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Coevolution of costly mate choice and condition-dependent display of good genes

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Females often choose their mates, instead of mating at random, even when a father contributes nothing but genes to his offspring. Costly female preferences for males with exaggerated traits that reduce viability, such as the peacock's tail, are particularly puzzling. Such preferences can evolve if directly favoured by natural selection or when the exaggerated trait, although maladaptive *per se*, indicates high overall quality of the male's genotype. Two recent analyses suggested that the advantage to mate choice based on genetic quality is too weak to explain extreme cases of exaggeration of display traits and the corresponding preferences. We studied coevolution of a female mate-preference function and a genotype-dependent male display function where mutation supplies variation in genotype quality and mate preference is costly. Preference readily evolves, often causing extreme exaggeration of the display. Mate choice and trait expression can approach an equilibrium, or a limit cycle, or exaggeration can proceed forever, eventually causing extinction.

Keywords: good gene; mate choice; sexual selection; deleterious mutation; condition dependence

1. INTRODUCTION

The idea that mate preference for traits in the opposite sex can evolve solely because of genetic benefits to the potential offspring ('good genes') is controversial. The idea is appealing because there is abundant evidence that animals, usually females, prefer particular mates even when there is no evidence that mates contribute anything other than genes to their offspring (Bradbury & Andersson 1987; Kirkpatrick & Ryan 1991; Andersson 1994). For convenience, we will refer throughout this paper to female choice based on male displays, although either sex may exhibit mate choice. Zahavi (1975, 1977) proposed the first modern version of the good-genes hypothesis. He noted the important point that stable preference can only evolve for costly male traits that allow high-quality males to give larger displays than low-quality ones. This is the handicap principle.

There was initially controversy over whether good-genes handicap models could work in principle (reviewed by Pomiankowski 1988). Subsequent analyses have revealed that they can cause stable exaggeration of mate preference and display and that the handicap principle is essential to the operation of the process (Pomiankowski 1988; Iwasa *et al.* 1991). In combination with the Fisher process, good-genes models can cause unlimited exaggeration of male displays (Iwasa & Pomiankowski 1994; hereafter referred to as I&P) and cycles of exaggeration and the minimization of display traits (I&P 1999).

Recent scepticism of the good-genes handicap model has taken two related forms. First, some investigators have questioned whether natural populations have enough genetic variance for fitness to make such choice worthwhile. This is the traditional 'lek paradox' (Borgia 1979; Taylor & Williams 1982). Others, however, propose that there are a number of mechanisms whereby substantial amounts of genetic variance in fitness can be maintained (Muller 1950; Hamilton & Zuk 1982; Kondrashov 1988*b*; Burt 1995; Rowe & Houle 1996). In addition, various empirical results suggest the presence of genetic variance for fitness in most populations (Charlesworth 1987; Kondrashov 1988*a*; Houle 1992; Burt 1995). This genetic variance is similarly reflected in the display traits that could be the targets of mate choice (Pomiankowski & Møller 1995). It seems probable that enough genetic variation is present to drive the evolution of some mate choice through the good-genes mechanism.

The second argument against the importance of good-genes handicap choice is that the strength of the selection on mate preference that it can generate is limited, and thus easily counteracted by natural selection (Kirkpatrick 1996; Kirkpatrick & Barton 1997). For example, Kirkpatrick & Barton (1997) demonstrated that the rate of response of mate choice through good genes is limited to a small percentage of its genetic standard deviation per generation. Kirkpatrick (1996) developed a numerical model which indicated that exaggeration of display by more than a few phenotypic standard deviations is improbable when mate preference is subject to Gaussian stabilizing natural selection. These two quantitative arguments against the importance of the good-genes process are related, as one of the important factors that leads to the limitation on the rate of evolution of choice is the amount of genetic variation for fitness. The model described by Kirkpatrick & Barton (1997) shows that selection is weak when genetic variance for fitness is in the range that is currently considered to be realistic.

An important difficulty in comparing the results of models that favour the good-genes process, such as those of I&P (Iwasa *et al.* 1991; I&P 1994, 1999), with models whose result challenge it, such as Kirkpatrick (1996), is

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that the parameters used are difficult to relate directly to empirical data. This problem is primarily due to our lack of knowledge about the evolution of mate choice. Kirkpatrick (1996) pointed out that one well-known aspect of sexually selected systems is the degree of exaggeration of male display traits, and he chose to relate his results to this exaggeration in units of phenotypic standard deviations. For example, the exaggeration of male tail length in three families of birds averages 30 s.d. over the unexaggerated traits (Alatalo *et al.* 1988). The results of the I&P models have not been carefully compared to such empirical benchmarks. The published numerical results of I&P show exaggerations of male traits to the order of one genetic standard deviation (I&P 1994, 1999), but because the position of the equilibria in these models does not depend on genetic or phenotypic variances, the significance of the difference is not clear.

