Evolution of sexual cooperation from sexual conflict

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In many species that form pair bonds, males display to their mate after pair formation. These displays elevate the female's investment into the brood. This is a form of cooperation because without the display, female investment is reduced to levels that are suboptimal for both sexes. The presence of such displays is paradoxical as in their absence the male should be able to invest extra resources directly into offspring, to the benefit of both sexes. We consider that the origin of these displays lies in the exploitation of preexisting perceptual biases which increase female investment beyond that which is optimal for her, initially resulting in a sexual conflict. We use a combined population genetic and quantitative genetic model to show how this conflict becomes resolved into sexual cooperation. A cooperative outcome is most likely when perceptual biases are under selection pressures in other contexts (e.g., detection of predators, prey, or conspecifics), but this is not required. Cooperation between pair members can regularly evolve even when this provides no net advantage to the pair and when the display itself reduces a male's contributions to raising the brood. The findings account for many interactions between the sexes that have been difficult to explain in the context of sexual selection.

cooperation | differential allocation | sensory bias | sexual conflict | sexual stimulation

In pair-bonding species, displays between the sexes often continue after pair formation (1). Ethologists have long argued that a main function of ongoing displays by males is to bring the females into, and maintain them at, prime reproductive condition (2–4) as corroborated by many subsequent experiments (5). Nevertheless, it is unclear why such displays evolve because the pair as whole should benefit if the male were to direct his energy into the brood, rather than display. To date, explanations have been focused on display maintenance rather than origination and are based on the idea that display intensity correlates with mate quality (6, 7). Notably, the differential allocation hypothesis states that if a female is paired with a high-quality male, she is under selection to invest more in the brood than when paired with a low-quality male (6–12) and that male displays are present because they indicate male quality to the female, which she cannot otherwise observe. Here we show how displays may regularly become established and maintained even in the absence of differential allocation, with their role simply to bring females into optimal reproductive condition.

Our model is predicated on the many experimental studies in birds which show that exaggeration of a male behavior, color, or vocalization stimulates females to increase their investment (*SI Appendix*, Table S1) (13, 14). The origin of such stimulatory effects is thought to lie in perceptual biases, arising from "properties of the environment, signals and neural systems" (15). More than 100 examples of such biases are now known from all of the major sensory systems (sound, sight, and smell) (16). When a male display exploits a perceptual bias that causes a female to increase her investment in her offspring, it can provide an advantage to the male but be detrimental to the female because it reduces her future reproductive success. This is a sexual conflict: the male display starts to increase in the population, but females are under selection to resist the display (17, 18). Such conflicts have been modeled using computational approaches (i.e., neural nets) (19, 20). In these models a signaler, which in our case is the male, exploits a receiver's perceptual bias by producing displays that stimulate the receiver to the receiver's detriment. At some point in the future a mutation in the receiver (female) population leads to a failure to be stimulated by the display (19). This mutation increases, raising female mean fitness, reducing male mean fitness, and leading to the subsequent loss of the display. As these evolutionary adjustments continue, new biases arise, and the process starts over. Because each sex increases its fitness at the expense of the other, the fitness of both sexes is not simultaneously maximized.

Here we consider a route by which such conflicts evolve into a stable cooperative system. We follow Mesterton-Gibbons and Dugatkin (21) in defining cooperation as an outcome that despite individual costs is good in some appropriate sense for the members of a group and whose achievement requires collective action. Other definitions have required cooperative acts to have evolved specifically for the benefits they provide (22), but this precludes behaviors that originate out of conflict, the focus of this study. The essential idea is that selection on female investment returns her investment to its optimal level, even as females continue to respond to the display (1). Suppose a male display increases in the population because it causes females to lay more eggs in their clutch (Fig. 1). Clutch size is now above the female optimum so females that do not respond to the novel display are favored. In one outcome, resistance to the display evolves, as in models of sexual conflict (lower right arrow, Fig. 1).

Significance

The past 50 y have seen much research on sexual selection. However, in many species, displays between the sexes continue long after pair formation, even if pairs have been together for years. As shown experimentally, such displays result in cooperation between the sexes, whereby displays by one partner affect investment into the brood by the other. How one gets to this cooperative outcome is not understood. We show such outcomes evolve if a novel display exploits a preexisting sensory bias that raises receiver investment. Once established, displays are maintained because they are required to stimulate the partner optimally. The pair bond is strengthened, and displays between the sexes accumulate over evolutionary time, even in the absence of sexual selection.

