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The sexual selection continuum

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The evolution of mate choice for genetic benefits has become the tale of two hypotheses: Fisher's 'runaway' and 'good genes', or viability indicators. These hypotheses are often pitted against each other as alternatives, with evidence that attractive males sire more viable offspring interpreted as support for good genes and with a negative or null relationship between mating success of sons and other components of fitness interpreted as favouring the Fisher process. Here, we build a general model of female choice for indirect benefits that captures the essence of both the 'Fisherian' and 'good-genes' models. All versions of our model point to a single process that favours female preference for males siring offspring of high reproductive value. Enhanced mating success and survival are therefore equally valid genetic benefits of mate choice, but their relative importance varies depending on female choice costs. The relationship between male attractiveness and survival may be positive or negative, depending on life-history trade-offs and mating skew. This relationship can change sign in response to increased costliness of choice or environmental change. Any form of female preference is subject to self-reinforcing evolution, and any relationship (or lack thereof) between male display and offspring survival is inevitably an indicator of offspring reproductive values. Costly female choice can be maintained with or without higher offspring survival.

Keywords: Fisher process; runaway evolution; good genes; mate choice; indirect benefits; sexual selection

1. INTRODUCTION

Any trait evolves in direct response to natural selection and in indirect response to selection on genetically correlated traits. In the case of mating preferences for exaggerated sexual displays, direct fitness benefits and costs impose direct selection on mate-choice behaviour, but indirect selection due to genetic covariation between mate choice and other fitness components is also thought to be widespread (Andersson 1994). Fisher (1930) pointed out that it would be adaptive for females to prefer mating with males that bear a trait that is favoured by natural selection. Furthermore, Fisher recognized that as a preference increases in frequency, the attractiveness of the trait itself will amplify the advantage of mate choice. The ensuing 'runaway' process of coevolution would exaggerate the display trait beyond its naturally selected optimum. Display exaggeration is halted by a trade-off between male attractiveness and other components of fitness, and preferences fail to exaggerate when male survival is so curtailed that there is no longer any benefit to females of mating with attractive males.

Fisher's name has become associated in the sexual-selection literature with the second component of his theory—the runaway coevolution between preference and display (Fisher 1930). Early attempts to model this process demonstrated that in a population where some mate choice occurs already, and where preference and display are heritable, the build-up of a genetic correlation between preference and display is inevitable (Lande 1981) and leads to runaway coevolution (Lande 1981; Kirkpatrick 1982). Positive preference–display genetic correlations have been found in nature (Bakker 1993; Wilkinson & Reillo 1994; Houde 1994; Gray & Cade 1999) and their rapid build-up under experimental conditions has been empirically verified (Blows 1999).

In recent years, attention has shifted again to the first component of Fisher's theory—the evolution of preferences for male traits that indicate fitness in contexts other than mate choice. This has been spurred by many factors, including the articulation by Zahavi (1975) of the handicap principle, a considerable body of theoretical modelling (e.g. Pomiankowski 1988; Grafen 1990*a*,*b*; Iwasa *et al.* 1991; Houle & Kondrashov 2002), the observation that in many species preferred males are more vigorous and long-lived than non-preferred males (Jennions *et al.* 2001) and often produce offspring of higher viability (Møller & Alatalo 1999) and arguments that additive genetic variation in fitness components can be maintained by processes such as host–parasite coevolution (Hamilton & Zuk 1982), genotype by environment interaction (Kotiaho *et al.* 2001) and mutation–selection balance (Rowe & Houle 1996). An unfortunate consequence of the success of good-genes indicators has been an overemphasis of the difference between these so-called 'good genes' or 'indi-

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cator' models and the Fisherian runaway process. One could be forgiven for thinking, upon reading the contemporary literature, that Fisherian runaway and good-genes indicators were alternative theories for the evolution of mate choice and that the main goal of the field is to distinguish between these as alternative hypotheses.

Considerable empirical attention has focused on the phenotypic and genetic relationships between male sexual display and survival, because viability is one of the most important fitness components that may be indicated by sexual displays. A large number of studies estimate the phenotypic (Jennions *et al.* 2001) or genetic (Reynolds & Gross 1992; Norris 1993; Petrie 1994; Jones *et al.* 1998; Møller & Alatalo 1999; Wedell & Tregenza 1999; Brooks 2000) association between attractiveness, survival, fecundity and other fitness components (Petrie 1994; Møller & Alatalo 1999; Wedell & Tregenza 1999; Brooks 2000). A positive relationship between male attractiveness and offspring survival (or other aspects of fitness) is thought to support the good-genes hypothesis (Norris 1993; Petrie 1994; Møller & Alatalo 1999; Jennions *et al.* 2001), whereas a negative relationship combined with significant heritability of attractiveness is interpreted as favouring a Fisherian mechanism alone (Etges 1996; Jones *et al.* 1998; Wedell & Tregenza 1999; Brooks 2000). However, it is conceivable within a purely good-genes framework that males with the highest genetic quality advertise so intensely that their survival becomes worse than that of males of poorer quality (Grafen 1990*a*; Kokko 1998, 2001; Eshel *et al.* 2000).

In dealing with the relationship between sexual attractiveness and survival, it is crucial to remember that costly sexual advertisement is a life-history trait subject to tradeoffs with other components of reproductive effort and with future survival and fecundity (Partridge & Endler 1987; Grafen 1990*a*; Gustafsson *et al.* 1995; Kokko 1997, 1998, 2001; Höglund & Sheldon 1998). A negative relationship between reproductive effort (including advertisement) and survival is consistent with life-history theory (Hansen & Price 1995; Kokko 1998). Thus, under many conditions, it is conceivable that a preference for males with high levels of costly advertisement and poor survival prospects can still deliver an indirect fitness benefit to females, based on superior fitness of offspring. It would follow that a distinction between genetic benefits due to enhanced survival (in addition to mating success) and due to mating success alone is spurious, and that there is really a unitary process of preference evolution by indirect benefits.

Here, we present a model that captures the essence of sexual selection for indirect benefits: males vary in a display trait that females may find attractive (if it pays for them to do so). This trait is heritable and it may correlate with male and offspring viability (expressed as annual survival), either positively or negatively. We also assume that there is a process that maintains genetic variation in the trait (and possibly in viability) and that female choice incurs direct costs that reduce female fecundity. We demonstrate that females should prefer males that display more intensely if the display indicates male breeding value for fitness and the indirect benefits of mating with males of high fitness exceed the direct costs of choosing rather than mating randomly. Moreover, we show that there is nothing qualitatively different in the process of mate-choice evolution whether the viability of attractive males is greater than, less than or equal to that of unattractive males.