Here we propose a model of good-genes choice that uses many of the assumptions employed by I&P. Our model permits a more informative parametrization of both the costs of mate choice and the maintenance of variation in genotypic quality. We also perform direct comparisons with the degree of exaggeration of male traits in natural populations. Results based on this model suggest that good-genes choice is capable of promoting male display to the degree seen in the most extreme natural examples.

2. THE MODEL

We consider the evolution of three traits: overall genotype quality; a display function expressed only in males; and a female mate-choice function based on this display trait. Quality is determined by the number of deleterious mutations an individual carries, x. Genetic variance in fitness is supplied by deleterious mutations that appear at the rate U per genome per generation. Mutations are not sex linked, so at the beginning of a generation, the distribution of x, $p(x)$, is the same in females as in males. We assume a linear decline in viability with increasing mutation numbers. The viability of females is given by $w(x) = 1 - x/(X + 1)$, where X is a parameter giving the maximum mutation number that allows survival and thus controls the effect of a single mutation. The viability of a male depends on both his mutation number and his display level, D, symbolized by $W(x, D)$.

We assume that the optimal male display under viability selection is a decreasing function of x, as might be the case if individuals with fewer mutations were larger, and natural selection favours a display trait value that is proportional to size. In the simulations shown here we arbitrarily assume that optimal display decreases as $O(x) = 3 - x/X$, from a value of 3 for a mutation-free individual to 2 for the maximum mutation number. The model's results depend on this function having a slope that is large enough so that females can recognize the difference between male genotypes (see below). Changing the intercept of $O(x)$ changes the size of the initial male display but does not otherwise affect the results. Viability falls further when D deviates from this optimum, as shown in figure 1. We investigated cases where fitness falls off exponentially from the optimum

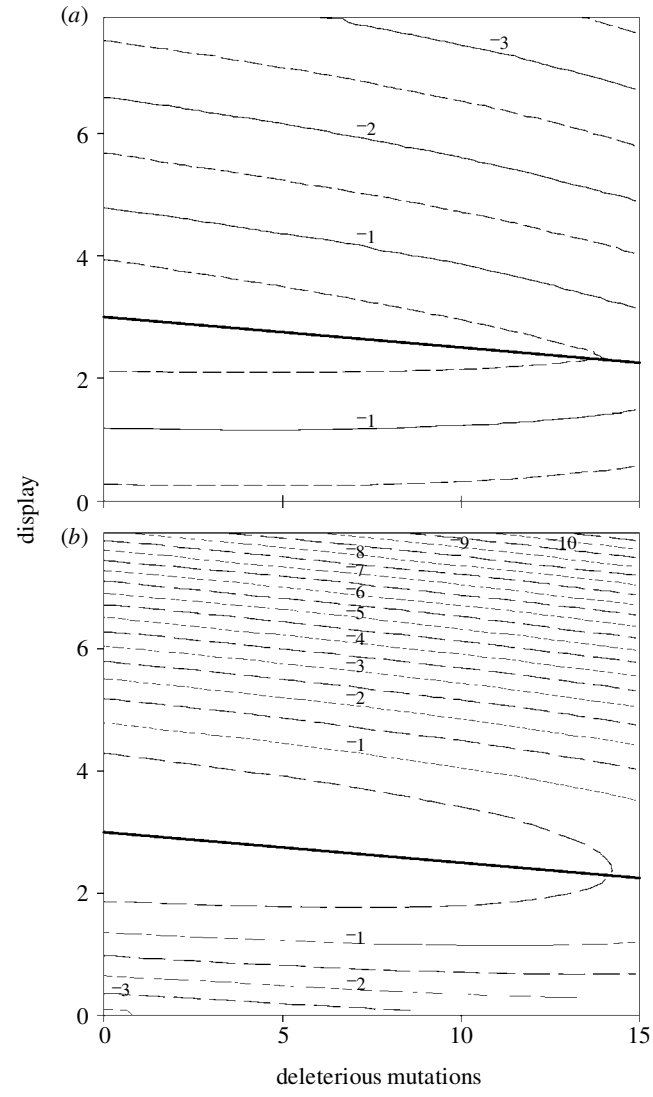

Figure 1. Log fitness surfaces, $W(x, D)$, describing viability selection in males. The optimal level of display, $O(x)$, is shown by the thick solid line and corresponds to the case where $X = 20$ and $O(x)$ declines linearly from $O(0) = 3$ to $O(X) = 2$. Along this ridge, fitness declines from $W(0, 3) = 1$ to $W(20, 2) = 0.048$. When D deviates from $O(x)$, viability of males with a given x declines either exponentially (*a*) or as a Gaussian curve (*b*). In each case $S = 0.8$.

$$W(x, D) = O(x) \exp\left[\frac{-|O(x) - D|}{S}\right] \tag{2.1}$$

according to a Gaussian curve

$$W(x, D) = O(x) \exp\left[\frac{-(D - O(x))^2}{2S^2}\right]. \tag{2.2}$$

The parameter S determines the rate at which fitness decreases away from the optimum; large values of S cause weak selection for the optimum display. We therefore assume that the handicap is that high-quality individuals have a higher viability at any given value of the display trait above $O(x)$.

