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Mutual Mate Choice Can Drive Costly Signaling Even Under Perfect Monogamy

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Models of sexual selection by mate choice have emphasized the evolution of sexually dimorphic costly signals, such as elaborate plumage or courtship display, in the sex exhibiting higher reproductive skew, usually males. Less well explored is the action of mutual mate choice in driving signal evolution in socially monogamous or near-monogamous populations. We present a simulation model of condition-dependent investment in a signal trait under conditions of perfect monogamy, equal initial offspring number, and differential offspring mortality based on inherited genetic quality minus signal cost. The model demonstrates persistent evolution of high-cost sexual ornaments through mutual mate choice, even under strict monogamy, as long as the phenotypic condition is sufficiently heritable, and the monomorphic ornament reflects condition with sufficient accuracy to allow positive assortative mating. We discuss implications for research on sexual selection, mate choice, mutation-selection balance, and human evolution.

Keywords sexual selection · mutual mate choice · assortative mating · monogamy · costly signaling · simulation

Please go to <http://adb.sagepub.com> for the Appendix of this article

1 Introduction

Adaptive behavior must be adapted not just to the physical environment of one's habitat and ecological niche, but also to the psychological environment of other animals. For sexually reproducing species, this includes being adapted to evaluate the phenotypic condition and genetic quality of potential mates, and being adapted to display one's own condition and quality, often through investment in sexual ornaments (also known as fitness indicators or costly signals). Thus, mate choice and mating displays as studied by sexual selection research are core aspects of adaptive behavior. Analogous issues apply in designing cognitive agents and robots as com-

mercial products: their success depends not just on performing some task efficiently, but on marketing tactics that make them attractive to consumers.

Ever since Darwin's work (1871), sexual selection research has focused on sexually dimorphic ornaments, usually male ornaments that evolve through female choice. In many species, however, both sexes show conspicuous, costly ornaments and courtship behaviors. These are traditionally interpreted as "species recognition markers," but we propose that these non-dimorphic ornaments might instead arise through mutual mate choice as indicators of genetic quality and phenotypic condition in both sexes (Amundsen, 2000; Miller, 2000; Zahavi & Zahavi, 1997).

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So far, few formal models have addressed ornament evolution through mutual mate choice. Most sexual selection models either assume dimorphism in choice and ornaments (e.g., Houle & Kondrashov, 2002; Kokko, Brooks, Jennions, & Morley, 2003), or examine the effects of mutual mate choice only on short-term mating-market dynamics or long-term speciation (e.g., Bergstrom & Real, 2000; Kirkpatrick, 2000), rather than long-term ornament evolution. This leaves models of mutual mate choice disconnected from models of costly signaling, and makes it hard to understand ornament evolution in socially monogamous species, including many birds, prosimians, gibbons, and humans. Although a small number of models have examined the factors promoting both mutual choosiness and mutual signaling (Johnstone, 1997b; Johnstone, Reynolds, & Deutsch, 1996; Kirkpatrick, Price, & Arnold, 1990; Kokko & Johnstone, 2002), theory has lagged behind recent empirical work on ornament evolution through mutual choice in many species. (Table 2 presents empirical evidence for mutual mate choice and display across taxa; this list is extended in the online appendix.) Models of ornament evolution through mutual choice may also prove useful in the human behavioral sciences, given the substantial evidence for mutual mate choice in humans (Borgerhoff Mulder, 2004; Buss, Reis, & Rusbult, 2004; Kanazawa & Kovar, 2004), and for many human morphological and behavioral traits functioning as costly fitness indicators (Gangestad, Bennett, & Thornhill, 2001; Grammer, Fink, Møller, & Thornhill, 2003; Haselton & Miller, 2006; Penton-Voak et al., 2001; Prokosch, Yeo, & Miller, 2005; Shaner, Miller, & Mintz, 2004; Smith & Bliege Bird, 2000).

As a first step towards understanding costly signaling under mutual choice and monogamous mating, we developed a simple evolutionary computer simulation based on the 'fitness matching' model by Miller (2000, pp. 196–203). Miller (2000) proposed that the expression of preferences for high-quality mates in a monogamous mating system can give rise to positive assortment, or a correlation between the traits of mated pairs. As genetic quality is not directly observable, however, choice must be based on phenotypic traits that correlate with genetic quality. This makes it worthwhile for individuals to allocate more resources to the development of these phenotypic traits as sexual ornaments, to gain the benefits of greater offspring survival and attractiveness that result from inheriting

the good genes of a high-quality mate. This can lead to the exaggeration of the trait as a conspicuous costly signal, even if every individual is constrained to a single pairing. Some readers found the fitness-matching model plausible and compelling; others did not. The history of theoretical biology suggests that verbally plausible arguments often turn out to be wrong when they are modeled formally. Our simulation strategy was to develop a "proof of concept" that the fitness-matching model can work.

That is, can evolution favor significant positive investment in an indicator trait, even under conditions that render traditional models of sexual selection irrelevant? Indicator evolution is easy to achieve given large sex differences in choosiness and reproductive skew, and large variance in reproductive success. We did not pursue such well-studied routes to signaling for our model, but rather chose parameters that would make costly indicator evolution most unlikely and surprising by standard models. Specifically, we imposed conditions of perfect sexual equality, perfect monogamy, no extra-pair copulation, no mate switching, and no variance in initial offspring number.

As with most costly signaling models, the results need not be analyzed with complex statistics. Individuals' investment in the sexual ornament will usually evolve either toward zero (if costly signaling is not favored in a particular socioecology), or to be significantly positive (if costly signaling is favored). Under most assumptions about sexual selection, costly indicator evolution should be impossible under such conditions of perfect monogamy and equal initial offspring number. So if we observe any significant positive investment in costly signaling evolving in our simulations, this would constitute a novel and surprising demonstration that fitness matching can suffice to drive sexual selection. On the other hand, if our model does not lead to the evolution of higher investment in the indicator trait when heritable condition and positive assortment are present, that negative result would render the fitness-matching model much less plausible.

2 The Model

The model was developed as a simple genetic algorithm written in Visual Basic running on Windows XP; source code is available from the first author by e-mail.

The simulation was implemented as follows (see Figure 1 and Table 1). Each individual has a 100-locus genome containing either functional (wild-type) or dysfunctional (mutated) alleles. The number of dysfunctional alleles represents one's mutation load. Each generation, an individual's relative "genetic quality" is calculated by sorting the population in order by mutation load: the fittest individual with the lowest mutation load receives a genetic quality score of 1; the one with the highest mutation load receives a score of 0; intermediate qualities are distributed uniformly between the two extremes. Phenotypic "condition" after development, interpretable as one's health, strength, or energy budget, is a joint function of this genetic quality score and a uniformly distributed random variable ranging from 0 to 1. The relative strength of these two factors is scaled by the exogenous simulation parameter "condition accuracy," which may vary from 0 to 1. This is the same for all individuals within a simulation run but can be set to different values between runs. Condition is thus given by:

$$\begin{aligned} \text{condition} &= \text{condition accuracy} \times \text{genetic quality} \\ &+ (1 - \text{condition accuracy}) \times \text{random}. \end{aligned}$$

If condition accuracy = 1, then condition perfectly reflects genetic quality (and inverse mutation load); if condition accuracy = 0, condition is random, and uninfluenced by genetic quality. This was the simplest way we could see to manipulate how accurately heritable genetic quality determines sexually mature condition.