2. THE MODEL

We consider a population in which births and deaths occur continuously and the primary sex ratio is 1 : 1. Mate choice for indirect benefits can operate only when males vary in some heritable trait. To provide a conceptually simple example, we assume the existence of a gene with two alternative alleles, $i = 0$ and 2, that is expressed in males only. The gene influences the male's appearance in ways described in the following paragraphs, and it can covary with survival positively, negatively or not at all. It can thus also be thought to reflect the 'quality' of a male. However, to avoid any unnecessary connotations with terminology that is biased in favour of one (runaway) or the other (indicator) direction, we simply refer to males carrying these alleles as male 'types' $i = 1$ and 2, and note that we do not necessarily assume a correlation between male type and survival.

We assume haploid inheritance of the gene. Any model of sexual selection for indirect benefits will require a mechanism to maintain variation in males. As our focus is not on solving the lek paradox, we simply assume that such a mechanism exists: allele 1 mutates to allele 2 with a rate of m_1 per generation, and allele 2 to allele 1 with a rate of m_2 (see table 1 for a full list of variables and their definitions).

The type of a male cannot be observed directly. However, a male of type i also expresses a sexually selected trait denoted by D_i (for 'display'; if $D_i = 0$ the male lacks the display trait). Additionally, both males and females carry a preference gene P that dictates female preferences for large values of D_i. Female preferences can vary continuously from absent ($P = 0$) to strong (large P). A high value of P means that a female spends much effort in her mate choice to find a male with a large D, but this effort also reduces her fecundity, $F(P)$: $\partial F/\partial P < 0$ (so that the cost of choice $C(P) = (F(0) - F(P))/F(0)$; see figure 1). Based on the function $F(P)$, we distinguish between two concepts of costs of choice. The environmentally determined costliness of choice, E, is a parameter that specifies the shape of $F(P)$, i.e. how quickly fecundity drops with stronger female preferences. E is high if, for example, low population density causes high energetic expenditure in females that attempt to sample several males. The fecundity cost actually paid by the female, C, equals the reduction in fecundity that the female suffers when her preference equals P: $C(P) = (F(0) - F(P))/F(0)$. Note that C depends both on E and on P, and it can therefore be small even if the environment dictates that choice is costly, as a female can opt not to be particularly choosy (small P) when E is large (figure 1).

We next need to specify male mating success. If females are not choosy ($P = 0$), males have equal mating success regardless of their display, whereas high P values imply that the number of offspring that a male sires depends strongly on his display, D. We specify that male mating success (the number of offspring he sires) is proportional to a function $M(P,D)$, where $\partial/\partial P(\partial M/\partial D) > 0$; this means that high P values describe females who discriminate

Table 1. List of variables and their definitions.

i	allele specifying 'type' of individual ($i = 1, 2$)
x	proportion of newborn offspring that are of type 1
D_i	display of male of type i
P	female preference
F	female fecundity
E	environmentally determined costliness of choice
$C(P)$	fecundity cost paid by a female whose preference equals P
$M(P,D)$	function that relates male display D to his mating success, when female preference equals P
m_1	mutation rate (type 1 → type 2)
m_2	mutation rate (type 2 → type 1)
p_i	relative number of males of type i, compared with the number of females
$\mu_i(D)$	mortality rate of male of type i, with a display trait D ('evolvable display' model)
q_i	parameter ('quality') determining the mortality function for type i males
μ_i	mortality rate of male of type i ('constrained display' model)
μ_F	mortality rate of females
K_i	proportion of offspring that are type 1, when father is type i
$k_i(P)$	proportion of offspring that are type 1, when mother is type i and her preference equals P
$W(P',P)$	success of mutant strategy P' against resident strategy P

strongly against males with small displays, D. In all of our examples, we use $M(D,P) = \exp[(1 + D)^P]$. Our method generalizes to other functions that yield similar results as long as they are able to generate strong mating skews with high P values.

A general sexual-selection model must be able to answer the following questions:

(i) assuming that a preference allele, P, predominates in the population, then will an allele $P' \neq P$ spread? Which alleles P^* are uninvadable by alternative alleles?
(ii) assuming that females use preference P^*, what is the distribution of male types and display traits, D_i, in the population?

We first outline the general method for seeking uninvadable preference alleles, when the preference influences fecundity (direct cost) and the probability of mating with males of types 1 or 2 (indirect benefit). This method assumes that the mortality of various types of offspring is known. We then consider two versions of the model that differ in the way that male mortality is determined. In the 'evolvable display' model, males evolve to express the display level, D_i, to optimize a trade-off between mating success and mortality. In the 'constrained display' model, type i males always express a specific value D_i, and consequently suffer a specific, unalterable level of mortality.

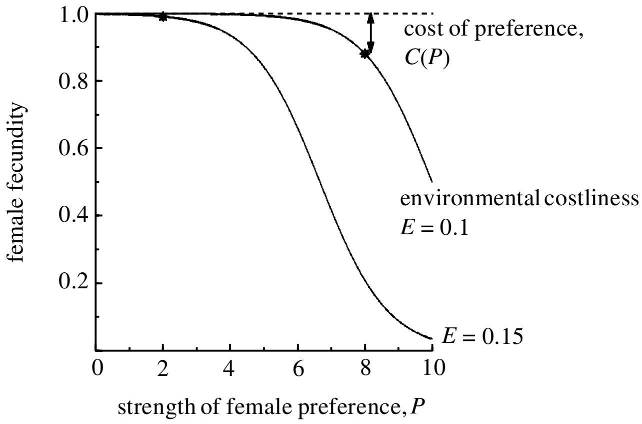

Figure 1. The two concepts of female choice costs. We assume that stronger mate-choice preferences P in females lead to lower fecundity, $F(P)$. All of our examples are based on the function $F(P) = 1 - \{1 + \exp[-(P - E^{-1})]\}^{-1}$. The parameter E describes whether the environment permits strong preferences without a strong decline in fecundity (low E), or whether fecundity declines with preferences sooner (high E). The actual cost of preference $C(P) = (F(0) - F(P))/F(0)$ depends both on the environmental costliness E and the strength of preference actually used by the female. Thus, a higher environmental cost, E, may be associated with a smaller cost paid, $C(P)$, if the females evolve to be less choosy in this situation (in the hypothetical examples marked, $P = 2$ and $E = 0.15$ lead to a smaller cost than $P = 8$ and $E = 0.1$).

(a) *Finding uninvadable preference alleles*

To determine which P' can invade P, we need to contrast the direct cost that females pay with the indirect benefits of mate choice. The indirect benefits depend both on the probability that a female's preference actually leads to mating with the preferred male and on the long-term success of offspring, either female or male, produced when mating with the preferred versus non-preferred males. Both components of the benefit require some non-trivial calculations. First, the probability of mating with the preferred male depends not only on P, but also on how many males of the preferred type are in the population. If, for example, female choice has depleted the variation in male types, even $P = 0$ guarantees mating with the preferred male type. Second, the invasion prospects of a genotype depend on the survival and attractiveness of first-generation offspring, but also, for example, on the attractiveness of male grand-offspring and grand-grand-offspring. Hence, a female offspring that carries an allele that makes grandsons more attractive can be more valuable than a female offspring without this allele. The appropriate technique to find endpoints of evolution in such settings is to calculate reproductive values of offspring based on a resident strategy P, and ask whether mutant P' exist that have higher fitness than the resident strategy (e.g. Taylor & Frank 1996; Houston & McNamara 1999; Pen & Weissing 2000). Reproductive values are defined as contributions of an individual to the population far into the future and hence take into account all appropriate genetic effects.