For simplicity we assume that the expected male display function is a linear function of x, $D(x) = \alpha - x(\alpha - \beta)/X$ where $\alpha = D(0)$ and $\beta = D(X)$. A female perceives the expected display as $d = D(x) + N(0, E^2)$ where $N(0, E^2)$

denotes a Gaussian distributed random deviation with mean 0 and variance E^2. E^2 is the combined error from deviations of male display from $D(x)$, caused for example by environmental effects, and errors in female perception of the male display. Females are monogamous, and mate choice occurs during sequential encounters. Females acquire information about the distribution of male traits in the population before breeding. Mating at each encounter occurs with probability $m(d^*)$, where d^* is the standardized deviation of the perceived display from the population mean $d^* = (d - \bar{d})/\sigma(d)$ where $\sigma(d)$ is the standard deviation of d. We assume that a proportion ν of encounters end in mating, regardless of the male display and female choice. Similarly, for a proportion ν of the time no mating takes place; thus $\nu \leq m(d^*) \leq 1 - \nu$.

A key feature of the model is that costs of female choice arise as a direct consequence of mate search or interaction, rather than through pleiotropic effects. For every potential mate that a female rejects, she incurs a direct fitness cost C, for example as a result of increased mortality. A female that rejects mates with probability r will therefore have fitness proportional to

$$F(C, r) = (1 - r) + r(1 - r)(1 - C) + r^2(1 - r)(1 - C)^2 + \ldots = \frac{1 - r}{1 - r + rC}. \quad (2.3)$$

If mate rejection is costly, we expect the mate-choice function $m(d^*)$ to evolve to threshold form (Parker 1983; Real 1990). Indeed, in simulations where $m(d^*)$ was allowed to take an arbitrary form, it rapidly approached a threshold. Consequently, the function $m(d^*)$ was restricted to a step function with a single variable τ, the truncation threshold. If $d^* < \tau$, $m(d^*) = \nu$; if $d^* > \tau$, $m(d^*) = 1 - \nu$. For this choice function, the probability of rejecting a potential mate is $r = \nu + (1 - 2\nu)\Phi(\tau, 1)$, where $\Phi(\tau, 1)$ is the probability that a Gaussian random variable with mean 0 and variance 1 is less than τ. The probability that a male genotype x will mate in an encounter with a female depends on that genotype's expected standardized display, $\bar{d}^*$, as

$$M(\bar{d}^*) = \nu + (1 - 2\nu)[1 - \Phi(\bar{d}^* - \tau, E^2/\sigma^2(d))], \quad (2.4)$$

where $\Phi(\bar{d}^* - \tau, E^2/\sigma^2(d))$ is the probability that a Gaussian random variable with mean 0 and variance $E^2/\sigma^2(d)$ is less than $\bar{d}^* - \tau$. For given values of ν and E, τ determines the probability that a female mates, the distribution of male genotypes that mate, and, together with C, the strength of direct selection on mate choice (figure 2).

We treat α, β and τ as the mean values of independent quantitative traits with constant small additive genetic variances V_α, V_β and V_τ. The dynamics of the model involve coevolution of the distribution of mutation number, x, with these display and preference variables.

We numerically investigated the behaviour of the model, assuming that the population was infinite and haploid, generations were discrete and the life cycle was mutation→viability selection→mating→reproduction with free recombination. Transformations of the distribution of mutation numbers, $p(x)$, by all these processes were modelled explicitly (Kimura & Maruyama 1966; Kondrashov 1982).

To focus purely on good-genes sexual selection, the possibility of the Fisher runaway process was excluded by