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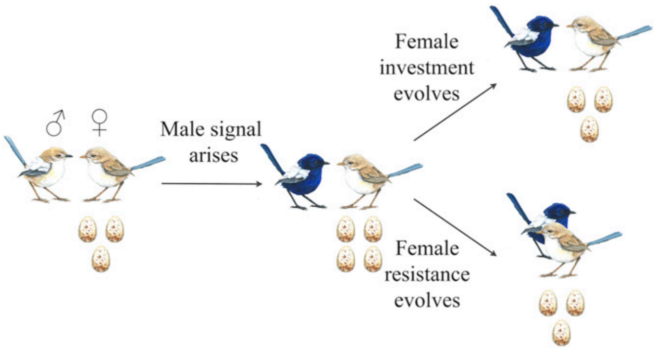

Fig. 1. Alternative outcomes when appearance of a novel male display causes a female to invest above optimal levels. (*Left*) Ancestrally, females invest optimally by laying 3 eggs in a clutch. Males do not display in an exaggerated manner to the female and have little ornamental plumage. (*Center*) A male develops ornamental blue plumage associated with a display to his mate, stimulating her to invest more in the brood (4 eggs). The display increases the male's fitness but lowers that of his mate. (*Lower Right*) In traditional models, the engendered sexual conflict results in females evolving to ignore the new display (males should subsequently lose the display as it provides no benefit). (*Upper Right*) Instead, we consider an alternative outcome whereby investment evolves back to the female optimum even as females respond to the display. In this case the display is retained because without it females would produce fewer than the optimal number of eggs, detrimental to both sexes. Illustration courtesy of Allison Johnson (artist).

However, an alternative possibility is that a clutch size above the female optimum generates selection on females to reduce their investment, even as they continue to respond (upper right arrow, Fig. 1). In this second case, investment of responding females may evolve back to what it was before a display arose. This becomes a cooperative system that is evolutionary stable, because a mutation that causes the male to display at a lower rate will reduce female investment below that which is optimal for either sex.

Results

We evaluate conditions under which the alternative outcomes in Fig. 1 are expected, based on a mathematical model with haploid genetics. A quantitative trait with mean $\bar{z}_f$ describes basal female investment in her clutch (all symbols are defined for easy reference in the text, in the legend to Fig. 2 and *SI Appendix*, Table S2). The mean is initially allowed to evolve to its optimum, $\bar{z}_{opt}$, which depends on both the fecundity benefit of the investment (number of surviving offspring) and its viability cost to females (c_f). The viability cost is paid after reproduction, implying some females survive to breed to the following year, resulting in overlapping generations (*Methods* and *SI Appendix*, Fig. S1). A novel male display and the female response to it are each modeled by freely recombining, diallelic, single-locus modifiers, thus combining quantitative and population genetic approaches (23, 24). At the locus which controls a response in females, **A**, there is initially a high frequency of the responder allele (A_2), corresponding to the existence of a preexisting perceptual bias (the nonresponder allele A_1 is at a low frequency). The display locus **B** is initially fixed for the allele for no display, B_1. We then introduce the allele B_2 that causes a male to display. The male display comes with a viability cost to the male (s_m) but elevates investment of an A_2 female partner by a value α. For example, α may represent extra eggs laid by a responding female (Fig. 1), but increased investment could also come through provisioning and other positive effects she may have on her offspring (*SI Appendix*, Table S1). Consequently, a pair in which the male carries the display allele and the female carries the responder allele (i.e., A_2B_2 pairs) have extra female investment and hence higher fecundity than the other 3 combinations. The number of offspring surviving to breed the next year is affected by density dependence within the brood (mediated by parameter a), and density dependence after fledging (b), driven by total population size.

After offspring production males and females undergo mortality determined by their investment in the brood (c_m and c_f, respectively), the cost of display (s_m), and a nonselective extrinsic death rate (d_m for males and d_f for females). Surviving pairs may then undergo divorce, at a constant rate (v). Death and divorce result in males and females not always being paired to the same partner each year, which is a necessary condition for sexual conflict. Widows, widowers, juveniles, and any formerly single individuals (extras of the more common sex after pairing) combine to form new mated pairs, and the yearly cycle is complete (see *Methods* for the full presentation of the equations). We