Each individual also has a set of heritable allocation variables that determine investment in the fitness indicator. Their evolving values and the distribution of signal magnitudes they produce are the most important outcomes of the simulation. The basic logic of honest signaling theory in biology and economics suggests that optimal investments in a signal will vary according to an individual's condition (Houle & Kondrashov, 2002; Kokko et al., 2003; Spence, 1973). To allow the possibility of condition-dependent signal investment while remaining agnostic as to the specific shape of the investment function, we assumed that each agent carries a set of genes that specify the coefficients b_0 , b_1 , and b_2 of a second-order polynomial function of condition. Total signal investment is then defined as:

$$\begin{aligned} \text{signal investment} &= b_0 + (b_1 \times \text{condition}) \\ &+ (b_2 \times \text{condition}^2). \end{aligned}$$

Although each coefficient may be positive or negative, negative total investments in signaling are impossible and are thus treated as zero. This function allows signal investment that is independent of condition (i.e., $b_1 = b_2 = 0$), or that is positively or negatively and linearly or non-linearly dependent on condition. Selection thus shapes a reaction norm that takes an agent's phenotypic condition as its input and gives the magnitude of signaling as its output.

The probability of surviving to reproduction is concave in condition minus signal investment, and is given by:

$$\text{survival} = \sqrt{\text{condition} - \text{signal investment}}$$

The concavity of the survival function ensures that the marginal cost of signal investment is smaller

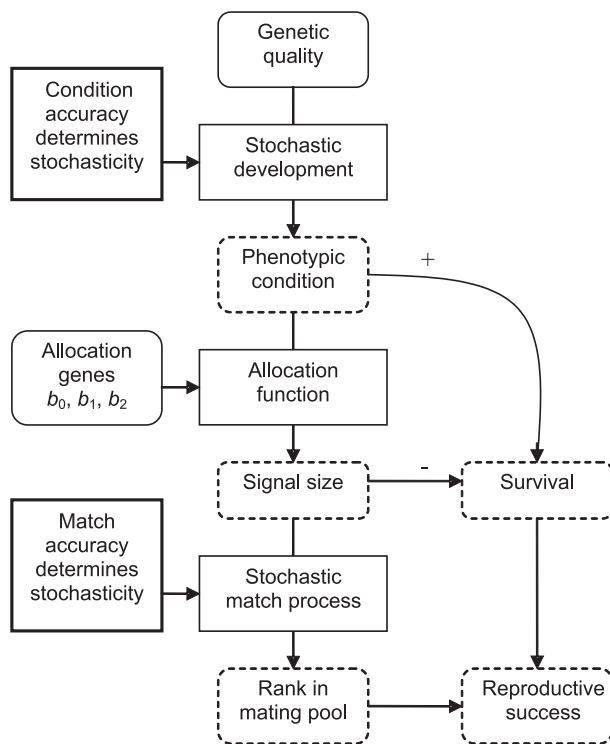


Figure 1 The role of run-specific parameter values (thick rectangular boxes), evolved heritable traits (rounded boxes), and emergent phenotypic traits (dashed rounded boxes) in development, indicator investment, survival, and mate assignment.

Table 1 Key simulation variables and parameters.

Key variables for each individual	
Directly heritable traits:	
genetic quality (based on mutation load in a 100-locus simulated genome)	
condition-dependent signal investment function defined by the variables b_0 , b_1 , and b_2	
Emergent (indirectly heritable) traits:	
condition = condition accuracy \times genetic quality + (1 – condition accuracy) \times random value	
total signal investment = $b_0 + (b_1 \times \text{condition}) + (b_2 \times \text{condition}^2)$	
probability of surviving to reproduction = $(\text{condition} - \text{signal investment})^{1/2}$	
mate ranking variable = match accuracy \times signal investment + (1 – match accuracy) \times random value	
Key parameters for each simulation run	
condition accuracy (how precisely genetic quality determines phenotypic condition at sexual maturity)	
match accuracy (how precisely signal investment determines relative ranking in the mating pool)	

for individuals in good condition than for those in poor condition, an essential feature of most stable signaling models (Johnstone, 1997a; Spence, 1973). Each individual's probability of survival is standardized by a dynamic scaling variable used to maintain a stable adult population size. (Basically, when the population grows too large, the simulation's death rate automatically increases; biologically, this could be construed as reflecting increased ecological competition, but computationally, the point is simply to avoid a simulation-crashing exponential increase in population size.)

Those individuals that survive development enter the mating market. This consists, on average, of 100 individuals (50 males, 50 females), with minor fluctuations because death is a stochastic function. Sexual pairing proceeds based on each individual's signal investment and a simulation parameter called "match accuracy," which may range from 0 to 1 and affects how accurately an individual's relative ranking in the mating market reflects total signal investment. Like condition accuracy, match accuracy is an exogenous parameter: it is the same for all individuals within a simulation run, but can vary between runs.

To determine one's relative rank in the mating market, each individual is assigned a "ranking variable," defined by:

$$\begin{aligned} & \text{ranking variable} \\ &= \text{match accuracy} \times \frac{\text{signal investment}}{\text{signal investment}_{\max}} \\ &+ (1 - \text{match accuracy}) \times \text{random}, \end{aligned}$$

where "random" is another uniformly distributed random value in the range 0 to 1. (Standardizing the individual's signal investment by the population's maximum signal investment sets the signal variable and the random variable to comparable orders of magnitude; this is important to ensure that the noisiness of the ranking variable is not dependent on the current level of signaling in the population, but on the match accuracy parameter alone.) All individuals in each sex are then sorted by their ranking variables and paired with the opposite-sex individual of equal rank. Thus the most attractive female mates with the most attractive male, the second most attractive female mates with the second most attractive male, and so on down through the population.

This perfect assortative mating by rank is critical to testing the fitness matching model. First, where match accuracy is high, it produces a correlation between the degree of female and male ornamentation within a pair, which, if larger ornaments are associated with greater offspring viability, can potentially yield returns to

ornament growth. Second, it guarantees that each individual reproduces with exactly the same number of mates (i.e., one), so that traditional models of sexual selection, which depend on differential mating success, cannot explain whatever costly indicators may evolve. Of course, imperfect match accuracy means that even “perfect” assortative mating by attractiveness rank does *not* imply perfect assortative mating by signal investment, much less by actual condition or genetic quality.