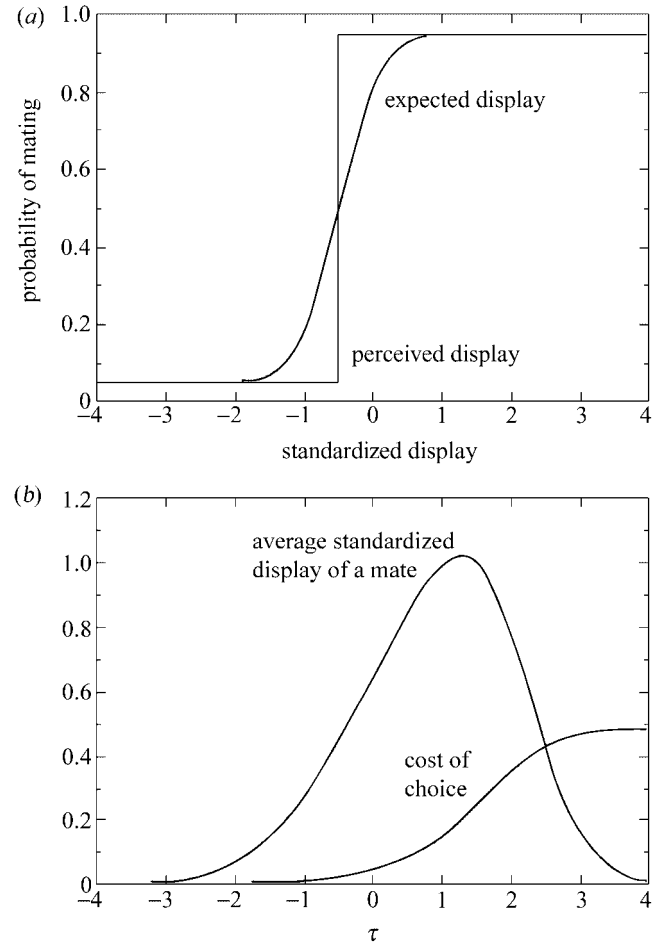

Figure 2. (*a*) Probability that a male will mate during an encounter as a function of his standardized perceived display d^* or his standardized expected display under threshold-like mate choice with $\tau = -0.5$, $\nu = 0.05$ and E equal to half the standard deviation of d^*. (*b*) The effect of the mating threshold, τ, on the expected standardized display of successful males (the effectiveness of choice) and the cost of mate choice, $1 - F(C, r)$. We assume a Gaussian distribution of expected display, $\nu = 0.05$, $C = 0.05$ with E half the standard deviation of d^*. A modestly stringent choice ($\tau < 0.0$) was effective yet had very little cost. The effectiveness of choice declines at high τ values because of the possibility that rejected males will still be able to mate ($\nu > 0$).

calculating the selection gradients on τ, α and β in a population that varies for only one of these variables. At each time-step, an independent selection gradient was calculated for each variable in turn, assuming only variation in the variable (say z) and x. Linkage disequilibrium between alleles affecting choice and display variables was therefore never present, but disequilibria between alleles influencing $m(d^*)$ or $D(x)$ and x were allowed to develop and are essential for the model. The fitness gradients for variables $z(\mathrm{d}\ln(W)/\mathrm{d}z)$ were calculated by introducing alleles that slightly increased and decreased the value of the variable in question from the population mean. These alleles were allowed to reach equilibrium with the deleterious mutations in the population, which usually took place within 30 generations. The selection gradient was then measured from the difference between the fitnesses of the two introduced alleles and the resident allele. Thus, we assumed that

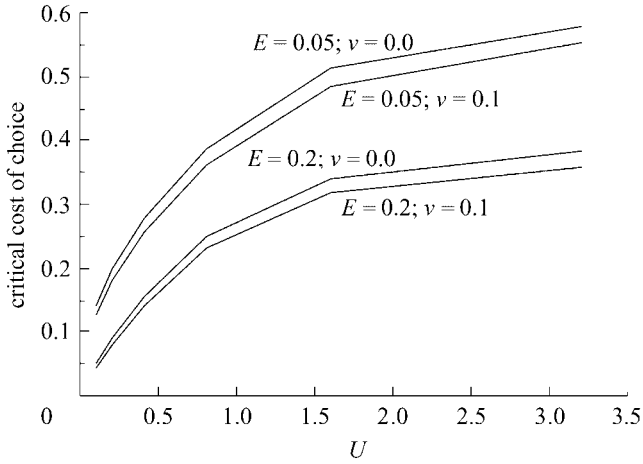

Figure 3. The maximal value of C where τ increases from -2, as a function of U. We assume $D(x) = O(x)$ for $X = 20$, $O(0) - O(X) = 1$, as in figure 1.

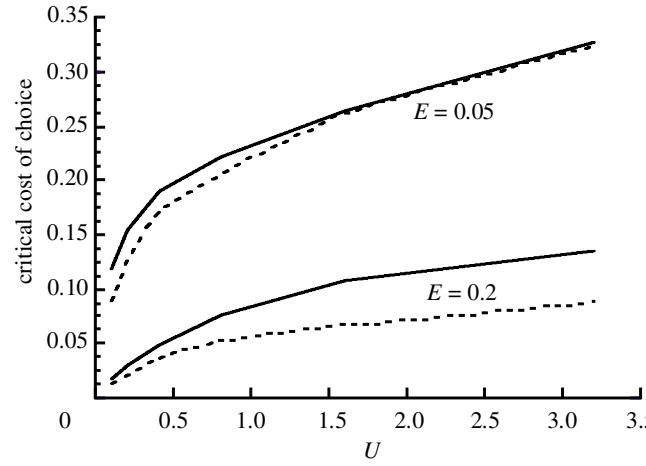

Figure 4. The maximal value of C under which exaggeration of β over $O(X)$ (solid lines) and α over $O(0)$ (dashed lines) occurs, as a function of U. The fitness ridge has exponential form (figure 1*a*), $S = 0.5$ and $v = 0.1$; otherwise conditions are the same as in figure 3.