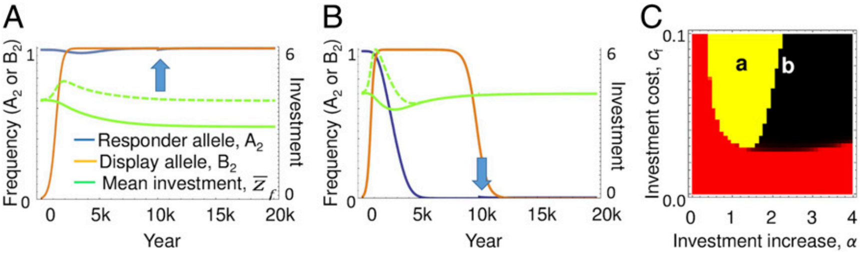

Fig. 2. Evolution of display, responder, and investment. (*A*) The responder allele, A_2, starts at high frequency (0.99). A display allele B_2 is introduced at low frequency (0.01). Basal investment (green), $\bar{z}_f$, represents mean female investment without the added effects of the response to the male trait (α); dashed green line is mean realized investment. We confirm stability of the equilibrium by introducing a perturbation (frequency of $A_1 = 0.01$) at 10,000 y (blue arrow). Parameters are as follows: $\alpha = 1.2$, viability cost to males of displaying; $s_m = 0.01$, scaled cost of investing in eggs for females; $c_f = 0.08$ and for males, $c_m = 0.01$, nonselective density dependence in the brood before fledging; $a = 0.09$ and after fledging, $b = 0.00007$, nonselective mortality rate for both females and males; $d_f = d_m = 0.1$, divorce rate; $v = 0.3$, heritability of z_f; $h^2 = 0.5$, phenotypic variance of z_f; $\sigma^2 = 1$, recombination rate between the display and responder loci; $r = 0.5$. (*B*) Case in which the additional investment, $\alpha = 2.4$, induces a level of investment too high for females to sustain the response, A_2, before the quantitative investment trait z can respond. The responder A_2 is lost, and the display allele B_2, which evolves to be close to fixation when the responder is still present, is slowly lost due to selection against the display. Perturbation at 10,000 y (A_2 reintroduced at a frequency of 0.01) confirms stability. (*C*) Alternative outcomes after 100,000 y as a function of costs of female investment, c_f, and investment induced, α. Perturbations occur every 10,000 y to reintroduce at frequency of 0.001 any allele that is within that frequency of loss. The points a and b correspond to the parameters of the dynamic panels to the left. In the yellow region, display (B_2) and responder (A_2) alleles are fixed. In the red region, display never increases, and the responder allele remains at high frequency (A_2 and B_1 high). In the black region, cost of the induced female response causes the responder allele to be lost, followed by loss of the display (A_1 and B_1 high). See https://powers.shinyapps.io/pqreadr/ (*SI Appendix*, Fig. S4), for a complete interactive version of both panels of this figure, where the effect of altering the parameters can be examined and both initial and equilibrium basal clutch size are listed.

assume random mating at pairing and strict social and genetic monogamy, thereby removing all forms of sexual selection (i.e., selection associated with competition for mates).

We find that a stable equilibrium can indeed be attained where all males display and all females respond to the display. At equilibrium, realized investment is restored to the same value as it was prior to the display appearing (as in Fig. 1, *Top Right*; in our evaluations of long runs, initial investment and investment at the end of the run differed only at the sixth decimal place). An example of the evolutionary dynamics is shown in Fig. 2*A*, where investment back to the optimum for females results from evolution of the quantitative investment trait (dashed green line is realized investment, and solid green line is investment as it would be stripped of any female responses). An example of the alternative outcome where the sexual conflict results in loss of responder and display is shown in Fig. 2*B*. In Fig. 2*C* we delineate the role of 2 parameters in affecting these outcomes: the increase in investment promoted by the display α and the costs to the female of investment, c_f. In the red region, the display never increases because its costs outweigh the benefits. In the yellow and black regions the display rises in frequency, resulting in increased costly investment by the female. In the yellow region, the response to this selection occurs by reduction in the quantitative investment trait, resulting in the permanent fixation of both the display and responder alleles. In the black region, where there is higher induced investment by the responding females, the responding allele is quickly lost, followed by the display, as in traditional sexual conflict models (Figs. 2*B* and 1, *Lower Right*).

The roughly vertical border between the red and yellow regions represents the point where benefits to males of extra investment by the female balance the costs of the display, such that the display is too costly in the red region. The horizontal border separating the yellow and black regions from the red one arises similarly but for a subtler reason. When female costs of investment c_f are low, optimal investment $\bar{z}_{opt}$ is relatively high, and hence, female investment is high at the initial conditions. The consequence is that a display gives the male a proportionally smaller benefit from the investment it induces, again countered by its costs. The parameter space over which the display and response are fixed (yellow) varies depending on the strength of selection and genetic variance in the responder allele. For example, when the initial frequency of the responder allele is 0.9, instead of the frequency of 0.99 shown in Fig. 2, introduction of a display results in more efficient selection against responders (initial genetic variance is higher), and the black region extends farther to the left (*SI Appendix*, Fig. S2).

Selection on Perceptual Biases. The model so far assumes that perceptual biases are not subject to any selective forces other than those which affect their response to the display. In fact, many biases are thought to be present because they facilitate predator, prey, or conspecific detection (15, 16, 25). A small selective advantage (e.g., a viability advantage of $s_p = 1\%$) favoring the responder allele, A_2, increases the parameter space that allows the permanent fixation of the display (compare Fig. 2*C* with Fig. 3*C*). If both induced investment α and costs to investment c_f are high, the display, response, and to a slight extent investment may cycle, depending on the frequency of perturbations (Fig. 3*B*), as follows. First, when the display is absent, natural selection maintains the responder allele at high frequency. Consequently, an introduced display will increase. Next, the responder allele declines because of high costs of investment, which overwhelm its natural selection advantage. Once the responder allele is at a low enough frequency, the display declines as it gives little advantage to males. When the display is at a sufficiently low frequency, a mutation favoring the response increases under natural selection, and the cycle is repeated.