Each mated pair produces the same number of offspring, by default set to 4. The standardized death rate means that, on average, half of these offspring will survive to breed. (When each mated pair produces the same initial number of offspring, reproductive variance, which drives sexual selection in most traditional models, is minimized.) For each locus of the 100-locus genome, an offspring has an equal chance of inheriting the allele from one parent or the other. Thus, offspring tend to inherit a genetic quality around the average of their parents’ qualities. Random deleterious mutations are introduced with constant probability (equal to two mutations per individual per generation, on average). This maintains some heritable variation in genetic quality, despite selection. Each offspring likewise has an equal chance of inheriting the signal investment variables b_0 , b_1 , and b_2 from either parent. Upon inheritance, these traits (which may take on any real value) are subject to mutation, with mutation size and direction drawn from a normal distribution with mean 0 and a standard deviation determined by a mutation-scale parameter with a default value of 0.005. To allow more radical experimentation across the fitness landscape, with some small probability (0.02 by default) an individual’s investment variables are replaced with values drawn from a random distribution with mean 0 and a standard deviation of 0.25. One modeling cost of specifying a more flexible signal investment function in which the coefficients can fall far below zero is that populations occasionally enter periods of phenotypically meaningless genetic drift through the trait space, where b_0 , b_1 , and b_2 are all highly negative. In order to limit this evolutionarily uninteresting behavior, when the values of all three of an agent’s allocation traits drift below -0.1 , they are reset to $b_0 = -0.1$ and $b_1 = b_2 = 0$. (The effect of lifting this constraint is a somewhat higher fraction of generations in which zero signaling occurs in areas of the parameter space that

otherwise yield positive signaling, making it more difficult to differentiate ornament-favoring conditions from the null model.)

The life-cycle above repeats after reproduction is finished and all offspring inherit their (possibly mutated) values of genetic quality and signal allocation. Genetic quality plus condition accuracy again influences phenotypic condition; condition and the three allocation variables jointly determine investment in the indicator trait; condition minus indicator investment determines the probability of survival to sexual maturity; and indicator investment interacts with match accuracy to determine relative mating rank, which in turn determines the rank-based formation of breeding pairs (see Figure 1).

Typical simulations (illustrated in Figures 2 and 3) were run for 1,000 generations, with varying values of condition accuracy and match accuracy. Metrics of genetic quality, condition, b_0 , b_1 , b_2 , and correlations between traits within individuals and pairs were recorded for each generation. As given levels of condition accuracy and match accuracy produce consistent mean correlations between individual genetic quality and condition, and (where variance in signal investment exists) between signal investments within couples, we present the results using the more easily interpretable Pearson correlation coefficient associated with a given parameter value rather than the value itself.

3 Results

Our results show that higher offspring survival due to mutual mate choice can indeed drive the exaggeration of costly traits that correlate with genetic quality. Figure 2 shows two example simulation runs with different values of match accuracy: in the top graph, match accuracy is zero, and there is no assortative mating; in the bottom graph, match accuracy is 1, producing a correlation between signal investments within pairs of about 0.55. In both runs, condition accuracy is set to 1, producing a correlation between genetic quality and condition of about 0.96. The graphs show mean ornament investment, ornament investment by individuals in the best condition, and mean mutation load across time.

The two runs show very different patterns of signal evolution. When the population assorts totally ran-

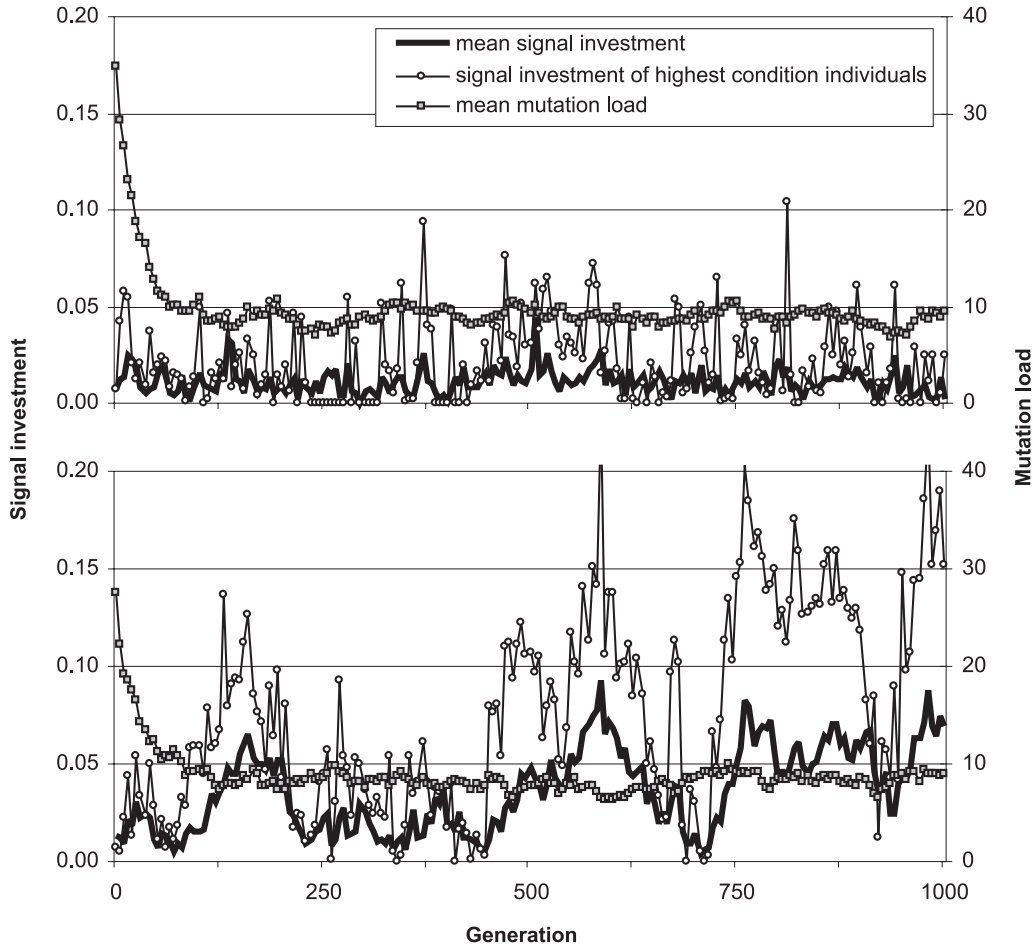


Figure 2 Mean signal investment, signal investment by individuals with the highest phenotypic condition, and mean mutation load in two typical runs of 1,000 generations. In the top graph, condition accuracy is one and match accuracy is zero, meaning that while condition is heritable, there is no assortment by signal investment: all signal investment is the result of noise. In the bottom graph, condition accuracy and match accuracy equal one (producing correlations between individual quality and condition of about 0.96, and between signal investments within pairs of about 0.55). Mean signal investment and signal investment by high-condition individuals are both significantly higher than in the null model, while mean mutation load is slightly lower. Fluctuations in signaling are apparent across generations, with the population shifting through periods of strong and weak signal investment.

domly (top graph of Figure 2), average signal investment stays very low, with a mean across the run of 0.009. This reflects only the noise produced by random mutations in the investment variables b_0 , b_1 , and b_2 . In this population, investment in the indicator increases mortality, but does not yield any mating benefits, as it does not raise the likelihood of attracting a high-quality mate. On the other hand, when there is maximal assortment (bottom graph of Figure 2), both mean investment and investment by high-condition individuals evolve to be much higher (although there are significant fluctuations in signal magnitudes across time).