coevolution of choice and display occurs when the distribution of the genotype quality is at quasi-equilibrium with respect to the alleles affecting each variable (Kondrashov 1995). Evolution of variables then followed the standard quantitative genetics equation $\Delta\bar{z} = V_z\, \mathrm{d}(\ln W)/\mathrm{d}z$, where z is the trait (τ, α or β), and V_z is the additive genetic variance of z.

3. RESULTS

If mating is effectively random ($\tau < -3$), $D(x)$ evolves to match the ridge of optimum fitness $O(x)$. This match creates the correlation between display and quality that is necessary for the good-genes process to proceed (Andersson 1986, 1994; Iwasa *et al.* 1991), because $O(x)$ is a decreasing function of x. Once this correlation is established, choice readily evolves (τ increases), unless its cost is very high (figure 3). Initial evolution of choice is favoured when the mutation rate and the efficiency of mate choice (v and E low) are high (figure 3).

Once choice ($\tau > -3$) evolves, sexual selection favours males with larger displays. The impact of this selection depends on the shape of the male fitness ridge. If fitness declines exponentially away from the fitness ridge (figure 1*a*), small values of τ are insufficient to displace $D(x)$ from $O(x)$, because the one-sided derivatives of fitness with respect to $D(x)$ at $O(x)$ are negative. Once τ is large enough to affect $D(x)$, exaggeration of $D(x)$ begins with changes in β (figure 4), because the low-quality males having low levels of display have the most to gain from exaggerated displays. When displays of low-quality individuals approach to within *ca.* E of $D(0)$, the mating success of high-quality males falls to the point where an increase in α also begins. As with the evolution of preference, more efficient mate choice favours exaggeration of $D(x)$ (figure 4). With the exponential fitness ridge, the rate of decline of relative viability is constant with increasing deviation of $D(x)$ from $O(x)$. Thus if α increases at all, both α and β will increase indefinitely, leading to an unlimited decline in male viability. In reality, the cost of mate choice might increase as male viability declines, countering this extreme scenario. When the slopes of the fitness ridge are Gaussian (figure 1*b*), the rate of change in fitness near $O(x)$ is small, and any $\tau > -\infty$ causes some displacement of $D(x)$. However, the evolution of $D(x)$ will be limited because the rate of decline of relative viability increases as $D(x)$ deviates more and more from $O(x)$. Still, parameter combinations can always be found that lead to a finite loss of fitness. Therefore, when selection against increasing display is an increasing function of deviation from the optimum, as in the Gaussian case, exaggerations of both mate choice and display are expected.

The time-course of this exaggeration is shown for two parameter combinations in figure 5. As with the exponential function $W(x, D)$, the increase in β is initially more rapid than that of α, therefore sexual selection for increasing display of high-quality individuals is weak until low-quality individuals gain a large proportion of matings. Evolution of mate choice and exaggeration of $D(x)$ reduce the viability of males but increase the viability of females because of the decline in the average number of mutations per individual.

Coevolution of mate choice and display can lead to equilibrium (figure 5*a–c*) or to stable cycling if the genetic variance of τ is higher than that of α and β (figure 5*d–f*). Overshoot of τ can then cause the display to evolve so far that low-quality males are essentially absent at the time of mating, making costly mate choice disadvantageous. Once τ drops, $D(x)$ returns to $O(x)$ (α often returns faster than β, temporarily making high levels of display an indicator of low genotype quality), after which the choice–exaggeration cycle may be repeated.

The importance of sexual selection is usually assessed in terms of the difference in the display trait between male and female, which is readily measured. A more meaningful measure of the effect of sexual selection is the fitness cost paid by the displaying sex. Measured in this way, the importance of sexual selection is quite sensitive to the values of U and C (figure 6). Interestingly, the fitness cost of sexual selection to males is greatest with an intermediate width of the fitness ridge, S (figure 7). When S is small, low-quality males cannot evolve a high enough display to