Fecundity Selection on Males. Male displays may become established even if they come with a cost that reduces male investment into the current brood (parameterized by s_{fec}), thereby directly affecting both male and female fitness rather than reducing the male's survival. Outcomes across parameter space are similar whether costs to the male affect fecundity or viability (Fig. 4). In the fecundity case, when the display is fixed (in yellow), all males are now investing less into the brood than they were prior to the introduction of the display. In this case, female investment evolves to be greater than it was before the display was present ($\bar{z}_f + \alpha$ is higher than was $\bar{z}_f$ prior to the evolution of the display). A higher female investment when male display costs operate through fecundity rather than viability raises the average number of offspring fledged per pair, but this does not completely compensate for the lower number of offspring fledged per pair due to the presence of the display. Increased female investment over time raises the average number of offspring fledged per female but reduces mean female viability, resulting in a new balance between these 2 forces, where the average number of offspring is lower than both the viability case and the initial conditions. For example, for the parameters of Fig. 2*A*, with male display imposing a fecundity cost of 1%, rather than a survival cost, female investment is raised by 1.3%, female mortality is increased by 0.5%, and offspring fledged per pair are reduced by 0.16%, compared to the viability case.

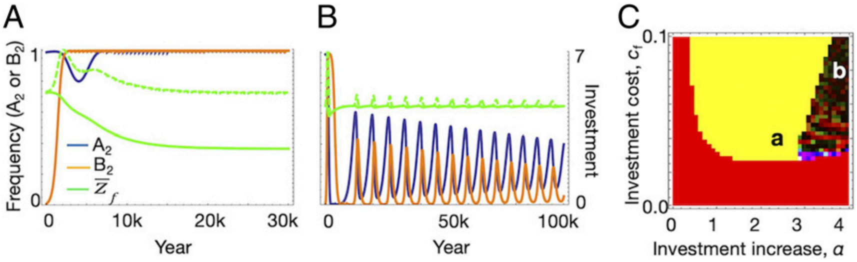

Fig. 3. Natural selection on the perceptual bias. Here natural selection favors the responder allele, A_2 ($s_p = 0.01$). As in Fig. 2 the responder allele is initially at a frequency of 0.99 and the display allele introduced at a frequency of 0.01. If close to fixation or fixed, both the display and responder alleles are perturbed away by 0.01 for *A* and *B* and 0.001 for *C*, every 500 y. (*A*) $c_f = 0.04$, $\alpha = 2.5$. (*B*) $c_f = 0.08$, $\alpha = 4$. All other parameters are as in Fig. 2. (*C*) Colors are as in Fig. 2 with the yellow region indicating permanent fixation of the display. The colors represent a snapshot of the frequency of the display allele (green channel) and responder allele (red channel) as they were at 10,000 y. A blue overlay indicates strong cycling, where A_2 and B_2 were simultaneously low (<0.2) and then simultaneously high (>0.8). The cycling is induced by reintroduction of the display/responder alleles. Labels a and b are the positions for the dynamic runs illustrated in the corresponding panels. It can be seen that the cycles in *B* are dampening; an extended run shows that there are eventually polymorphisms at both the A and B loci with these parameters. Note that both points a and b are in the black region of Fig. 2*C*, so without selection on the perceptual bias the display would not be established.

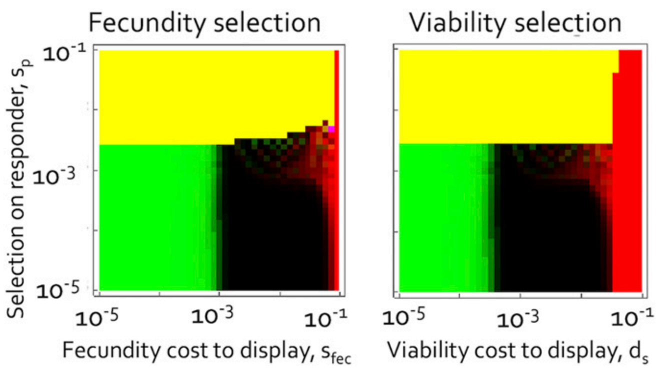

Fig. 4. Comparison of fecundity and viability costs to the display. The responder allele is initially at a frequency of 0.99, the display allele is at a frequency of 0.01, and perturbations to a frequency of 0.001 occur every 500 y. Selection coefficients are plotted on a log scale. In the yellow region, both display and responder alleles are permanently maintained through their effects on investment. In the red region, the display is lost. A region of cycling at the display and responder loci is indicated by the stippling. In the black region both responder and display alleles are lost, as in the green region, but here the display initially rises to a high frequency and is lost only slowly. Parameters are as in Fig. 2 but with $c_f = 0.07$, $\alpha = 2.3$. (*Left*) Fecundity selection on the male display. (*Right*) Viability selection on the male display.