When deriving reproductive values, we assume constant female mortality, μ_F, regardless of her genotype, and mortalities μ_1 and μ_2 in males of types 1 and 2, respectively. An alternative preference allele can spread if the allele produces a larger sum of reproductive values of all offspring produced. The details of the calculation of offspring reproductive values and the invasion criterion for P' are presented in Appendix A.

(b) *The relationship between traits and mortalities in the 'evolvable-display' model*

To find the relationship between male type and its mortality, we need to specify how the display D influences male survival prospects. In the 'evolvable display' model, we assume a function $\mu_i(D)$ for each type, where mortality μ_i increases with the display D ($\mathrm{d}\mu_i/\mathrm{d}D > 0$). This relationship depends on male type. We then allow for the evolution of reaction norms between the display D_i and male type i. For each type i, the display D_i evolves to maximize that type's fitness. Assuming that males will mate with any female that accepts them, increasing display does not change the type distribution of a male's offspring but influences their number. After Houston & McNamara (1999; see also J. M. McNamara, A. I. Houston, M. Marques dos Santos, H. Kokko and R. Brooks, unpublished data), an uninvadable allele for the display, D_i^*, therefore maximizes $M(P, D_i)/\mu_i(D_i)$, where $M(P, D_i)$ is proportional to the number of offspring that he sires (see Appendix A for details). Males will suffer mortality $\mu_i^* = \mu_i(D_i^*)$ at this equilibrium. An evolutionarily stable strategy (ESS) is found when the values D_i^* that are the best responses to female preferences, P^*, also make P^* uninvadable by any alternative P'.

(c) *The relationship between traits and mortalities in the 'constrained display' model*

We also consider evolution in a simplified setting where the genetic architecture constrains males of type i to express a display trait D_i, in addition to experiencing a mortality rate μ_i. In this model, we do not assume that reaction norms can evolve to exploit the relationships between D_i, μ_i and male type. The trait, D_i, and mortality, μ_i, can covary positively, negatively or not at all. We are thus exploring female preferences for traits that either increase, decrease or have no effect on viability, but these correlations are fixed and do not evolve.

3. EVOLUTION OF PREFERENCES AND DISPLAYS

In the 'evolvable display' model, random mating $P^* = 0$ is always evolutionarily stable. If a population of females does not exhibit any preferences ($P = 0$), males do not evolve to show any costly displays ($D_i = 0$). Therefore, in the absence of any displays distinguishing between males, female preferences cannot invade (figure 2*a*). If costs of choice are high ($E > 0.165$ in figure 2), $P^* = 0$ is the only ESS and mate choice cannot evolve at all. However, when costs of choice are smaller, female preferences ($P^* > 0$) can evolve if females show an initial preference P that exceeds an invasion barrier. For the ESS with $P^* > 0$, females pay a fecundity cost for their preferences, but the cost $C(P^*)$ is predicted to remain small (in the example of figure 2, females never evolve preferences more costly than a 0.8% reduction in fecundity; the results of this magnitude are typical in all versions of our model).

Figure 2*a* plots the invasion barrier measured as the required initial preference P, whereas figure 2*b* measures it as the cost $C(P, E)$ that females pay for this initial preference. If the costs of being somewhat choosy are small (indicated by a small or moderate E value in figure 2), the invasion barrier is narrow and can be crossed relatively easily. As an example, evolution towards male displays and costly female preferences can be initiated at any $E < 0.15$ if it is facilitated by a 'moderate preference' allele that reduces fecundity by no more than 0.01% compared with random mating (figure 2*b*). Such low, cheap levels of initial preference can become established exaptively, e.g. via passive processes (Wiley & Poston 1996), sensory biases (Payne & Pagel 2000) or species recognition (Veen *et al.* 2001). At this initial preference P, evolution in males produces displays D_i that favour further increases in the preference P (and, as a consequence, in the displays D). The increase eventually stops at the evolutionarily stable equilibria for P^* and D_i^*, due to the increasing costs of further elaboration of preferences or displays.

While females are not predicted to evolve very costly preferences, these preferences are able to select for display traits causing high mortality in males. At the evolutionarily stable equilibria for P^* and D_i^*, the preferred males have larger displays D_i (figure 2*c*), but they can have either higher or lower mortality than the non-preferred males (figure 2*d*). The case where preferred males suffer from higher mortality occurs when the environment permits relatively cost-free female choice (low E, enabling a combination of high P with small C).

Figure 2 also shows the solutions for the 'constrained display' model. To aid comparison, we have calculated the evolutionarily stable preferences P^* and the invasion barrier for the spread of the preference for values $D_i = D_i^*$ and $\mu_i = \mu_i(D_i^*)$ that were reached in the 'evolvable display' model (for each value of E). The preferences P^* that were to be found stable in the 'evolvable display' model remain the best response to these display and mortality values of males in the 'constrained display' model, and hence the ESSs with $P^* > 0$ are the same in these two models. The invasion barrier has a different shape, however, as the 'constrained display' model assumes that displays are present even if the preference P is low (figure 2*a*,*b*). Specifically, the invasion barrier can disappear if male displays covary positively with survival (figure 2*a*,*b*).

The solutions for the 'constrained display' model in figure 2 are special cases, as they assume a specific relationship (one derived from the 'evolvable display' model) between the environmental cost of choice E and the covariation of male display with his mortality. More generally, the 'constrained display' model can be solved for any combination of E, D_i and μ_i. If male display is correlated with good survival ($\mu_1^{-1} - \mu_2^{-1}$ is positive) and the costs of choice are not too large (E is small), female preferences for the display can invade without the need to cross an invasion barrier (figure 3). If the correlation

