

Sexual selection when the female directly benefits

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Why do females of many species mate with males on the basis of traits apparently detrimental to male survival? The answer may lie in the fact that these male traits are correlated with male condition. We consider the argument that high male condition directly benefits female fecundity and/or viability (e.g. through lower transmission of parasites, improved control of resources, or better paternal care). Using a quantitative genetic model we show how female preferences for male traits that indicate condition can evolve, even if the male traits themselves have deleterious effects on both the male and the female's fecundity. So-called 'arbitrary preferences' can spread in this way because male traits subject to sexual selection are often under additional selection to become correlated with condition. At equilibrium the positive effects of male condition on a female's fecundity and the negative effects of the male trait on her fecundity are balanced and the female preference is under stabilizing selection. The male trait will often be correlated with viability, but not with fecundity, even though the preference evolved as a result of differences in male fecundity. The mean fecundity of females is not maximized, and can steadily decline as the male trait and female preference evolve. If the male trait has no direct deleterious effects on female fecundity, as may happen in species with no paternal care, female preferences are under continuous directional selection to increase.

ADDITIONAL KEY WORDS:—Fecundity selection – handicaps – mean fitness – female preferences – condition – paternal care – quantitative genetics – theoretical models – birds.

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INTRODUCTION

The bright colours, exaggerated tails and energetic courtship displays exhibited by males of many species are thought to have evolved through sexual selection by female choice (Darwin, 1971; Pomiankowski, 1988; Kirkpatrick & Ryan, 1991). The challenge has been to understand how female preferences for traits detrimental to male survival could evolve. The existence of such preferences is especially puzzling in species in which the male provides parental care. For example, the male quetzal is one of the most beautiful and conspicuous birds of Central America (Janzen, 1983), yet provides substantial parental care, as does the male paradise flycatcher which is burdened with a tail up to 2.5 times the length of his body (Ali & Ripley, 1983). Such extravagant male traits may compromise the level of parental care or attract predators to the nest, and consequently negatively affect the fecundity of the female.

What does the female gain by choosing a male with an extravagant secondary sexual trait? One possible answer is that she gains nothing directly. Instead, it is hypothesized that the female preference evolves as a correlated response to (1) sexual selection on the male character, with which the female preference is genetically correlated (the 'Fisher Process'; Lande, 1981; Kirkpatrick, 1982); (2) higher offspring viability, inherited from males expressing the exaggerated trait to highest degree, and with which the female preference is also correlated genetically ('good genes'; Pomiankowski, 1987; Iwasa, Pomiankowski & Nee, 1991) or (3) natural selection on other female traits (Kirkpatrick & Ryan, 1991). Here we consider a second possibility: that the evolution of a female preference for a male trait directly affects her survival or the number of offspring raised (fecundity). Using a theoretical model we show that an initial low preference for an elaborate male trait will evolve to higher levels despite deleterious effects of the male trait to female fecundity, provided that (1) the degree of expression of the male trait indicates his overall physical condition and (2) high condition in the male is directly beneficial to the female, thereby compensating for any deleterious effects of the male trait on female fecundity. The direct benefits of mating with a male in high condition may include superior male parental care, or a reduced probability of acquiring from the male a sexually-transmitted disease or contagious parasite (Heywood, 1989; Borgia & Collis, 1990; Reynolds & Gross, 1990). In our model we assume that a female

bases her choice only on the degree of elaboration of the male trait, and that she is otherwise unable to assess a male's condition.

We also assume that while the male trait is heritable, his condition is not. Non-heritable condition is one way in which this model differs from good genes models of sexual selection (Pomiankowski, 1988). Good gene effects are unlikely to be completely absent in nature, but we exclude them in order to examine the consequences of the alternative hypothesis, that female choice evolves mainly by direct natural selection (Kirkpatrick & Ryan, 1991). Given our assumptions, the female preference and male trait evolve jointly to ever higher degrees of exaggeration, until a point is reached at which the benefit to females from pairing with males in good condition is exactly balanced by the costs to her of the elaborate trait on which her choice is based. Interestingly, at this equilibrium sexual selection holds the male trait well off the value that would maximize his contribution to her survival or fecundity. Since mean male condition cannot evolve, the mean fitness of females may actually decline as the preference evolves. In other cases, when the female suffers no cost from the male trait (e.g. because parental care is absent), but still receives a benefit from her choice (e.g. fewer parasites), the preference may continue to evolve indefinitely (and mean female fitness always increases). Under these circumstances we expect the most extraordinary degrees of exaggeration in the male sexually selected trait.