Cooperation Can Arise Directly in Changing Environments. Finally, we identified a situation in which displays promoting investment become established under a particularly broad range of parameter space because benefits immediately accrue to the female (*SI Appendix*, Fig. S3). This happens if mean female investment is initially below the optimal level, e.g., as a consequence of a changing environment. Then a male's display that increases her investment also increases her fitness. The display is immediately cooperative, and it can be subsequently maintained at equilibrium. The fact that displays and responses may more easily become established in changing environments than in static ones suggests they can contribute to speciation events, which may often be associated with entry into novel environments (26). We caution that our conclusion that establishment may be easier under these conditions is based on a broadening of the parameter space under which we get the fixation of display, but the question of what parameter spaces are reasonable is always an empirical one, and we encourage further study of these conditions.

Discussion

Our models show that a simple explanation for the presence of displays after pairing is that they are required to stimulate females to invest adequately in offspring, as has long been proposed (1–3). Here we show how such a requirement could evolve. In words, male displays induce the female to overinvest thereby placing selection on females to reduce their investment. Provided a reduction can be made by evolution at loci affecting investment, rather than loci affecting response to the display, there is the possibility for both the male display and female response to be maintained. Under such conditions, the male display is now required to optimally stimulate the female. We find this outcome is most likely when costs to female investment are high, but levels of investment induced by the display are moderate. On the other hand, when both costs and the induced investment by a displaying male are high, strong selection against the responder allele results in its loss, as in standard sexual conflict models. We explored this process using a model which assumes that the responder and display are determined by single loci of large effect. Large-effect loci are realistic for some visual display traits (27). An alternative approach would be a full quantitative genetic model, which would require an additional set of simplifying assumptions. Qualitatively, we expect to find similar outcomes, especially when a perturbation in the display induces at least a moderate increase in investment. Specifically, in the continuous formulation, if the mean display is perturbed, then this will induce selection on loci affecting both investment and response, and both should evolve. To the extent investment evolves, we expect at least some element of the display and response to be maintained to raise investment back to the optimal level.

A complementary explanation for the presence of displays after pairing assumes they are present to indicate male quality. In this idea, a female increases her investment when paired to a male with an exaggerated display because he is likely to be of high quality, which her offspring will inherit (6, 7). Theoretical models demonstrate that elevated female investment when paired to a high-quality male is expected in some situations, but in other cases the adaptive solution is no change in investment, or a reduction, because high-quality males may invest more, which compensates (8–10). We suggest mate stimulation may explain many of the experimental findings documented in *SI Appendix*, Table S1, without recourse to differential investment arguments. Nevertheless, if differential investment is important, our results provide a model for how it may evolve. Once costly displays have become established, they are generally under selection to become condition dependent and thereby correlate with male quality (28).

Any evolutionary model necessarily comes with assumptions about the spectrum of permissible mutations. It is possible to devise scenarios whereby mutations we have not allowed would destroy the displaying equilibrium. For example, a reader suggested that after the displaying equilibrium is reached, a mutation that causes a female to ignore the male but maintain optimal investment should be favored because such a mutant would not underinvest when paired with a weakly displaying male or overinvest when paired with a strongly displaying male. It remains an empirical question as to whether such mutations, or others along similar lines, are plausible. We consider this particular example to be unlikely because of the pleiotropic effects implied: if a mutation causes the female to ignore the male display, we expect this to also lower her investment, as we have modeled. In consequence the mutation would have to simultaneously increase investment to exactly compensate for the loss due to lack of male stimulation. Even if mutations such as these do occur, they need not be favored. For example, the female may be less able to assess the optimal clutch from environmental cues than from the male, or evolution subsequent to the establishment of the display may have resulted in other selective pressures favoring its maintenance, as would be the case if differential allocation secondarily evolves.

In the model we have eliminated all forms of sexual selection, that is, selection associated with competition for mates. In reality, both sexual selection and sexual stimulation are present in many species. Often the same displays and traits are employed in both cases, presumably because perceptual biases influence both attraction and stimulation, as exemplified by several of the studies in *SI Appendix*, Table S1. Given this reasoning it is possible that in sexually selected systems, females are not only choosing displaying males but also being reproductively stimulated by viewing displays. A link between stimulation and preference provides a novel explanation for the lek paradox, which asks how female mating preferences can be maintained in the absence of obvious benefits to choice (29). We suggest direct benefits may be present in the form of the reproductive stimulation display imparts to females. For example, in a controlled experiment in the peafowl *Pavo cristatus,* attractive males induce females to lay larger eggs containing more testosterone (30). The inference is that in the absence of peafowl display they would underinvest in their fecundity.