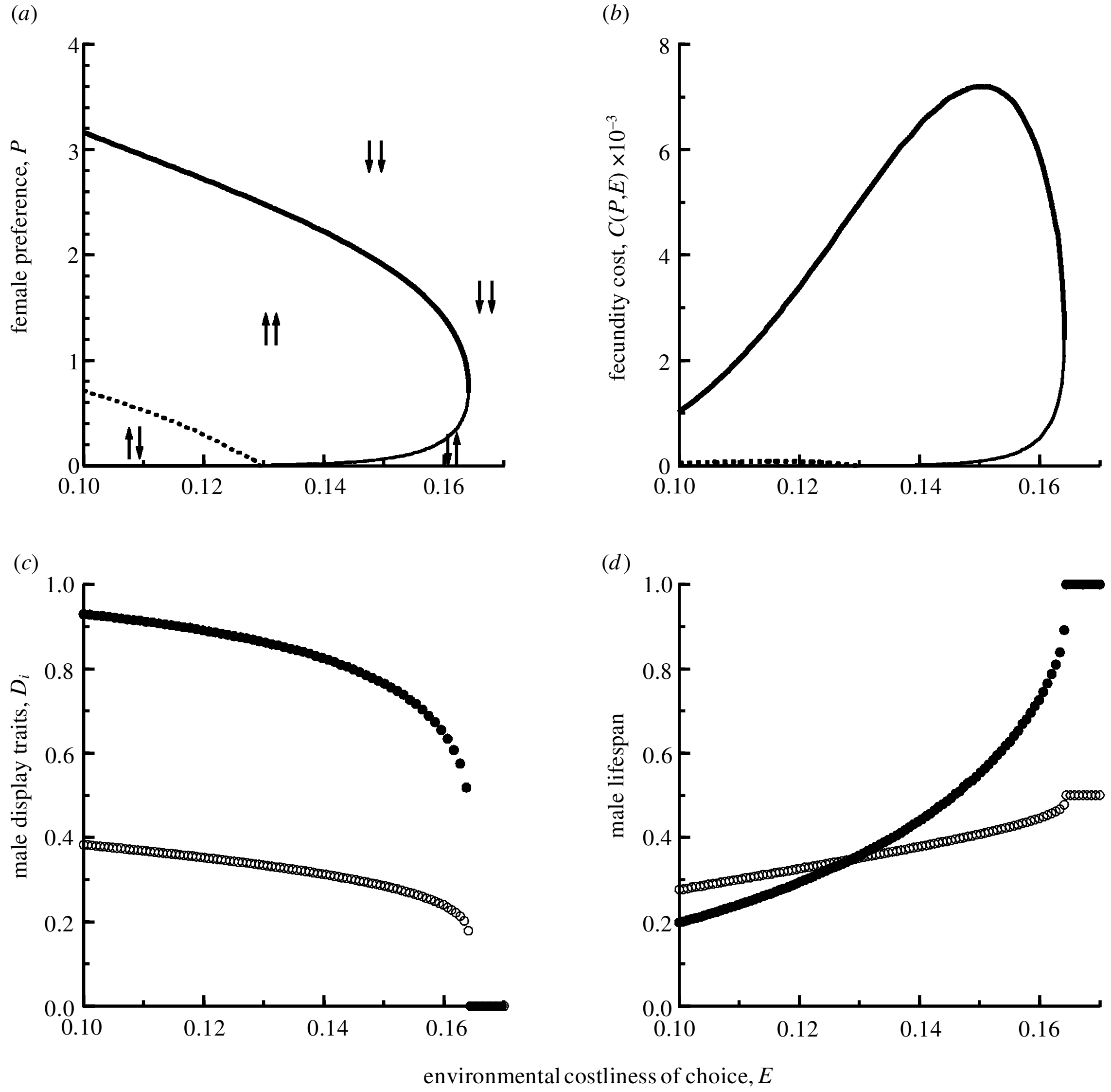

Figure 2. Evolution of female choice measured as (*a*) preference P, and (*b*) fecundity cost, $C(P)$, paid by a female with a preference P. The parameter E (x-axis) measures the speed by which increasing mate preferences reduce fecundity. In (*a*), the arrow pairs indicate the invasion of alleles for larger or smaller levels of female effort in the 'evolvable display' model (left arrows) and in the 'constrained display' model (right arrows); thick solid line, ESS; thin solid line, invasion barrier, evolvable display; dashed line, invasion barrier, constrained display. In addition to the ESS indicated, $P^* = 0$ is an ESS except between $E = 0.130$ and $E = 0.164$ in the 'constrained display' model. It is the only ESS if $E > 0.164$. (*c*) Display traits, D_i^*, and (*d*) expected lifespans, $1/\mu_i^*$, of type 1 (filled circles) and 2 (open circles) males at the ESS with $P^* > 0$ (or $P^* = 0$ where this is the only ESS). The results for the 'evolvable display' model are derived assuming the mortality functions $\mu_i(D) = [q_i(1 - (D/q_i)^3)]^{-1}$ (we assume that $D \leqslant q$), $q_1 = 1$ and $q_2 = 0.5$. The other functions and parameters used are $M(P,D) = \exp[(1 + D)^P]$, $m_1 = 0.05$, $m_2 = 0.01$ and $\mu_F = 1$. Preferred males always display more strongly than non-preferred males (*c*), but their lifespans can be longer or shorter (*d*).

between display and survival is zero or negative, female preferences can still invade but only after crossing an initial invasion barrier, which becomes wider with more negative correlations and with increasing choice costs (figure 3).

4. SEXY SONS AND VIABILITY INDICATORS: TWO ENDS OF A CONTINUUM

For female choice to be uninvadable by less costly random mating, it must lead to an increase in the reproductive values of offspring. Males and females of the preferred type indeed have higher reproductive values, but our models do not specify *a priori* whether the increase is due to high mating success, low mortality or both. The models show solutions where preferred type 1 males have higher mortality than type 2 males (figure 2*d*, small E; figure 3, left-hand side) and vice versa (figure 2*d*, large E; figure 3, right-hand side). It would be consistent with published work on this topic to classify the former as an example of a preference for a Fisherian trait and the latter as a preference for a good-genes indicator. Our modelling produces both kinds of outcomes from a single process, however, where indirect consequences of choice encompass both offspring viability and the mating success of sons in future generations—including sons produced by daughters, granddaughters etc. that have inherited alleles whose expression makes them more attractive.

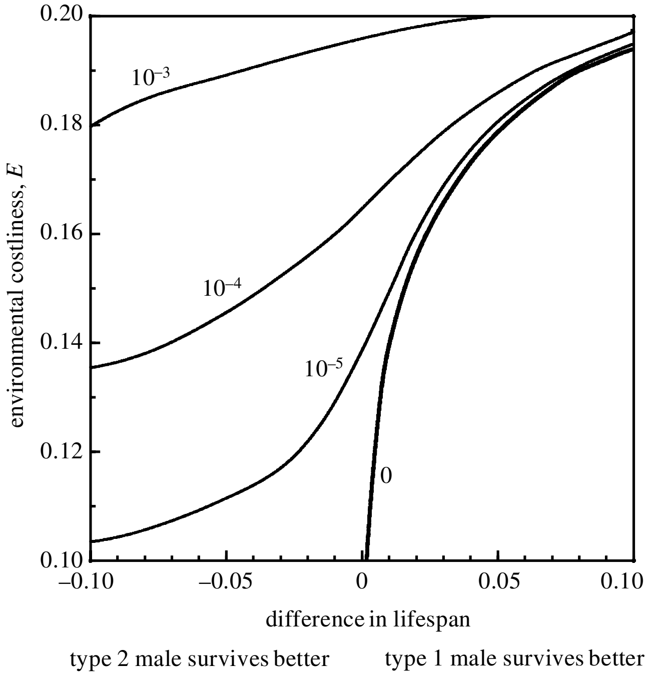

Figure 3. The width of the invasion barrier in the 'constrained display' model, when males of type 1 develop a display trait $D_1 = 1$, whereas type 2 males lack this trait, $D_2 = 0$. The width is calculated for various values of environmental cost of choice E and differences in lifespan caused by the trait, $1/\mu_1 - 1/\mu_2$ (we set $1/\mu_2 = 1$). The barrier width is indicated as the fecundity cost $C(P)$ that the population of females has to pay for its preferences P, before an increase in the strength of preference P is favoured by selection. To the right of the zero contour, $C(P) = 0$, i.e. there is no invasion barrier. The other parameters used are $m_1 = 0.02$ and $m_2 = 0.01$, with $M(P,D)$ as in figure 2.