The mean signal investment across the run is 0.036, which is about four times higher than the null model. The mean signal investment by the highest-quality individuals is around 0.08, which entails a 4% loss in survivorship. At the maximum, around generation 580, high-quality individuals are investing 0.23 of their phenotypic budget in signaling and thus taking a 12% reduction in survivorship. In this case, where there is significant positive assortment and a strong relationship between genetic quality and phenotypic health, the current survivorship costs of sexual display ultimately pay off in the form of securing a higher

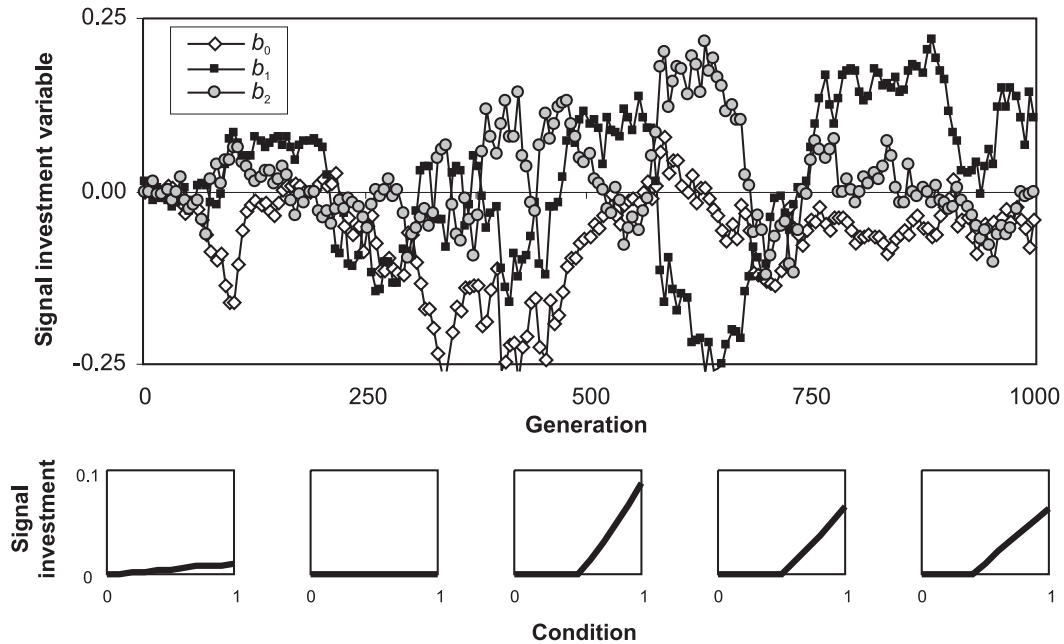


Figure 3 The mean signal investment values (b_0 , b_1 , and b_2) and the investment functions they produce for the same run represented in the bottom of Figure 2. When signaling is present, these variables generally combine to produce a signal investment function that is increasing in condition. The five investment functions represent those produced by the mean trait values at generations 5, 250, 500, 750, and 1,000.

quality genetic endowment for one's lineage into the future.

Figure 3 displays the change in the mean signal investment traits b_0 , b_1 , and b_2 throughout the same run shown in the lower graph of Figure 2. The small boxes below the main graph show the resulting signal investment functions produced by these three investment variables at 5, 250, 500, 750, and 1,000 generations. All three variables show fluctuation above and below zero. Parameter b_0 , which defines the constant in the investment function, remains negative throughout much of the run, indicating a negative y-intercept. This yields a range of low phenotypic conditions at which individuals do not bother signaling at all. With the exception of periods around generation 250 and 700 (where there is effectively no signal investment), either b_1 , b_2 , or both are above zero, producing positive signal investment for high-condition individuals. Typical investment functions for the positive signaling regime are displayed in the small boxes corresponding to the 500th, 750th, and 1,000th generations in Figure 3.

How does long-run signal investment respond to variation in the heritability of condition and the degree

of assortative mating? Figure 4 displays mean signal investment as a function of the correlation between genetic quality and condition (manipulated by the condition accuracy parameter) and the correlation between signal size within pairs (manipulated by the match accuracy parameter). The effects of the two parameters clearly interact, with no costly indicators evolving at the lower extremes of either parameter. Past the minimum threshold for indicator evolution, total indicator investment increases monotonically with both match accuracy and condition accuracy. The slightly ragged contours in the graph result from the simulation's stochastic elements: the sampling error due to probabilistic offspring death in a limited population size, and the randomness affecting phenotypic condition and sexual attractiveness for each individual (see Figure 1).

While the population's mean signaling investment reveals aggregate levels of ornamentation in the population, what can we understand about the evolution of the individual reaction norms that govern ornament investment as a function of phenotypic condition? Figure 5 plots the shift in mean signal investment by condition across different values of condition accu-

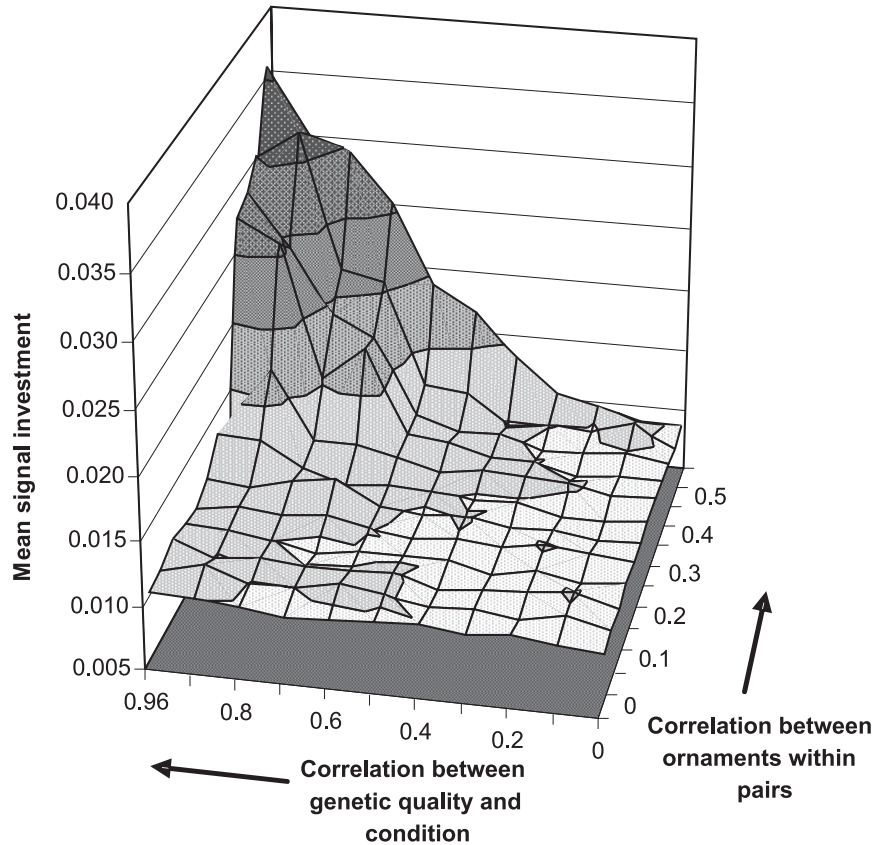


Figure 4 Mean signal investment as a function of the heritability of condition and assortment by ornament size. (Each point in the grid represents the mean signal investment for given values of condition accuracy and match accuracy across five independent runs of 1,000 generations.)