We have shown how sexual conflicts evolve into permanent sexual cooperation, a scenario previously considered impossible (ref. 18, p. 220). We find that evolution of cooperation from conflict is enhanced when perceptual biases are subject to selection for other reasons ($s_p > 0$). Natural selection pressures have been widely invoked as the cause of perceptual biases (16), but once displays have become established, biases may alternatively be maintained as a result of social selection pressures, including social stimulation, as we have modeled. These biases may be general across whole clades (31) or restricted to certain species that occupy specific environments (16, 32). The presence of general biases does not in itself place a strong restriction on signal design: many different signals may stimulate the same perceptual bias (33). Indeed, multiple components of a display may each become sequentially established in response to the same bias, with each component initially pushing the female above her optimal level of investment that is subsequently restored by selection for lower basal investment. Ultimately, this may lead to displays whose absence results in a failure of the female to ovulate (4, 34). Male displays that stimulate investment also set the stage for self-stimulation by the female, e.g., by using similar vocalizations (35); through female stimulation by signals from other conspecifics, as in colonially breeding species (36); and through feedback mechanisms, whereby females stimulate males who then stimulate females (24). In many of these cases, the presence of a male attending the female is required, and hence, evolution of such displays can also lead to increases in other cooperative behaviors, such as brood provisioning, and a general strengthening of the pair bond (37).

Methods

We consider the evolution of 3 traits, 2 of which are each controlled by a single locus and 1 of which is polygenic, expanding on models in refs. 23 and 24. Specifically, we assume that a responder locus (A) and display locus (B) are each autosomal and haploid and contain 2 alleles. Both are sex-limited in their expression. The third trait is controlled by the combination of a normally distributed, haploid, continuously varying, sex-limited trait expressed by females, z_f, and the genotype of the mated pair at the responder locus (in the female) and display locus (in the male), together producing female investment, z. Females mate with males to form a diploid zygote that undergoes free recombination between the signal and response loci and the quantitative trait. We track numbers of single individuals and mated pairs, assuming a life cycle with overlapping generations (the events in the life cycle, described below, are also shown in *SI Appendix*, Fig. S1). Pairing is random, breeding occurs once each year, and pairs are strictly monogamous within a breeding season.

Life Cycle, Demographic, and Genotypic Equations. The life cycle begins right after pairing. Numbers of single males and females of each genotype at the responder and display loci are denoted by n_{mi} and n_{fi}, respectively, where the first index in the subscript refers to the sex of the individual and the second index, i, ranges from 1 through 4 referring respectively to the genotypes A_1B_1, A_1B_2, A_2B_1, and A_2B_2. The number of individuals in each mated pair consisting of a female of genotype i and a male of genotype j is designated by N_{ij}. Directly after pairing, only the more common sex contains unmated individuals.

In each mated pair combination with a female responder genotype i and a male display genotype j, female investment, z, has a normal distribution $p_{ij}(z)$ with phenotypic variance σ^2, and heritability h^2, and mean $\bar{z}_f + \alpha_{ij}$ where z_f is the basal value in females before modification. The component of the mean $\bar{z}_f$ is set at the beginning of each year based on the response to selection in the previous year (see below). Weak selection justifies the assumption of normality in the adult generation, when different age classes are combined, as are the distributions of z_f in pairs with different display and response genotypes. The alternative is to track the phenotype within each genotypic category and cohort across years, which becomes very complex. Weak selection also justifies the assumption of constant variance. Individual phenotypes are assumed not to change with age. The additional component of the mean, α_{ij}, is set by the genotype at the responder and display loci in each pairing N_{ij}. Specifically, if the female in a pair carries the responder allele A_2 (i = 3 or 4) and the male expresses the display allele B_2 (j = 2 or 4), then increased investment in the clutch is triggered, and $\alpha_{ij} = \alpha$. If either of these conditions is not met, females make no additional investment, and $\alpha_{ij} = 0$.

Right after the census at the time of pairing, fecundity selection occurs, associated with offspring production. The number of offspring that survive to recruitment, as produced by each combination of mated pairs, is

$$F_{ij} = (1 - s_{fec,j})e^{-bN_{tot}} \int p_{ij}(z)w(z)dzN_{ij}, \qquad [1]$$

where N_{tot} is the total number of adult individuals in the population, $w(z) = ze^{-az}$, and $s_{fec,j}$ is a fecundity cost to the pair when the male displays (such that $s_{fec,j} = s_{fec}$ when j is even and $s_{fec,j} = 0$ otherwise). Note that s_{fec} is set to 0 for most of the results discussed above. Here a represents the effect of density dependence within the brood on offspring survival, whereas b represents the density dependence of offspring survival after fledging on the number of adults present. The fact that females with allele A_2 increase their investment in offspring if mated to males with allele B_2 is reflected in whether the extra investment $\alpha_{ij} = \alpha$ is triggered (added to the z_f expressed by female i) for that mated pair i, j when the integral is taken.

The number n_i^{off} of offspring of each genotype and each sex is generated from the matrix F using standard equations for free recombination and segregation in haploids. The sex ratio of offspring is set to 1:1, which is accomplished by multiplying the total number of offspring from each pairing F_{ij} by 1/2 in the calculation of n_i^{off}.