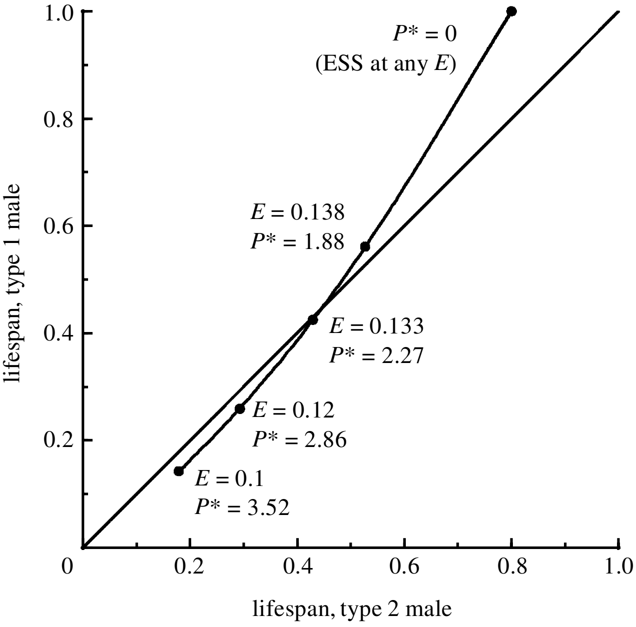

Figure 4. The coevolution of female choice and male mortality in the 'evolvable display' model. The functions and parameters are as in figure 2, except there is a smaller difference in mortality functions among males $q_1 = 1$, $q_2 = 0.08$ and symmetrical mutation: $m_1 = m_2 = 0.02$ (zero back mutation, $m_2 = 0$, produces a virtually indistinguishable outcome). The random-mating equilibrium ($P^* = 0$) is always stable. Male mortalities are expressed as the expected male lifespan, $1/\mu_i^*$. The coevolution of preferences and displays shifts male mortalities along the curve, provided that the invasion barrier is first overcome. Some possible endpoints (stable equilibria) are indicated with the values of the environmental cost parameter, E, and the corresponding female preference, P^*; see § 4 for further explanation.

The process can produce either outcome, regardless of whether we assume that males evolve to exploit a trade-off between mating success and costs of developing the attractive trait ('evolvable display'), or that they simply differ with respect to a genetically coded trait that also has survival consequences ('constrained display'). The balance between the importance of 'sexy-son' or 'good-genes' benefits can be altered simply by varying an environmentally determined cost factor E that specifies how easily females produce a strong mating skew and, hence, how competitive a mating environment the sons will experience.

We further illustrate the arbitrariness of distinguishing the two hypotheses and the generality of our modelling, by another example of the 'evolvable display' model (figure 4). As above, random mating is evolutionarily stable. Under random mating, males of type 2 suffer higher mortality than males of type 1. Consider a case where the environmental cost of choice is small, $E = 0.1$. If female preference crosses a very small $C(P) < 0.0005\%$ for $P = 0.1$) invasion barrier, coevolution of the male display and female choice increases male mortalities until their expected lifespan is less than 20% of the original value (figure 4). Here, the preferred males' display decreases their lifespan to fall below that of the less preferred males (figure 4, $C = 0.1$) and the mating skew is strong: $P^* = 3.52$ predicts that type 1 males with display $D_1 = 0.95$ enjoy 34.7 times as high-mating success as type 2 males with display $D_2 = 0.74$. The reproductive value of attractive offspring is high; not because they survive well, but because females prefer to mate with them—an erstwhile 'Fisherian' outcome.

Consider now that the scenario with $E = 0.1$ has been established. The high-mating skew might now shift the cost of choice, E, upwards. This can happen because of the accumulation of sexually antagonistic genes that benefit males (Rice 1992, 1996), more widespread sexually transmitted disease (Boots & Knell 2002; Kokko *et al.* 2002) or increased inbreeding (Farr 1983; Amos *et al.* 2001*a*,*b*). Also, external changes in environmental factors may alter search costs by increasing search time, the energetic costs of searching or exposure to predators (Pomiankowski 1987). Any process increasing E now leads to reduced female choice effort P, smaller male display traits D and increased male lifespan $1/\mu_i$. This eventually restores the function of the display as an indicator of viability (at $E > 0.133$, figure 4). However, the switch in relative male mortalities at $E = 0.133$ does not involve any qualitative change in the process responsible. Further environmental change can again cause coevolution of P, D and μ up and down the curve (figure 4).

5. DISCUSSION

We have built a general model of the evolution of female preferences for traits that indicate indirect benefits. The same process is responsible for the evolution of female preferences for males whose offspring survive either better or less well than those of unattractive males. Moreover, the correlation between male attractiveness and survival can switch from positive to negative (or vice versa) with changes in the environmentally determined costliness of female choice, and thus the intensity of sexual selection that females impose on males. At equilibrium, female preferences are maintained despite direct costs that we have modelled as reduced fecundity.

Based on the results of our model, viewing Fisherian runaway and good-genes indicators as competing alternatives is a hindrance to understanding the evolution of mate choice for indirect benefits. Instead, a single process favours female choice for males who sire offspring of high reproductive values. If female choice is cheap, and thus leads to strong mating skews among males, male attractiveness may become negatively correlated with survival or other fitness components. If the costs of strong preferences are prohibitive, preferred males are also expected to provide genetic benefits in other components of fitness. There is no qualitative difference between these outcomes; rather, they are endpoints of a continuum (figure 4).

As a device to illustrate that it is not useful to distinguish Fisherian and good-genes models of sexual selection, we respond to five important counterarguments that we anticipate might be raised.

(a) *Counterargument 1. Only Fisherian runaway evolution can account for female preferences for traits that lead to lowered survival rates in their offspring*

This view is simply wrong, as has been repeatedly pointed out (Grafen 1990*a*; Kokko 1998, 2001; Eshel *et al.* 2000; Jennions *et al.* 2001). If males vary in quality and optimize their display in a condition-dependent manner—standard assumptions in any 'good-genes' model—high-quality males may benefit from signalling with such intensity that their survival falls below that of low-quality males. Thus, negative correlations between attractiveness and survival are consistent with 'good-genes' signalling.