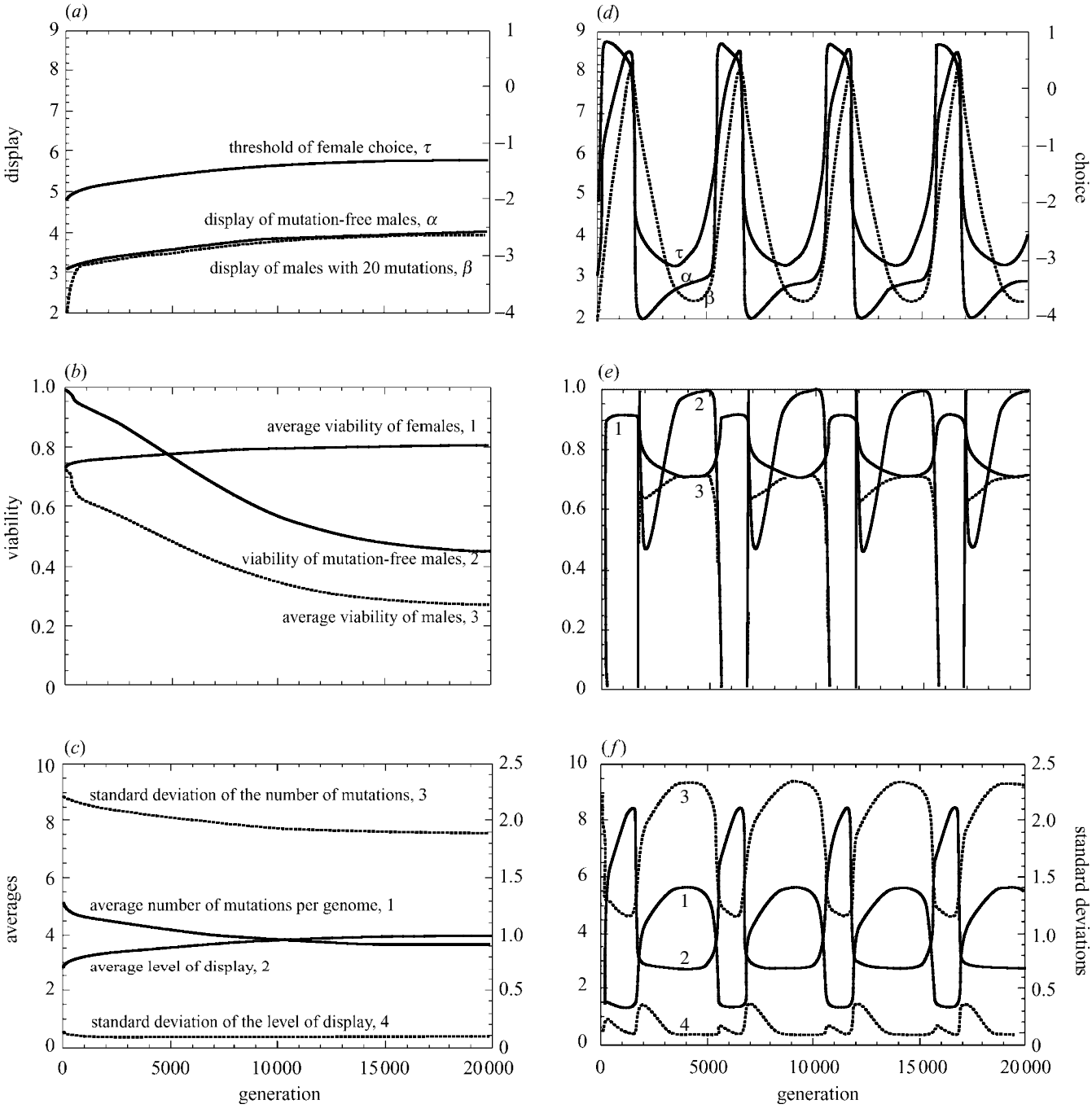

Figure 5. (*a–c*) Dynamics of sexually selected display in a population with a Gaussian viability surface (figure 1*b*), with $X = 20$ and $S = 0.8$, $U = 0.4$, $C = 0.01$, $E = 0.1$, $\nu = 0.05$, $V_\alpha = V_\beta = V_\tau = 0.09$. Initially, mating is close to random ($\tau = -2.0$), and male display coincides with $O(x)$ ($\alpha = 3.0$ and $\beta = 2.0$). (*a*) τ, α and β. (*b*) Average viability of females, 1; viability of mutation-free males $W(0, \alpha)$, 2; and average viability of males, 3. (*c*) Average and standard deviation of the number of mutations per genotype before selection and of male display level. (*d–f*) The same variables as in (*a–c*), except that $V_\tau = 0.36$.

challenge high-quality males. When S is large, the handicap on the low-quality males imposed by the slope of $O(x)$ is less. Conversely, τ is maximized when S is small, as male phenotypes are most informative when most constrained by selection. Nevertheless, the absolute exaggeration of display increases with S. The equilibrium degree of exaggeration is inversely related to ν and E, so the greater the ability of females to choose the phenotypes of their mates, the greater the degree of exaggeration (data not shown).