eracy. While an increase in the heritability of phenotypic condition yields a general increase in mean signal investment across all conditions, signaling by high-condition individuals increases more steeply than for low-condition individuals. Averaging over time, high heritability of condition yields an ornament that increases in condition at an increasing rate. This pattern is partly a result of occasionally positive values for the multiplier b_2 on condition², as well as the floor effect for low-condition individuals that results from consistently negative values for the y-intercept b_0 . Adjusting the correlation between signals within couples (by manipulating the match accuracy parameter) has the same qualitative effect as adjusting heritability: the more accurately the population assorts, the taller and steeper the reaction norm.

What are the main factors influencing mutation load in the simulation? Both socio-ecological parameters, condition and match accuracy, are important, but

condition accuracy influences both survival selection (death's ability to cull harmful mutations that directly reduce phenotypic condition) and sexual selection (mate choice's ability to cull harmful mutations that indirectly reduce ornament quality), whereas match accuracy influences only sexual selection. Figure 6 plots equilibrium mutation loads across the same runs and conditions as plotted in Figure 4. When both parameters vary, condition accuracy is clearly the stronger determinant. If the correlation between quality and condition stays above 0.6, however, stronger assortment also decreases mutation load. In Figure 6, increasing match accuracy from 0 to 1 reduces mean mutation load by 0.3 to 0.5 mutations.

For a given match accuracy value, there is also variation in signal investment across time and across runs, which affects the population's ability to assort accurately by quality. Figure 7 illustrates the negative relationship between mean ornament size and mean

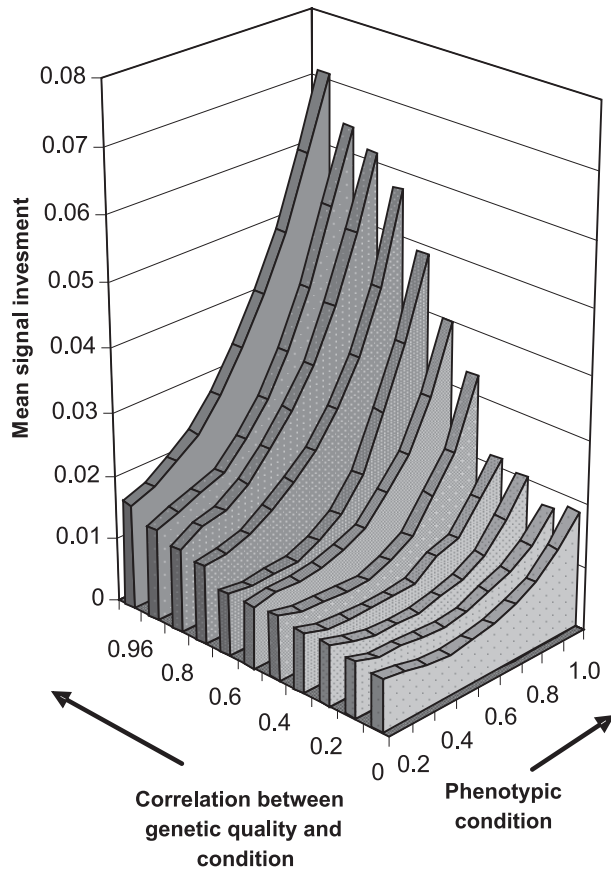


Figure 5 The evolution of the signaling reaction norm in response to increasing heritability of phenotypic condition. As the heritability of condition increases, there is a general increase in signaling by all individuals regardless of condition, but high-condition individuals come to invest much more heavily in the signal than low-condition individuals. (Signal investment by condition was generated by averaging across 1,000 generations in five independent runs for different values of condition accuracy; match accuracy was held constant at one.)

mutation load across runs where condition and match accuracy are both maximal. When these populations evolve higher-cost signals, they assort more accurately by quality. This ensures that individuals of poor genetic quality (high mutation load), even if they manage to survive development, will be snubbed by high-quality mates. They must settle for lower-quality mates, which damns their offspring to similarly high mortality and low attractiveness in the next round. Indeed, the fitness-matching process tends to concentrate harmful mutations in minimal-quality offspring, who are then much more likely to die before mating.

The result is that higher cost signals promote fitness matching and purge harmful mutations from the population more effectively.

These results were not greatly affected by changes in the other simulation parameters of deleterious mutation rate, adult population size, and offspring number. Deleterious mutation rate can be higher or lower, as long as some variance in genetic quality is maintained in the population. If the mutation rate is too low, all mutations are cleansed from the population, leaving no incentive for mate choice. If the mutation rate is too high, the population saturates with dysfunctional alleles, again eliminating all variation in quality. In either case, mate choice and costly signaling become irrelevant. Larger populations reduce between-run variance in equilibrium trait values, but at the cost of slower simulation runs. If each mated pair produces a larger number of offspring (requiring a higher death rate during development), computation also slows, but there is no observable effect on outcomes. Changing the size of mutations in the indicator investment traits (b_0 , b_1 , and b_2) affects the pace of evolution and, to some degree, the stability of outcomes. If very large, these mutations produce noisier drift in areas of the parameter space that disfavor signal investment, and noisier signal evolution where signaling is favored.

4 Discussion

This is the first explicit simulation of the fitness-matching model of costly indicator evolution through mutual mate choice (Miller, 2000). Even under perfect monogamy and equal initial offspring numbers, selection favors investment in costly indicators by both sexes because a mate's heritable genetic quality predicts offspring survival and sexual attractiveness. Under a broad range of conditions, the genetic ("indirect") benefits of a high-quality mate can compensate for substantially increased mortality due to costly sexual ornamentation or display. At the population level, this fitness-matching process also increases selection's ability to purge harmful mutations, because assortative mating for genetic quality tends to amplify genetic variance, concentrating mutations in a few low-fitness offspring that tend to die young.