(b) *Counterargument 2. Only 'good-genes' models with condition-dependence can account for female preferences for traits that indicate higher survival rates in their offspring*

Our modelling shows that displays that indicate the 'type' of a male via a reaction norm can evolve to covary with high survival rates of their offspring. Here, 'type' can be interpreted as a male's genetic quality, because it determines the mortality cost of a display of certain magnitude. In this sense, the 'evolvable display' model corresponds to standard good-genes modelling. However, the 'constrained display' model also easily yields preferences for displays that are correlated with higher survival rates of offspring. This model simply assumes that a gene has pleiotropic effects: it is fully conceivable that a visible (or otherwise detectable) trait can also confer survival advantages. It is easy to see that females can benefit by using such a trait as a mate-choice cue. The preference can be maintained even if it is costly, as long as there is a mechanism (in our models, mutation) that maintains additive genetic variation in the male trait.

(c) *Counterargument 3. Preferences for Fisherian traits are arbitrary; preferences for viability indicators are not*

In polarizing Fisher and good-genes indicators, some authors characterize the Fisherian runaway process as the 'arbitrary traits' model (e.g. Møller 1991; Møller & Höglund 1991). The 'arbitrariness' of a preference or a trait seems to lack a consistent definition in the literature, however. Neither Fisher (1930) nor Lande (1981) used the word 'arbitrary'. Fisher (1930) did not consider male sexual displays to be arbitrary in any sense, and the runaway process (that is halted by decidedly non-arbitrary costs) is merely the second component of his theory of the evolution of mate choice. There is nothing in the results of our model that is inconsistent with the theory set out in Fisher (1930).

To our knowledge, the first usage of the expression 'arbitrary' traits was by Heisler (1985). She explicitly used it as shorthand for 'characters that may not themselves be the cause of variation in fitness, but merely reflect that variation owing to genetic correlations with other, directly selected characters' (p. 188). In this sense, Heisler (1985) uses 'arbitrary' to mean male traits that are not directly selected themselves, but indicate breeding value for other fitness components—i.e. a form of indicator trait. Kirkpatrick & Ryan (1991) described the Fisher process as 'a runaway [that] will generally establish preferences that are arbitrary with respect to male survival' (p. 34).

According to our results, females can evolve to favour traits that covary with survival of offspring positively, negatively or not at all. The process of evolving preferences does not establish itself equally easily in all of these cases. If survival is negatively correlated with the display, the benefits through attractiveness must override this cost, in addition to any direct cost of choosiness. If one defines arbitrary as 'having any correlation with male survival', one loses the distinction that survival will have an influence on how easily preferences will evolve. Signals are all arbitrary under this meaning. If one instead considers 'arbitrary traits' to be those that do not improve offspring survival, one is left with the result that preferences for 'arbitrary traits' can favour males who are of genetically high quality and signal this so intensely that their survival remains meagre (Grafen 1990*a*; Kokko 2001). We therefore conclude that distinguishing between preferences for 'arbitrary' and 'non-arbitrary' male traits is, in itself, arbitrary.

(d) *Counterargument 4. Even if both 'good-genes' and 'Fisherian' models make similar predictions, traits evolve in the former as a result of condition-dependent signalling of overall genetic quality; this is absent in Fisherian theory*

Models designed to explore Fisherian trait evolution have typically assumed a fixed relationship between male traits and viability, in this respect resembling our 'constrained display' model. 'Good-genes' models have assumed this relationship to vary depending on male quality. They therefore correspond to our 'evolvable display' model, if male 'type'—i.e. the trait that determines the display–mortality trade-off—is interpreted as his genetic quality.

As we have shown, both the 'constrained display' model and the 'evolvable display' model have female preferences that evolve as a response to the genetic correlation between male display and breeding value for total fitness. Both models also require a mechanism that maintains variation among males. Consequently, the preferred males will, at equilibrium, be fitter, either through their attractiveness alone or through a combination of improved viability and attractiveness. These results do not depend on whether the display is condition dependent. Therefore, the preferred males can also be said to be of higher genetic quality in the 'constrained display' model.

Despite this equivalence in terms of the ESS level of choice in the two models that we present, we agree that the genetic architecture of signalling will have an influence on the ease with which preferences become established. The 'evolvable display' model and 'constrained display' model yield different predictions in one respect: the width of the initial invasion barrier. In the 'evolvable display' model, the evolution of costly traits always requires some initial (albeit miniscule and conceivably exaptive) mate choice in females, regardless of the costliness of choice and the sign of the correlation between male advertisement and survival at the evolutionary endpoint. By contrast, a fixed level of sexual advertising (and concomitant relationship with survival), such as in our 'constrained display' model, generates some cases where the preference can spread without an invasion barrier. This can happen if the display trait is positively correlated with male survival. This finding echoes Fisher's original suggestion that female choice spreads initially because preferred males are favoured by natural selection.

The underlying genetics will determine how easily additive variation is maintained. Most probably, the general condition of a male, i.e. his 'type' in the sense of the 'evolvable display' model, is subject to a larger mutation rate than a single or a few genes that determine display trait expression in the constrained display model (see Rowe & Houle 1996; Kotiaho *et al.* 2001). The conditions for the maintenance of female choice are thus perhaps more likely to be met in the scenario where male traits evolve as a reaction norm to their overall condition. While we agree that this is a biologically meaningful distinction, the logic of the preference evolution process is not fundamentally different in the condition-dependent versus simple pleiotropic scenarios. Both require a process maintaining variation in male fitness and a detectable trait that separates fit males from unfit ones. Both also rely heavily on the benefits of producing 'sexy sons' and require that sexiness be a component of a male's fitness.

(e) *Counterargument 5. Self-reinforcing runaways or positive preference–display genetic correlations are found only in Fisherian models of sexual selection*

Female choice is self-reinforcing in both variants of our modelling: the benefit of producing attractive sons increases with female preference P, and stronger preferences P are favoured by selection as the importance of sons' attractiveness as a determinant of their mating success increases. Lande (1981) demonstrated that where heritable variation in mate choice and male display exist, the build-up of a genetic correlation between them, and thus some Fisherian runaway, is an inevitable consequence of choice. Eshel *et al.* (2000) showed that this sexy-son benefit is inherent in all good-genes models.

If self-reinforcing runaways are taken to mean open-ended evolution of male traits, it is true that those have been found in models of the runaway process only. However, as Fisher (1930) pointed out, the runaway process is likely very rapidly to reach an equilibrium where it is halted by ever-increasing costs. Existing runaway models mention this but have simply not incorporated these costs. In our model, self-reinforcing evolution of preferences does eventually halt and there are no differences between the different versions of our model in this respect. We did not, however, find cases of cyclic evolution of preferences in our model (cf. Iwasa & Pomiankowski 1995; Houle & Kondrashov 2002), but we have no reason to believe that the conditions for this to occur should differ between the evolvable- versus constrained-display versions of the model.

