also essential for survival (34). For a male to be viable, his total investment must obey  $\|x\| < 1$ .

The probability that a breeding female's offspring are sired by any particular suitor is proportional to her "rating" of that male, which is a function of her preferences and his ornaments. In addition, ratings depend on the saliency of each ornament, which arises from the interaction between ornament expression and female perceptual and cognitive systems. We assume that ornaments may differ in their saliency to females, even when their sizes  $T_j$  are identical. We implement this assumption by assigning saliency coefficients to the  $n$  ornaments, represented by a vector  $s$  with positive entries. A higher saliency coefficient means that an ornament stands out more to females and is consequently given greater weight in female ratings. A female with preferences  $p$  assigns a male with ornaments  $T$  the following rating:

$$R(p, T) = \exp\left(\sum_{j=1}^n s_j p_j T_j\right). \quad [6]$$

This is an extension of Lande's "psychophysical" model of preferences (13).

**Causal Analysis.** We analyzed the causal structure of selection acting on investment in the male ornament  $x$  and on female preference  $p$  (see causal diagram in Fig. 7). For simplicity, we performed causal analyses on the output of simulations in which only a single ornament and preference coevolved ( $n = 1$ ). From Stein's lemma (31, 49, 50), if  $z$  is a normally distributed trait, then selection on  $z$  can be expressed in terms of the average marginal association  $\frac{d}{dz}\mathbb{E}(w | z)$  between  $z$  and fitness:

$$\text{cov}(z, w) = \sigma_z^2 \mathbb{E}\left(\frac{d}{dz}\mathbb{E}(w | z)\right). \quad [7]$$

The marginal association can, in turn, be partitioned into the marginal causal effects of  $z$  on fitness (i.e., the extended selection gradient,  $\eta_z$ ) and the marginal spurious association between  $z$  and fitness (31, 51, 52). The latter arises via non-causal pathways, including via genetic correlations between  $z$  and other traits that are not causally influenced by  $z$ . Let us write  $B$  for a set of traits that blocks all noncausal paths between  $z$  and fitness (i.e., a backdoor set) (53). We can then write (31)

$$\mathbb{E}\left(\frac{d}{dz}\mathbb{E}(w | z)\right) = \underbrace{\mathbb{E}\left(\frac{\partial}{\partial z}\mathbb{E}(w | z, B)\right)}_{\text{extended selection gradient } \eta_z} + \underbrace{\int \mathbb{E}(w | z, B) \frac{d}{dz} d\mathbb{P}(B | z)}_{\text{spurious selection}}. \quad [8]$$

The extended selection gradient  $\eta_z$  represents selection arising from (direct or indirect) causal effects of  $z$  on fitness (51, 52). It can be partitioned in turn into selection components arising via particular causal pathways (see Eq. 11 below). Although Eq. 7 only holds for normally distributed traits  $z$ , Eq. 8 provides an informative breakdown of selection, even for nonnormal quantitative traits.

To apply this framework to the output of our model, we first calculated genic values  $x$ ,  $p$ ,  $m$ , and  $q$  for all individuals, regardless of sex. The genic values correspond to the phenotypic trait value that an individual's genotype would express if the individual were of the relevant sex. In the current model, the genic values for preference are equivalent to breeding values; for the other traits, the genic values approximately equal breeding values if the proportion of negative-valued alleles is low. Since genes spend equal time in males and females, selection on a trait  $z$  is given by the average strength of selection in males and in females:

$$\text{cov}(z, w) = \frac{1}{2} [\text{cov}(z, w_f) + \text{cov}(z, w_m)]. \quad [9]$$

Let us first consider selection on investment in the male ornament  $x$ . In males, quality  $q$  blocks all backdoor paths from  $x$  to fitness. We can thus write

$$\mathbb{E}\left(\frac{d}{dx}\mathbb{E}(w_m | x)\right) = \underbrace{\mathbb{E}\left(\frac{\partial}{\partial x}\mathbb{E}(w_m | x, q)\right)}_{\text{extended selection gradient } \eta_x} + \underbrace{\int \mathbb{E}(w_m | x, q) \frac{d}{dx} d\mathbb{P}(q | x)}_{\text{spurious selection on } x \text{ via associations with } q}. \quad [10]$$

We can then further partition the extended selection gradient on  $x$  into selection via viability  $V$  and selection via ornament size  $T$ , as follows (31):

$$\eta_x = \underbrace{\mathbb{E}\left(\mathbb{E}(w_m | V, T) \frac{dV}{dx}\right)}_{\text{selection on } x \text{ via } V} + \underbrace{\mathbb{E}\left(\mathbb{E}(w_m | V, T) \frac{\partial T(x, q)}{\partial x}\right)}_{\text{selection on } x \text{ via } T}. \quad [11]$$

We can thus partition selection on ornament investment into four components:

- (in males) sexual selection via the effect of investment  $x$  on male ornament size  $T$ ,
- (in males) viability selection via the effect of  $x$  on  $V$ ,
- (in males) spurious selection via the association between investment  $x$  and quality  $q$ , and
- (in females) spurious selection via the association between  $x$  and female fitness, which arises via covariation between genes for  $x$ ,  $q$ , and  $m$ .

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Similarly, selection on preference genes  $p$  can be expressed in terms of associations with female fitness (via genetic correlations between  $p$ ,  $q$ , and  $m$ ) and male fitness (via correlations between  $p$ ,  $q$ , and  $x$ ). Note that, in the current model, there is no causal effect of preference genes on the no. of offspring an individual produces during their lifetime; this is the quantity we refer to throughout as "fitness." However, preference expression by females can increase the reproductive value of their offspring, which might be included under a more general definition of fitness.

For each simulated generation, we estimated the above selection components using the observed distributions of trait values and fitness components. We assumed the qualitative causal structure depicted in Fig. 7 but did not take into account the functional relationships among variables that were used to construct the simulations. We thus treated the simulation results analogously to empirical data, which typically are obtained without a detailed quantitative understanding of the data-generating process. Expressions like  $V(x)$ ,  $T(x, q)$ , and  $\mathbb{E}(w_m | V, T)$  were estimated using thin-plate regression splines in the R package mgcv (54), with all bivariate functions fitted using bivariate splines. We then smoothed these estimates with respect to generation using LOESS regression (R package ggplot2) (55).

**Data, Materials, and Software Availability.** All simulated data that were used to generate figures are available on Dryad (46). See *SI Appendix* for simulation code written for Julia v1.6.

**ACKNOWLEDGMENTS.** J.M.H. was supported by the German Federal Ministry of Education and Research (BMBF). We are grateful to K. Fitzsche for helpful discussions.