4. DISCUSSION

In our model, the good-genes process is effective at promoting female preferences that then cause the evolution of large male displays. For example, when the rate of decline in relative fitness of males for a given increase in display is constant, as it is when viability decreases exponentially with increasing display, the model predicts exaggeration of display without limit, leading to an infinitely large loss of male viability. The possibility of such 'Dar-

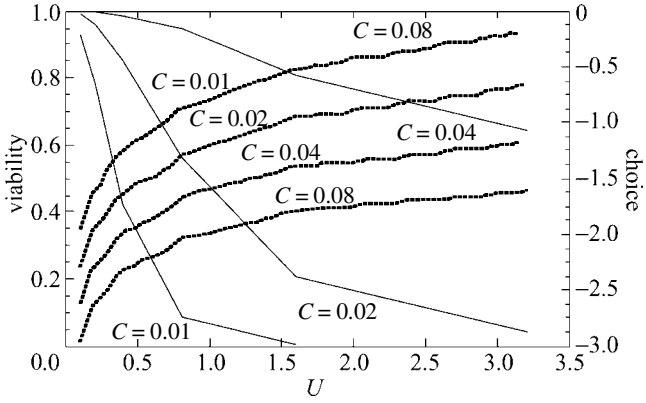

Figure 6. Equilibrium τ (broken lines with decreasing heights) and viability of mutation-free males $W(0, \alpha)$ (solid lines with increasing heights) as functions of U for $C = 0.01$, 0.02, 0.04 and 0.08, and $S = 0.8$. Other parameters as in figure 5*a–c*.

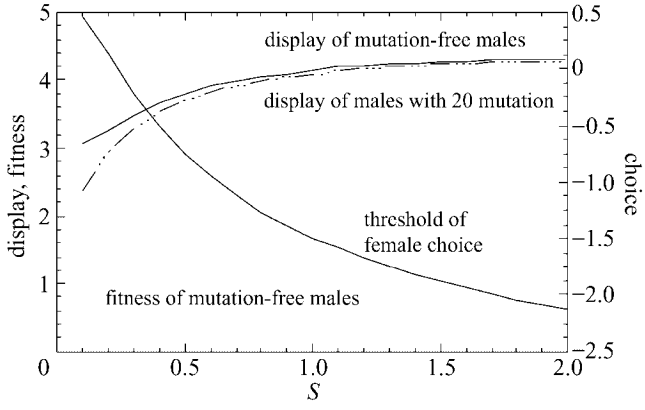

Figure 7. Equilibrium values of τ, α, β and $W(0, \alpha)$ as functions of S when $U = 0.4$ and $C = 0.01$.

winian extinction' has been suggested by earlier authors (Haldane 1932; Huxley 1938). Although extinction as an outcome may be peculiar to the current formulation of this model, it does suggest that the power of the good-genes process is very large. In nature other forces not included in the model, such as density-dependent costs of mate search for females, could limit the amount of exaggeration.

The striking exaggeration of choice and display in our model is achieved under standard and realistic assumptions about the maintenance of genetic variance by deleterious mutation, the strength and form of selection on displays, and levels of variation within populations (Kirkpatrick 1996; Lynch *et al.* 1999). For example, in figure 5 the coefficient of variation of display is initially 5%, the proportion of the variance in display that is accounted for by variation in quality is 20%, the cost to a female of rejecting a mate is 1% and we have made the conservative assumption that the genomic mutation rate is 0.5. Few data are available on the direct cost of rejecting a potential mate, but it seems probable that it can be considerably less than 1%, for example on a lek. The outcome of the models with these parameters is an increase in the mean male display of 45% or eight phenotypic standard deviations.

Several equilibrium properties of the populations in the model should be noted. First, the displays of the best and worst male genotypes often differ by less than the amount the females can unambiguously detect. For example, in figure 5*a–c* the equilibrium difference in display between the best and worst male genotypes is less than the uncertainty in female perception, whereas the actual variance in male quality is such that males with even half the maximal number of mutations are very rare. Thus, low-quality males may be displaying almost as much as high-quality males, although they may pay a very high viability cost to do so. This observation suggests that large phenotypic variance in male display traits is not necessary to maintain the good-genes process. This is seemingly at odds with large variance in display traits within natural populations. However, the size of variance in display should be judged in relation to the information contained in the display. Environmental effects on display might be so large that only extreme displays are informative. Alternatively, variation in natural populations could be due to the effects of male age and multiple breeding seasons, which we did not include in the model.

Second, the mean number of mutations is substantially lower with good-genes sexual selection than without it. For example, under the parameters used in figure 5*a–c*, at equilibrium the average number of mutations per genome before viability selection decreases by 29% (figure 5*c*). The average viability of females is therefore increased, despite the costs of choice, although male viability is reduced because of the costs of display. This outcome supports models that suggest that sexual selection can help alleviate the cost of sex (Geodaykan 1965; Trivers 1976; Agrawal 2001; Siller 2001).