In conclusion, our model replaces the Fisherian–good-genes dichotomy with a general process of indirect selection in which fitness components trade-off along a continuum. The most important prediction to test is that females prefer males with high breeding values for total fitness (i.e. high reproductive value). It is neither valid nor useful to measure a single fitness component such as attractiveness or survival as a test of the theory that mate choice can evolve by indirect selection. Nevertheless, it remains worthwhile for empiricists to ask whether females seeking indirect benefits usually gain merely by producing 'sexy sons', or if offspring survival, fecundity or other fitness components are also improved. One end of the sexual-selection continuum arises when cheap choice allows a strong mating skew, so that variation in offspring reproductive value is almost completely driven by 'sexiness' of sons. Empirical examples consistent with this are scarce (Etges 1996; Wedell & Tregenza 1999; Brooks 2000), possibly because very cheap female choice and extreme mating skews are rare. A testable prediction from our model is that the trade-off between mating success and other components of fitness will covary with the costs of mate choice and the mating skew that results.

It also remains valid to ask whether indirect benefits differ between offspring sexes (Rice 1992, 1996). To retain conceptual simplicity in our models, we have ignored any sire effects on daughters apart from the attractiveness genes that they carry and pass on to their male descendants. It is clear that when male genes also influence the survival or fecundity of daughters, these factors will have to be incorporated into the reproductive value equation. Again, we would expect no qualitative difference in the process: female choice is selected for when it leads to a higher total of offspring reproductive values. For example, if sexually antagonistic genes (Rice 1992, 1996) cause daughters sired by attractive males to survive poorly, the invasion barrier for such a preference is simply expected to be wider than if daughters survive well.

Several authors have preached a pluralistic understanding of indirect selection on female mate choice (e.g. Andersson 1994; Houde 1997). Others have recognized that the good-genes process can result in positive or negative correlations (both phenotypic and genetic) between attractive advertisement and survival (Höglund & Sheldon

1998; Eshel *et al.* 2000; Kokko 2001) and that 'sexy-son' benefits are also inherent in the good-genes process (Eshel *et al.* 2000; Jennions *et al.* 2001; Kokko 2001). Since Fisher (1930), however, we have mostly missed the point that self-reinforcement of preferences and the evolution of indicator traits are merely different components of one and the same process of indirect selection.

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APPENDIX A: CALCULATING REPRODUCTIVE VALUES AND THE EVOLUTION OF FEMALE CHOOSINESS

We assume a 1 : 1 primary sex ratio. When x is the proportion of offspring that are born type 1 and female mortality does not depend on type, females are type 1 with probability x, irrespective of their age. Offspring of a male of type 1 will therefore be type 1 with probability $K_1 = (1 - m_1)x + [(1 - m_1 + m_2)/2](1 - x)$, and offspring of a type 2 male will be type 1 with probability $K_2 = [(1 - m_1 + m_2)/2]\, x + m_2(1 - x)$. We let $k_i(P)$ denote a type i mother's proportion of offspring of type 1, when the strength of her preference equals P.

The number of offspring sired by a male is proportional to $M(P,D)$. To simplify notation, the mating success of a resident male phenotype with display trait D_i is denoted by $M_i(P)$. It is calculated as $M_i(P) = M(P,D_i)/\Sigma_{j=1}^{2} p_j M(P,D_j)$, where p_i is the number of resident males of type i relative to the number of females. When a fraction x of newborn individuals are type 1, the p_i obey the relationships $p_1 = x\mu_F\mu_1^{-1}$ and $p_2 = (1 - x)\mu_F\mu_2^{-1}$.

The rules of haploid inheritance yield

$$k_1(P) = \frac{(1 - m_1)p_1M_1(P) + \dfrac{1 - m_1 + m_2}{2}p_2M_2(P)}{p_1M_1(P) + p_2M_2(P)}$$

and

$$k_2(P) = \frac{\dfrac{1 - m_1 + m_2}{2}p_1M_1(P) + m_2p_2M_2(P)}{p_1M_1(P) + p_2M_2(P)}.$$

At equilibrium, the fraction x satisfies $x = xk_1(P) + (1 - x)k_2(P)$. In a temporally stable population, the reproductive values of males (ν_{M_1}, ν_{M_2}) and females (ν_{F_1}, ν_{F_2}) of types 1 or 2, respectively, are derived from

$$\begin{aligned}
&\nu_{M_1} : \nu_{M_2} : \nu_{F_1} : \nu_{F_2} = \\
&\quad M_1(P)\mu_1^{-1}(D_1)F(P)[K_1(\nu_{M_1} + \nu_{F_1}) + (1 - K_1)(\nu_{M_2} + \nu_{F_2})] : \\
&\quad M_2(P)\mu_2^{-1}(D_2)F(P)[K_2(\nu_{M_1} + \nu_{F_1}) + (1 - K_2)(\nu_{M_2} + \nu_{F_2})] : \\
&\quad F(P)\mu_F^{-1}[k_1(\nu_{M_1} + \nu_{F_1}) + (1 - k_1(P))(\nu_{M_2} + \nu_{F_2})] : \\
&\quad F(P)\mu_F^{-1}[k_2(\nu_{M_1} + \nu_{F_1}) + (1 - k_2(P))(\nu_{M_2} + \nu_{F_2})].
\end{aligned}$$

The values are solved iteratively, scaling values so that $\nu_{F_1} = 1$.

By the method of Houston & McNamara (1999) and J. M. McNamara *et al.* (unpublished data), a mutant allele P' for female effort can invade allele P if $W(P',P) > W(P,P)$, where

$$\begin{aligned}
W(P',P) = F(P')\mu_F^{-1}\{&[xk_1(P') + (1 - x)k_2(P')](\nu_{M_1} + \nu_{F_1}) \\
&+ [x(1 - k_1(P')) + (1 - x)(1 - k_2(P'))] \\
&\times (\nu_{M_2} + \nu_{F_2})\}.
\end{aligned}$$

Here, the reproductive values ν_{M_1}, ν_{F_1}, ν_{M_2} and ν_{F_2} are calculated using the resident strategy P. Where $(\partial W(P',P)/\partial P')\,|_{P'=P} > 0$, selection will lead to an increase in choosiness P and where $(\partial W(P',P)/\partial P')\,|_{P'=P} < 0$, choosiness will decrease.

REFERENCES

Amos, W., Worthington Wilmer, J., Fullard, K., Burg, T. M., Croxall, J. P., Bloch, D. & Coulson, T. 2001*a* The influence of parental relatedness on reproductive success. *Proc. R. Soc. Lond.* B **268**, 2021–2027. (DOI 10.1098/rspb.2001.1751.)

Amos, W., Worthington Wilmer, J. & Kokko, H. 2001*b* Do female grey seals select genetically diverse mates? *Anim. Behav.* **62**, 157–164.