These results are novel and perhaps surprising, because our simulation excludes most of the conditions (dimorphic reproductive rates and/or reproduc-

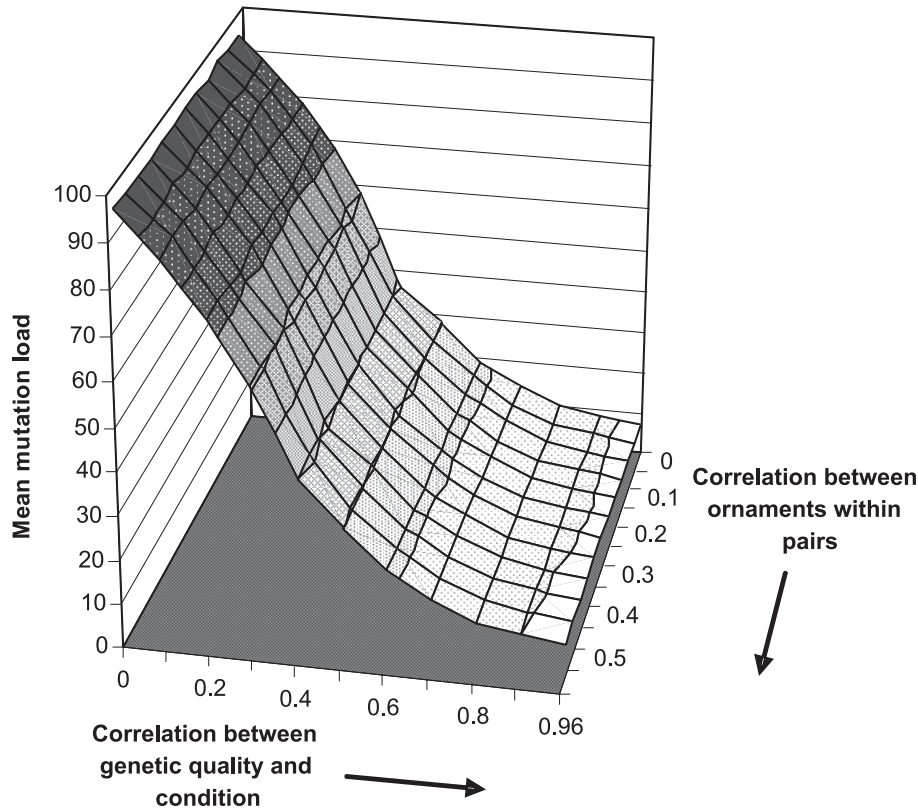


Figure 6 Mean mutation load as a function of the heritability of condition and assortment by ornament size, drawing from the same data as Figure 4. (The directions of the axes are reversed from Figure 4 to aid clarity.)

tive skew) that are normally thought to drive sexual selection. Evolutionary biology and evolutionary psychology sources routinely assert that such conditions are fundamental to sexual selection and the evolution of sexual ornaments. For example, a leading evolutionary psychology textbook (Gaulin & McBurney, 2004, p. 258) asserts unconditionally that “sexual selection is caused by sex differences in reproductive rate.” As our model shows, sexual selection for costly fitness indicators can occur without any sex difference in reproductive rate.

The process we describe suggests that sexual selection can also be important even in the absence of reproductive skew that arises through polygyny, polyandry, or extra-pair copulation. It also reinforces arguments for the need to go beyond traditional female-choice/male-display models of ornament evolution (cf. Houde, 2001; Kokko & Jennions, 2003; Sandvik, Rosenqvist, & Berglund, 2000) to understand sexual selection in socially monogamous species. Moreover, the model potentially expands the explanatory range

of sexual selection theory to include ornamental traits with low sexual dimorphism (e.g., “species recognition markers”) and populations with low reproductive skew.

This fitness-matching process leads to significant trait exaggeration when phenotypic condition is reasonably heritable, and when condition can be reasonably well-reflected in ornament quality. If good ornament quality is due more to good luck than good genes, then the process does not work – but neither do most other sexual selection models of costly indicator evolution. We suspect that good genes become more important than good luck in relatively larger, longer-lived (“K-selected”) species with higher parental investment, lower mortality, and greater resilience against transient environmental threats. As social monogamy and mutual choosiness generally covary with higher paternal investment and lower offspring mortality (Kokko & Johnstone, 2002), the conditions for the fitness-matching model to work ought to often hold for a socially monogamous species such as humans.

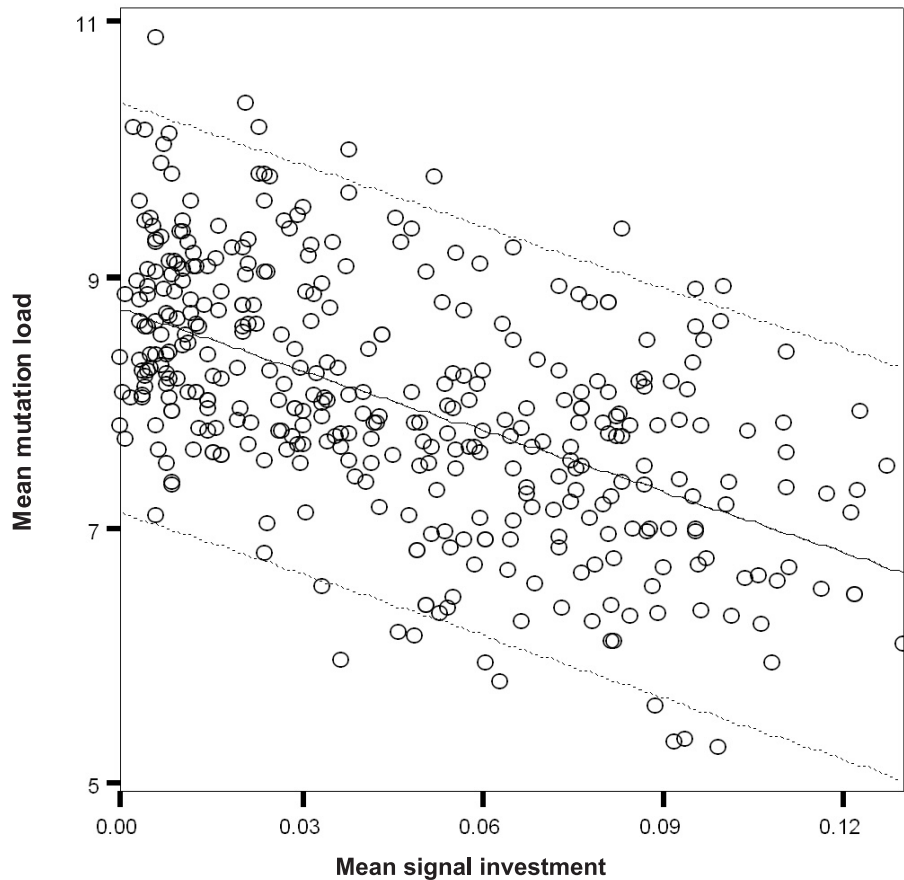


Figure 7 The impact of signaling on the mean genetic quality of a population. As populations evolve higher levels of signaling and assort more accurately by genetic quality, deleterious mutations are eliminated at a higher rate than in the absence of assortment. A 0.1 increase in mean signal investment is accompanied by a reduction of 1.6 mutations per individual (estimated by OLS regression; $p < 0.001$; $R^2 = 0.30$). The solid and dashed lines represent the regression estimate and 95% prediction limits, respectively. (These data were generated by recording mean signal investment and mutation load after 300 generations in 372 independent runs; both condition and match accuracy were held constant at one.)