Third, female preferences can evolve even when the costs of rejecting a mate are quite substantial.

Fourth, the stringency of female choice always remains modest, rarely leading to rejection of more than half the males in the population, even for parameter combinations that lead to large exaggeration of male traits and extremely low male viability. For the parameter set in figure 5*a–c*, an 8 s.d. exaggeration of male display occurs, even though females reject only about 9% of the potential mates.

I&P (1994, 1999) have analysed a model with several key similarities to ours: both models involve the evolution of a linear condition-dependent male display function; both models assume that female mate preference is based on the relative level of male displays rather than the absolute level of display. However our model differs from that of I&P in key ways. We have intentionally excluded the possibility of the Fisher process from our model, whereas some aspects of the dynamical behaviour of the I&P model are dominated by the effects of the Fisher process. If we had allowed the Fisher process in the model, I&P's results suggest that more rapid changes would have been seen with perhaps a larger amplitude of changes.

Another important difference between the current model and I&P's model is in selection on female choice. I&P assumed an arbitrary selection function on female preference where log fitness falls with a power coefficient that they assumed to be greater than 2 in most cases. The more specific but less arbitrary assumption was made that the selection on female preference arises directly through mating. This assumption results in a decrease in log fitness that increases with a power coefficient that is *ca.* 2 (figure

2*b*). I&P's (1994) assumptions prevent an analytical solution when the power coefficient is 2. This is unfortunate because the usual assumption about stabilizing selection is that log fitness falls with the square of the deviation from the optimum (cf. Kirkpatrick 1996). When the power coefficient is less than 2, I&P (1994) found that exaggeration of choice and display could proceed without limit. I&P treated such cases as unrealistic and instead chose to focus on cases where the power coefficient was substantially greater than 2. This results in very weak selection in the neighbourhood of the optimum that increases extremely rapidly away from the optimum.

Another interesting result of the current model is the emergence of cycling when the rate of evolution of female choice surpasses that of male display. I&P (1999) previously observed cycling in a good-genes model. The cause of this cycling appears to be different from that found in our model. They interpret their cycles as the result of alternating periods of Fisher runaway selection, followed by slow good-genes-dominated periods. They have also observed cycling in a model that only involves the Fisher process (I&P 1995). In both cases, the amplitude of the cycles observed was only about one phenotypic standard deviation in the display trait, much smaller than that shown in this model.

In our model, cycling only occurs when the genetic variance in female choice is larger than that in male display. The mechanism for cycling in this model is the near exhaustion of genetic variance in quality caused by good-genes choice, because of the high mortality of males, which removes the advantage to female choice. Choice then collapses relatively rapidly, aided by the tendency of poor-quality males to display more than high-quality males during this brief period. The rapidity with which the collapse takes place suggests that other kinds of disruptions to the good-genes process, such as density-dependent costs of choice or environmental changes, could also lead to cycling.

Our results are in sharp contrast with those of Kirkpatrick (1996). His numerical study suggested that exaggeration of male displays by more than a few phenotypic standard deviations was improbable under the good-genes process. Two key assumptions are responsible for this difference in results. First, mate choice in our model is made relative to the distribution of male display in the population. Therefore, choice of modest stringency suffices to drive the evolution of male traits indefinitely. Second, we assume that the costs of choice are related only to the proportion of males rejected and not to the absolute degree of exaggeration of the chosen males, so costs to females do not escalate with increased male display.

A more convincing explanation for the good-genes process was expressed by Kirkpatrick & Barton (1997), who demonstrated that the rate of response of mate choice to indirect selection based on good genes is limited to a small percentage of its genetic standard deviation. On this basis, they argued that selection on female mate choice through good genes is probably to be countered by opposing natural selection. In contrast, we assume that selection on cognitively complex organisms would be able to separate naturally selected aspects of the sensory system, such as the ability to find food or avoid predators, from those involved with mate choice. This is perhaps the most important difference in perspective between Kirkpatrick & Barton (1997) and ourselves.

These differences in perspective suggest that empirical evidence of the existence and nature of costs to female preferences is urgently needed before the importance of good-genes choice can be understood. Such evidence is probably relatively easy to obtain for costs that arise directly from the choice and rejection process. It is generally less clear what sort of experiments would allow reliable detection of pleiotropic costs of choice.

Several other aspects of the current model should be amenable to experimental investigation. Perhaps the most important and readily tested assumption is that of relative preferences for mates (Zuk *et al.* 1990; Hoikkala & Aspi 1993; Jang & Greenfield 1998). In some lek systems, one or a small number of males sometimes gain most of the matings. In our model, mate choice that is this stringent can only occur when both the costs of rejecting a mate and the frequency of forced copulations are very low. Although the former prediction is not novel, the rate of forced copulations is not usually incorporated into models of sexual selection.

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