After offspring production, adults in this overlapping-generation model undergo mortality that reflects, in part, the investment they have made in their offspring. There are several sources of mortality. Nonselective extrinsic death occurs with a constant death rate that may differ between the sexes. Selective death can also occur if there is an advantage to the responder allele in another ecological context (e.g., detection of predators, and food). These are the only sources of death on individuals that remain single (unpaired). Specifically, the numbers of single females and males that survive are $n_{fi}^s = (1 - d_f(1 - s_{pi}))n_{fi}$ and $n_{mj}^s = (1 - d_m(1 - s_{pj}))n_{mj}$, respectively, where d_f and d_m are the probabilities of death for each sex, and s_p reflects a perceptual bias survival advantage of the responder allele A_2. This latter advantage is given in both sexes; thus, $s_{pi} = s_p$ when i is 3 or 4, and $s_{pj} = s_p$ when j is 3 or 4 (otherwise, s_{pi} or s_{pj} are equal to 0).

Selective death in the context of pairing occurs due to viability selection against expressing the male trait (B_2 in males), with selection coefficient s_m, as well as due to selection against investment such that the survival rate due to investment is $e^{-c_k z}$, where k is an index for females or males (f or m) and c_k is an investment cost parameter (c_f will generally be greater than c_m because females pay a cost of egg production on top of a cost of provisioning the young, but we allow these parameters to vary freely). Note that costs of the display can be manifest as viability costs to the male, s_m, or fecundity costs to the pair, s_{fec}. Taking all of these sources of death into account, the number of mated pairs with both members surviving to the following year is

$$N_{ij}^s = (1 - d_f(1 - s_{pi}))(1 - d_m(1 - s_{pj}))(1 - s_{mj})\left(\int p(z)e^{-c_f z}e^{-c_m z}dz\right)N_{ij}, \qquad [2]$$

where $s_{mj} = s_m$ if j = 2 or 4 (indicating B_2 is present) and $s_{mj} = 0$ otherwise, $s_{pj} = s_p$ if j = 3 or 4 and $s_{pj} = 0$ otherwise, and $s_{pi} = s_p$ if i = 3 or 4 and $s_{pi} = 0$ otherwise. Similarly, the number of widows of genotype i who were mated to males of genotype j is

$$n_{fij}^w = N_{ij} \int p(z)(1 - d_f(1 - s_{pi}))e^{-c_f z}(1 - (1 - d_m(1 - s_{pj}))(1 - s_{mj})e^{-c_m z})dz, \qquad [3]$$

where the $(1 - d_f(1 - s_{pi}))e^{-c_f z}$ term accounts for survival of the female and the $1 - (1 - d_m(1 - s_{pi}))(1 - s_{mj})e^{-c_m z}$ term accounts for the death of the male. Likewise, the number of widowers of genotype j who were mated to female of genotype i is

$$n_{mij}^w = N_{ij} \int p(z)(1 - d_m(1 - s_{pj}))(1 - s_{mj})e^{-c_m z}(1 - (1 - d_f(1 - s_{pi}))e^{-c_f z})dz. \qquad [4]$$

The model allows for divorce, which is assumed to occur right before the next mating season irrespective of the number of offspring fledged from a particular nest. The number of mated pairs that remain after divorce is $N_{ij}^{r} = (1-v)N_{ij}^{s}$, while the number of single individuals of sex k created by divorce from each pair of i females and j males is $n_{kij}^{d} = vN_{ij}^{s}$.

We can now tally up all single females and males that are available to pair at the beginning of the next mating season:

$$n_{fi}^{tot} = n_{i}^{off} + n_{fi}^{s} + \sum_{j}\left(n_{fij}^{w} + n_{fij}^{d}\right) \text{ and } n_{mj}^{tot} = n_{j}^{off} + n_{mj}^{s} + \sum_{i}\left(n_{mij}^{w} + n_{mij}^{d}\right). \quad \textbf{[5]}$$

These include newly recruited fledglings, surviving individuals that were single in the previous year, widows and widowers, and divorcees.

Singles pair at random at the start of the next breeding season, with the number of pairs limited by the number of individuals of the rarer sex. We first calculated the total number of singles of each sex k as $n_{k}^{tot} = \sum_{i} n_{ki}^{tot}$ and then calculated the number of new couples with females of genotype j and males of genotype j as $N_{ij}^{new} = n_{fi}^{tot} n_{mj}^{tot} / n_{y}^{tot}$, where $y = f$ if $n_{f}^{tot} > n_{m}^{tot}$ and $y = m$ if $n_{m}^{tot} > n_{f}^{tot}$. The total number of pairs of each genotype, at the close of the life cycle, equals the sum of these newly paired individuals with the pairs that remained from the previous season after selection that did not divorce, as $N_{ij}(t+1) = N_{ij}^{new} + N_{ij}^{r}$. The more common sex also has single individuals remaining in the population, such that $n_{yi}(t+1) = n_{yi}^{tot}(1 - n_{y}^{tot}/n_{w}^{tot})$ and $n_{wi}(t+1) = 0$, where $y = f$ and $w = m$ if $n_{f}^{tot} > n_{m}^{tot}$ and $y = m$ and $w = f$ if $n_{m}^{tot} > n_{f}^{tot}$. These close the recursions for the numbers of individuals and pairs of each genotype in the population. The genotypic recursions can be turned into genotypic frequencies and then transformed into recursions for the allele frequencies for the responder A_2 and the display B_2, and the linkage disequilibrium between them, D, using standard equations for haploids.