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Bakker, T. C. M. 1993 Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature* **363**, 255–257.

Blows, M. W. 1999 Evolution of the genetic covariance between male and female components of mate recognition: an experimental test. *Proc. R. Soc. Lond.* B **266**, 2169–2174. (DOI 10.1098/rspb.1999.0904.)

Boots, M. & Knell, R. J. 2002 The evolution of risky behaviour in the presence of a sexually transmitted disease. *Proc. R. Soc. Lond.* B **269**, 585–589. (DOI 10.1098/rspb.2001.1932.)

Brooks, R. 2000 Negative genetic correlation between male sexual attractiveness and survival. *Nature* **406**, 67–70.

Eshel, I., Volovik, I. & Sansone, E. 2000 On Fisher–Zahavi's handicapped sexy son. *Evol. Ecol. Res.* **2**, 509–523.

Etges, W. J. 1996 Sexual selection operating in a wild population of *Drosophila robusta*. *Evolution* **50**, 2095–2100.

Farr, J. A. 1983 The inheritance of quantitative fitness traits in guppies, *Poecilia reticulata* (Pisces: Poeciliidae). *Evolution* **37**, 1193–1209.

Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford University Press.

Grafen, A. 1990*a* Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546.

Grafen, A. 1990*b* Sexual selection unhandicapped by the Fisher process. *J. Theor. Biol.* **144**, 473–516.

Gray, D. A. & Cade, W. H. 1999 Quantitative genetics of sexual selection in the field cricket, *Gryllus integer*. *Evolution* **53**, 848–854.

Gustafsson, L., Qvarnström, A. & Sheldon, B. C. 1995 Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature* **375**, 311–313.

Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

Hansen, T. F. & Price, D. K. 1995 Good genes and old age: do old mates provide superior genes? *J. Evol. Biol.* **8**, 759–778.

Heisler, L. 1985 Quantitative genetic models of female choice based on 'arbitrary' male characters. *Heredity* **55**, 187–198.

Höglund, J. & Sheldon, B. C. 1998 The cost of reproduction and sexual selection. *Oikos* **83**, 478–483.

Houde, A. E. 1994 Effect of artificial selection on male colour patterns on mating preference of female guppies. *Proc. R. Soc. Lond.* B **256**, 125–130.

Houde, A. E. 1997 *Sex, color and mate choice in guppies*. Princeton University Press.

Houle, D. & Kondrashov, A. S. 2002 Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. Lond.* B **269**, 97–104. (DOI 10.1098/rspb.2001.1823.)

Houston, A. I. & McNamara, J. M. 1999 *Models of adaptive behaviour: an approach based on state*. Cambridge University Press.

Iwasa, Y. & Pomiankowski, A. 1995 Continual change in mate preferences. *Nature* **377**, 420–422.

Iwasa, Y., Pomiankowski, A. & Nee, S. 1991 The evolution of costly mate preferences II. The 'handicap' principle. *Evolution* **45**, 1431–1442.

Jennions, M. D., Møller, A. P. & Petrie, M. 2001 Sexually selected traits and adult survival: a meta-analysis. *Q. Rev. Biol.* **76**, 3–36.

Jones, T. M., Quinnell, R. J. & Balmford, A. 1998 Fisherian flies: benefits of female choice in a lekking sandfly. *Proc. R. Soc. Lond.* B **265**, 1651–1657. (DOI 10.1098/rspb.1998.0484.)

Kirkpatrick, M. 1982 Sexual selection and the evolution of female choice. *Evolution* **36**, 1–12.

Kirkpatrick, M. & Ryan, M. J. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.

Kokko, H. 1997 Evolutionarily stable strategies of age-dependent sexual advertisement. *Behav. Ecol. Sociobiol.* **41**, 99–107.

Kokko, H. 1998 Good genes, old age and life-history trade-offs. *Evol. Ecol.* **12**, 739–750.

Kokko, H. 2001 Fisherian and 'good genes' benefits of mate choice: how (not) to distinguish between them. *Ecol. Lett.* **4**, 322–326.

Kokko, H., Ranta, E., Ruxton, G. D. & Lundberg, P. 2002 Sexually transmitted disease and the evolution of mating systems. *Evolution* (In the press.)

Kotiaho, J. S., Simmons, L. W. & Tomkins, J. L. 2001 Towards a resolution of the lek paradox. *Nature* **410**, 684–686.

Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725.

Møller, A. P. 1991 Viability is positively related to degree of ornamentation in male swallows. *Proc. R. Soc. Lond.* B **243**, 145–148.

Møller, A. P. & Alatalo, R. V. 1999 Good-genes effects in sexual selection. *Proc. R. Soc. Lond.* B **266**, 85–91. (DOI 10.1098/rspb.1999.0607.)

Møller, A. P. & Höglund, J. 1991 Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proc. R. Soc. Lond.* B **245**, 1–5.

Norris, K. J. 1993 Heritable variation in a plumage indictor of viability in male great tits *Parus major*. *Nature* **362**, 537–539.

Partridge, L. & Endler, J. A. 1987 Life-history constraints on sexual selection. In *Sexual selection: testing the alternatives* (ed. J. W. Bradbury & M. B. Andersson), pp. 265–277. Chichester: Wiley.

Payne, R. J. H. & Pagel, M. 2000 Inferring the origins of state-dependent courtship traits. *Am. Nat.* **157**, 42–50.

Pen, I. & Weissing, F. 2000 Sexual selection and the sex ratio: an ESS analysis. *Selection* **1**, 59–69.

Petrie, M. 1994 Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371**, 598–599.

Pomiankowski, A. 1987 The costs of choice in sexual selection. *J. Theor. Biol.* **128**, 195–218.

Pomiankowski, A. 1988 The evolution of female mate preferences for male genetic quality. *Oxf. Surv. Evol. Biol.* **5**, 136–184.

Reynolds, J. D. & Gross, M. R. 1992 Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proc. R. Soc. Lond.* B **250**, 57–62.

Rice, W. R. 1992 Sexually antagonistic genes: experimental evidence. *Science* **256**, 1436–1439.

Rice, W. R. 1996 Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**, 232–234.

Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond.* B **263**, 1415–1421.

Taylor, P. & Frank, S. 1996 How to make a kin selection model. *J. Theor. Biol.* **180**, 27–37.

Veen, T., Borge, T., Griffith, S. C., Saetre, G. P., Bures, S., Gustafsson, L. & Sheldon, B. C. 2001 Hybridization and adaptive mate choice in flycatchers. *Nature* **411**, 45–50.

Wedell, N. & Tregenza, T. 1999 Successful fathers sire successful sons. *Evolution* **53**, 620–625.

Wiley, R. H. & Poston, J. 1996 Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50**, 1371–1381.

Wilkinson, G. S. & Reillo, P. R. 1994 Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proc. R. Soc. Lond.* B **255**, 1–6.

Zahavi, A. 1975 Mate selection—a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.

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