We first illustrate these arguments in graphical form, and then develop them using a quantitative genetic model. Second, we consider the evolution of the correlation between degree of expression of the male trait and his condition; it is this correlation on which the present model depends. As discussed by Andersson (1982), Parker (1983), Nur & Hasson (1984), Grafen (1990a, b) and Michod & Hasson (1990), the correlation may evolve as an adaptive response to sexual selection. We show that under many situations the joint action of natural and sexual selection favours the strengthening of the correlation between the male trait and condition, and a concomitant increase in the non-genetic variance of the male trait. This gives a potential mechanism whereby preferences for apparently arbitrary male characters can spread in an adaptive manner. In the discussion we review the empirical evidence from birds supporting the proposition that many sexually selected traits are indices of condition.

We use the term 'condition indicator' (Andersson, 1982) rather than 'handicap' (Zahavi, 1977) for the male trait because the handicap has come to mean many different things and there appear to be at least four kinds (Grafen, 1990a; Iwasa *et al.*, 1991). The condition indicator is one class of handicap, albeit the class most often considered to work. The evolutionary quantitative genetic model we develop is similar to one locus and ESS models of the handicap mechanism in which the female directly benefits (Heywood, 1989; Grafen, 1990a, b), as summarized in Appendix 2. Our results confirm and generalize the results of these models.

Graphical illustration

We represent the essential features of the natural and sexual selection process in Fig. 1. Two attributes of the male are critical: condition (c), invisible to the female, and the visible trait (z) which positively correlated with c (and hence is referred to as the condition indicator, or simply male trait). An example of such

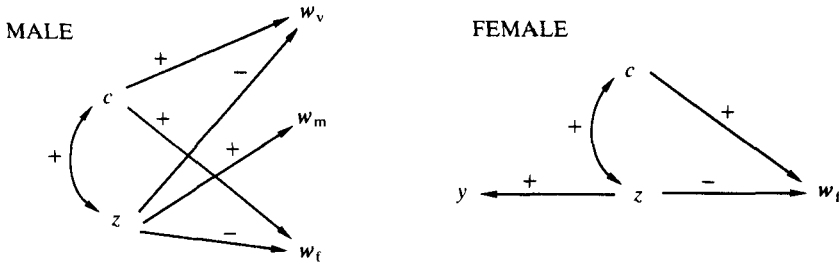


Figure 1. Selection on a male trait and female preference for that trait, when the male trait is correlated with condition. z , c and y are the male trait, male condition, and the female preference, respectively. w_v , w_m and w_f refer to the components of fitness: viability, mating success and fecundity, respectively. Signs of all path coefficients leading from condition (c) to the components of fitness are positive by assumption. Signs of other path coefficients have been assigned to represent a typical equilibrium situation. In 'good genes' models of sexual selection, the path from condition to fecundity is assumed to be zero.

a male trait might be tail length in the swallow, whose growth is known to be correlated with male condition (Møller, 1990). Following Kirkpatrick (1985), we assume a male experiences three bouts of selection over his lifetime, in the vertical sequence shown. The first bout is viability selection, assumed to take place prior to breeding. Male viability (w_v) increases with condition (as indicated by the '+' in the arrow from c to w_v) and decreases as the value of the male trait z increases beyond its viability optimum. Hence, the male trait is directly detrimental to his survival.

Next, males are subject to sexual selection: mating success (w_m) is greatest for males with large values of the trait, z . Finally, mated males experience fecundity selection: breeding success (w_f) increases with increasing condition, but again declines as the value of the trait z increases beyond the fecundity optimum. The evolutionary equilibrium is reached when the three separate forces of direct selection on z are balanced, i.e. when the mating advantage (w_m) of an increased value of the trait z is matched by the viability (w_v) and fecundity (w_f) disadvantage.

A female's preference is assumed not to affect her pre-reproductive viability or her ability to find a mate. Females experience a single episode of selection on the mating preference (y ; Fig. 1). A large value of y denotes a strong preference for males having a large value of the trait (z), whereas a small (positive) value of y indicates a weak preference for males of large z . The arrow from z to y thus indicates the positive association among matings of female preference and the male trait. We assume that selection on the preference works only through its association with the male trait and male condition, which determine the fecundity of the mated pair (Fig. 1). The negative effects of the exaggerated male trait on the pair's fecundity (w_f) will tend to favour a value of the male trait close to the fecundity optimum and (hence also of the preference), but the positive effects of the male's condition on fecundity, and the phenotypic correlation between condition and the male trait z will pull the mean value of the male trait upward (hence the mean value of the preference as well). Female preference reaches its evolutionary equilibrium when those two counteracting influences on fecundity are balanced.