Selection Differential and Evolution of $\bar{z}_f$. We calculate the selection differential on z_f, which is expressed only in females. Assuming weak selection and that selection on adults is not age dependent, as is outlined above, the selection differential is determined by taking a weighted average over paired and single individuals of that sex. To begin these calculations, we determine the mean after selection of the quantitative trait z_f in females of genotype j,

$$\bar{z}_{fij}^{s} = \frac{\int z p_{ij}(z) g_{fi}(z) dz}{\int p_{ij}(z) g_{fi}(z) dz}. \quad \textbf{[6]}$$

The equation for genetic fitness for females is

$$\begin{aligned} g_{fi}(z) = {} & \left(1 - d_f\left(1 - s_{pi}\right)\right)\left(1 - d_m\left(1 - s_{pj}\right)\right)\left(1 - s_{mj}\right)e^{-c_f z}e^{-c_m z} \\ & + \left(1 - d_f\left(1 - s_{pi}\right)\right)e^{-c_f z}\left(1 - \left(1 - d_m\left(1 - s_{pj}\right)\right)\left(1 - s_{mj}\right)e^{-c_m z}\right) \\ & + \frac{1}{2} w(z) e^{-bN_{tot}}. \end{aligned} \quad \textbf{[7]}$$

In the function $g_{fi}(z)$ the 3 terms represent the probability that both sexes in the mated pair survive given that the female has phenotype z, the probability that the female survived as a widow given that she has phenotype z, plus the number of newly recruited offspring that a female will contribute given that she has phenotype z, respectively. The factor of 1/2 in the last term accounts for the fact that the offspring of a female will share half of her genes in sexual haploids (as in sexual diploids).

The selection differential on females that started the life cycle as a member of a mated pair is $S_{fij}^{pair} = \bar{z}_{fij}^{s} - (\bar{z}_f + \alpha_{ij})$. The final selection differential on females is a weighted average of the selection differential of females in mated pairs and of female singles (which undergo no selection, so are not included in the numerator), across all genotypes, such that

$$S_f = \frac{\sum_i \sum_j S_{fij}^{pair}\left(N_{ij}^{s} + n_{fij}^{w} + \frac{1}{2}F_{ij}\right)}{\sum_i \left(\sum_j \left(N_{ij}^{s} + n_{fij}^{w} + \frac{1}{2}F_{ij}\right) + n_{fi}^{s}\right)}. \quad \textbf{[8]}$$

Since the quantitative character z_f is not expressed in males, $S_m = 0$. To calculate the change in $\bar{z}_f$ across a generation, $\Delta\bar{z}_f$, we must first calculate the generation time. We first determine the proportion of individuals in each sex k that survive, s_k^{*}:

$$s_k^{*} = \frac{\sum_p \left(\sum_q \left(N_{pq}^{s} + n_{kpq}^{w}\right) + n_{kp}^{s}\right)}{\sum_p \left(\sum_q N_{pq} + n_{kp}\right)}, \quad \textbf{[9]}$$

where $k = f$, $p = i$, and $q = j$ for females and $k = m$, $p = j$, and $q = i$ for males, and the multiplicative rate of increase, λ,

$$\lambda = \frac{\sum_p \left(\sum_q \left(N_{pq}^{s} + n_{kpq}^{w} + \frac{1}{2}F_{pq}\right) + n_{kp}^{s}\right)}{\sum_p \left(\sum_q N_{pq} + n_{kp}\right)}, \quad \textbf{[10]}$$

where $k = f$, $p = i$, and $q = j$ when females are the rarer sex and $k = m$, $p = j$, and $q = i$ when males are the rarer sex. The rarer sex is the limiting factor in population growth in the absence of extrapair copulations. Generation time is then determined for each sex k as T_k, where $T_k = 1 + s_k^{*}/(\lambda - s_k^{*})$, and the average across sexes $T = \frac{1}{2}(T_f + T_m)$ can be seen as an approximation of the average turnover rate of genes in the population (38, 39). Finally, we use the generation time T to modify the heritability h^2 of the trait z_f to calculate $\Delta\bar{z}_f = \frac{1}{2}h^2 S_f / T$ where the change in $\bar{z}_f$ comes only from selection in females, where these genes are expressed.

Numerical simulations were run by exact iterations of the recursion equations in 2 phases, one with B_1 fixed in order to calculate the optimal investment $\bar{z}_{opt}$ for each parameter set and the second starting at $\bar{z}_{opt}$ and introducing small amounts of B_2, with A_2 starting at a high frequency, to replicate the scenario described in the main text. Details of these analyses, performed using Mathematica (40), can be found in the *SI Appendix* and at an interactive reader (41) (https://powers.shinyapps.io/pqreadr/); see *SI Appendix*, Fig. S4, for more information.

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