Conversely, the fitness-matching model predicts lower signal investment when assortative mating is limited by high costs of mate choice, inaccurate quality assessment, or limited pools of potential mates (Benton & Evans, 1998; Johnstone, 1997b). When mate choice is cheaper and more accurate, the fitness-matching model should work better. Accurate quality assortment, for example, may be more easily achieved in human foragers, who live in multi-male, multi-female groups, exhibit wide and overlapping home ranges, and fission and fuse frequently and easily (Marlowe, 2005), than in New World night monkeys (genus *Aotus*) or titis (genus *Callicebus*), who live more commonly as solitary territorial pairs (Fuentes, 1998). Serially monogamous gibbons (genus *Hylobates*),

who show more flexible social groupings and partner changes, as well as elaborate duetting between mates, might represent an intermediate case (Geissmann & Orgeldinger, 2000; Sommer & Reichard, 2000).

Interestingly, the relationship between phenotypic condition and signal investment endogenously produced by the simulation, by which signal investment not only increases with condition, but at an increasing rate (see Figure 5), mirrors the form of the relationship found in nature. Kodric-Brown, Sibly, and Brown (2006) have shown that the size of male ornaments across the animal world, such as the horns of stag beetles and the dewlaps of *Anolis* lizards, nearly always increase super-linearly with body size. If we make the assumption that body size, which is not explicitly

Table 2 Fourteen species exhibiting mutual mate choice, mutual display, and/or positive assortment by quality-related traits. A more complete listing is available in the online appendix.

Species	Relevant mating pattern	Source
Burrowing parrot <i>Cyanoliseus patagonus</i>	Assortative mating by physical condition and red abdominal plumage; plumage color predicts male size and female condition.	(Masello, Pagnossin, Lubjuhn, & Quillfeldt, 2004; Masello & Quillfeldt, 2003)
Eastern bluebird <i>Siala sialis</i>	UV and melanin-based plumage associated with condition and reproductive success in both sexes.	(Siefferman & Hill, 2005)
Deep-snouted pipefish <i>Syngnathus typhle</i> (sex role reversed)	Ornament display by both sexes; female preferences for male size and brood patch thickness; greater offspring success where mate choice is allowed.	(Berglund et al., 2005; Sandvik et al., 2000)
European shag <i>Phalacrocorax aristotelis</i>	Assortative mating by crest size, which predicts condition and clutch success.	(Daunt et al., 2003)
Human <i>Homo sapiens</i>	Assortative mating by physical attractiveness and intelligence.	(Buss et al., 2004; Kanazawa & Kovar, 2004)
Jumping spider <i>Phidippus clarus</i>	Size assortative mating; male preferences for large females.	(Hoefler, 2007)
North American barn swallow <i>Hirundo rustica erythrogaster</i>	Assortative mating by ventral plumage coloration; plumage predicts annual reproductive success.	(Safran & McGraw, 2004)
Pied flycatcher <i>Ficedula hypoleuca</i>	Assortative mating by white forehead patch size, associated with low parasite load and number of surviving offspring in females.	(Morales et al., 2007; Potti & Merino, 1996)
Red grouse <i>Lagopus lagopus scoticus</i>	UV-reflecting combs in both sexes; brighter UV associated with fewer parasites in both sexes.	(Mougeot, Redpath, & Leckie, 2005)
Red-tailed tropicbird <i>Phaethon rubricauda</i>	Exaggerated tail streamers, mutual preferences for streamer length.	(Boland et al., 2004)
Rock sparrow <i>Petronia petronia</i>	Assortative mating by yellow breast ornament, correlated with body mass and fecundity in females.	(Griggio, Valera, Casas, & Pilastro, 2005; Pilastro, Griggio, & Matessi, 2003)
Soay sheep <i>Ovis aries</i>	More dominant males focus mating effort on heavier females with higher reproductive success.	(Preston, Stevenson, Pemberton, Coltman, & Wilson, 2005)
Two-spotted goby <i>Gobiusculus flavescens</i>	Male preference for large, brightly colored females; larger males pair with brighter females.	(Amundsen & Forsgren, 2003; Pelabon et al., 2003)
Yellow-eyed penguin <i>Megadyptes antipodes</i>	Assortative mating by carotenoid eye coloration and plumage.	(Massaro, Davis, & Darby, 2003)

modeled in the simulation, increases with condition (but not at a rate that overtakes the signal investment function), then our “in silico” species conforms to this real-world pattern as well. We are not aware of a study that has examined the scaling of ornaments across mutually ornamented species.

Observational and experimental evidence supports the plausibility of the fitness-matching process of ornament evolution. Mutual mate choice, mutual ornamentation, and positive assortment for quality have been observed across a large number of species showing different degrees of pair-bond stability and parental investment (see Table 2 and online appendix). Several empirical studies, moreover, support this fitness-matching model by demonstrating significant positive associations among genetic quality, phenotypic condition, ornament quality, sexual attractiveness, and/or offspring viability. For example, in the deep-snouted pipefish *Syngnathus typhle*, a sex-role reversed species in which both males and females show choosiness and competition over mates (Berglund, Widemo, & Rosenqvist, 2005), Sandvik et al. (2000) found that when males or females could choose between multiple partners, their offspring escaped more often from predators, and, when male choice acted on females, offspring grew faster. In the monogamous Inca tern *Larosterna inca*, both sexes invest in elaborate moustache plumage and fleshy wattles; Velando, Lessells, and Marquez (2001) demonstrated that moustache length in both sexes predicted offspring body mass and immunocompetence as well as individual condition and breeding success. European shags *Phalacrocorax aristotelis* show positive assortment by ornamental crest size, a trait associated with both individual condition and breeding ability (Daunt, Monaghan, Wanless, & Harris, 2003). Burrowing parrots *Cyanoliseus patagonus* mate assortatively by red abdominal patch size and physical condition, which are both associated with larger clutch size and faster nestling growth (Masello & Quillfeldt, 2003). These and many other studies of mutual display (see Table 2 and online appendix) beg for a better theoretical explanation, and support the viability of this fitness-matching process.

We do, however, caution that a simulation “proof of concept” that the fitness-matching model can work, plus empirical animal studies suggestive of mutual mate choice for costly fitness indicators, does not prove that fitness matching explains all, or even some, of the observed animal mating patterns. Receiver bias

theory (cf. Endler & Basolo, 1998; Ryan, 1998) might, in principle, explain some of the mutual mate choice patterns, at least at the proximate level. For example, European shags might have visual systems that happen to respond favorably to ornamental crest size for some other reason, so larger ornamental crests evolved in both sexes, and the positive correlations between crest size, phenotypic condition, and breeding ability (Daunt et al., 2003) might be accidental. We remain skeptical, however, that receiver bias theory can explain the long-term evolutionary stability of mate preferences for such traits, if the traits carry no information about a potential mate’s phenotypic or genetic quality (Fuller, Houle, & Travis, 2005; Kokko et al., 2003; Miller, 2000).

Alternatively, perhaps female ornaments are the genetically correlated by-product of female choice for male ornaments (Darwin, 1871). However, growing empirical evidence for male choice in mutually ornamented species (e.g., Amundsen & Forsgren, 2003; Boland, Double, & Baker, 2004; Table 2 and online appendix), the fact that females sometimes develop different ornamental traits than males (e.g., Hanssen, Folstad, & Erikstad, 2006; Weiss, 2006), and the apparent ability of selection to de-couple male and female life histories (Amundsen, 2000), suggest that mutual ornamentation is at least partially the result of adaptive response rather than the by-product of genetic or developmental constraints alone.

One strength of the model is its openness regarding the proximate mechanisms that lead to positive assortment (cf. Benton & Evans, 1998). Whereas the original fitness-matching model (Miller, 2000) assumed that assortment would be driven by mate choice alone, intra-sexual competition for access to high-quality mates, or a mix of competition and choice, could also drive patterns of positive assortment that lead to the evolution of armaments or “dual-utility” signals (Berglund, Bisazza, & Pilastro, 1996). Our model thus suggests that benefits from mate quality, not mate quantity alone, could support allocations to intra-sexual competition in addition to inter-sexual advertisement. Assortative mating by dominance rank might, for example, affect allocation to competitive behavior in the dwarf mongoose (*Helogale undulata rufula*), spotted hyena (*Crocuta crocuta*), wolf (*Canis lupus*), or mandrill (*Mandrillus sphinx*; Derix & van Hooff, 1995; Rasa, 1977; Setchell & Wickings, 2005; Szykman et al., 2001). The logic of this fitness-matching model would also extend

to the evolution of sexually dimorphic ornaments and mate preferences, as long as the expression of these preferences leads to positive quality assortment (e.g., Faivre et al., 2001; Roulin, Dijkstra, Riols, & Ducrest, 2001). Mate choice based on multiple indicators would presumably have similar effects (Candolin, 2003; Jawor, Linville, Beall, & Breitwisch, 2003).

The simulation approach has allowed us to represent the evolutionary dynamics of costly signaling when optimal signaling investment depends on individual difference in genetic quality and phenotypic condition, as well as the mate choice and signaling behavior of all other agents in the system. In analytical models (using mathematical population genetics), understanding such evolutionary dynamics often proves intractable without gross simplification, especially in costly signaling contexts. By explicitly modeling mutation loads, assortative mating patterns, and signal investment as an evolving reaction norm, we have been able to address some inter-related theoretical questions (such as the optimal scaling of ornaments with condition, the effects of condition and match accuracy, and the effect of choice and signaling on population-level mutation loads) as issues nested within the larger socio-ecological system rather than as decoupled, atomized problems.

Our model of course simplifies the dynamics of mutual mate choice in a number of ways. First, most species classified as socially monogamous, including humans, show at least modest levels of extra-pair copulation and/or polygyny, generally resulting in somewhat higher male reproductive skew (Griffith, Owens, & Thuman, 2002; Paul, 2002; Westneat & Stewart, 2003; Zeh & Zeh, 2003). Sexual selection for signaling in these populations would presumably combine the effects of both dimorphic reproductive skew (e.g., higher variance in male mating success) and fitness matching (differential offspring viability resulting from mutual choice). At the extreme, strong selection for male promiscuity (favoring quantity rather than quality of female partners) would probably disrupt the positive quality assortment that supports mutual display. We can, however, envision a broad range of intermediate conditions in which both fitness matching and more traditional forms of sexual selection can operate together in a population, yielding costly signaling by both sexes, perhaps through dimorphic traits with dimorphic costs.

Second, these simulations assume that assortative mating for ornament quality can occur, and do not

model specific mechanisms of mate search, mate choice, or sexual competition. We did not explicitly simulate the co-evolution of mate preferences and ornamental traits, but rather investigated whether high-cost ornaments can evolve given that mutual mate choice is operating. Our simulation did, however, allow the possibility of evolution to a “pooling equilibrium” (Gintis, 2000, p. 310) in which no effective signaling or mate choice occurs. We found that this does often occur in some areas of the parameter space (as in the top of Figure 2 and the front right quadrant of Figure 4). We hope to address the co-evolution of preferences and signals more explicitly in a future model.

Third, specific details of our model could be changed in future research to evaluate the robustness of the results. This could include changing the specific functions that map genetic quality onto condition and investment onto ornament quality, as well as the specific implementation of genetic quality, mutation, condition accuracy, match accuracy, death, and pair-formation. In the current model, differential offspring survival based on parental quality can also easily be reinterpreted as differential prenatal survival (leading to differential spontaneous abortion rates, or differential litter or clutch size), rather than different postnatal survival (from birth to sexual maturity).

Finally, given that monogamy and mutual mate choice are both associated with high levels of biparental investment, monomorphic indicators are likely to advertise both genetic quality (“indirect benefits”) and parenting ability and resources (“direct benefits”) (Kokko et al., 2003). Theoretical models have demonstrated the plausibility of good-parent processes of signal evolution (Iwasa & Pomiankowski, 1999; Kokko, 1998). A direct-benefits version of the fitness-matching model would focus less on how heritable genetic quality influences offspring survival and attractiveness, and focus more on how parental resource investment influences these outcomes, and would likely lead to different signal evolution patterns that depend on different parameters. Distinguishing the effects of direct versus indirect benefits on ornament evolution in biparental care species presents an empirical and methodological challenge, and many of the papers cited in the online appendix may be interpreted as supporting either benefits model.

To summarize, we demonstrate that higher offspring survival rates due to mutual good-genes mate choice can drive the exaggeration of costly traits that

advertise genetic quality. We also show that assortative mating by condition-dependent traits can drive down mean mutation loads in monogamous populations. In other words, sexual selection through fitness matching can increase average genetic quality in a population. Thus, indicator evolution in socially monogamous species may be driven by this fitness-matching process, in addition to traditional sexual selection processes based on sex differences in reproductive skew, reproductive rates, and mating effort. This has important implications for understanding sexually attractive traits with low sexual dimorphism, including what have been thought to be “species recognition markers” in many socially monogamous species. It may also be crucial in understanding the evolution of human capacities for intelligence, creativity, humor, language, morality, and conspicuous consumption (Geher & Miller, 2007; Griskevicius et al., 2007; Haselton & Miller, 2006; Miller, 2007; Miller & Penke, 2007; Miller & Tal, 2007), which show low dimorphism but high sexual attractiveness.

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