MODEL

Here, we develop a quantitative genetic model of the process described above. The model is similar to that of Kirkpatrick (1985), whose paper should be consulted for details of the assumptions. The difference between his model and the one outlined here is that we include effects of male condition. We choose specific functional forms relating fitness to the male trait, male condition and female preference (Fig. 1) to obtain an analytical description of the joint evolution of the female preference and male trait. For simplicity, we assume the male trait is sex-limited in its expression. At the start of each generation, before selection, the three characters z , c and y are assumed to be normally distributed with means μ_z , μ_c , μ_y and phenotypic variances σ_z^2 , σ_c^2 , σ_y^2 . The phenotypic covariance between c and z is written σ_{cz} . There is no phenotypic covariance between the characters expressed in males and in females prior to sexual selection.

Selection on the male trait: viability selection

This is the first bout of selection experienced by males. We denote the optimum value of the male trait for viability as θ_v , and assume that viability declines as a Gaussian (normal) function away from that optimum to either side. We assume that male viability increases exponentially with condition. Male viability, w_v , can then be written as:

$$w_v(c, z) = \exp\left(\alpha_v c - \frac{(z - \theta_v)^2}{2\omega_v^2}\right). \quad (1)$$

ω_v^2 is the width (variance) of the Gaussian function relating viability to the male trait (z). α_v is a positive coefficient relating viability to condition (c). The viability function (1) preserves the multivariate normal distribution of z and c after selection (Felsenstein, 1977), but it assumes that the form of the selection on the male trait, z , does not depend on his condition, c . This assumption is probably unrealistic, and we consider consequences of relaxing it later in the paper. The new means, variances and covariance for z and c after viability selection are (Felsenstein, 1977):

$$\mu_z^* = \frac{\alpha_v \sigma_{cz} \omega_v^2 + \omega_v^2 \mu_z + \sigma_z^2 \theta_v}{\omega_v^2 + \sigma_z^2} \quad (2a)$$

$$\mu_c^* = \mu_c + \alpha_v \sigma_c^2 - \frac{\sigma_{cz}}{\omega_v^2 + \sigma_z^2} (\alpha_v \sigma_{cz} + \mu_z - \theta_v) \quad (2b)$$

$$\sigma_z^{2*} = \frac{\sigma_z^2 \omega_v^2}{\omega_v^2 + \sigma_z^2} \quad (2c)$$

$$\sigma_c^{2*} = \sigma_c^2 - \frac{(\sigma_{cz})^2}{\omega_v^2 + \sigma_z^2} \quad (2d)$$

$$\sigma_{cz}^* = \frac{\sigma_{cz} \omega_v^2}{\omega_v^2 + \sigma_z^2} \quad (2e)$$

Sexual selection

After viability selection the males are subject to sexual selection. Females mate with males according to their phenotype, z . We assume polygamous mating and a 'psychophysical' (exponential) preference function (Lande, 1981). Results are expected to be similar if alternative mating preference functions are employed (see Kirkpatrick, 1985). In the presence of females with a particular phenotype y , the mating success of a male of phenotype z and condition c is:

$$w_m(c, z|y) = \frac{\exp(\gamma y z)}{\int_{-\infty}^{\infty} \exp(\gamma y z) p^*(z) dz} \quad (3)$$

where γ is a constant term representing the intensity of sexual selection on the male trait ($\gamma > 0$), and $p^*(z)$ is the probability distribution of the male trait z prior to sexual selection. To determine $w_m(c, z)$, the mating success of a male of phenotype z and condition c in the presence of the entire female population, one may integrate (3) over the distribution of the female preference. However, the distribution of the male characters after sexual selection is more easily calculated by first noting that the trait z in the presence of females with preference y is normally distributed with mean $\mu_z^* + \gamma y \sigma_z^{2*}$, following Felsenstein (1977). Similarly, the mean c given females of preference y is $\mu_c^* + \gamma y \sigma_{cz}^*$. The variances and covariances, given y , are unchanged. Thus, the z and c values for males mated to females of preference y can be written in regression form:

$$z = \mu_z^* + \gamma y \sigma_z^{2*} + \varepsilon_z \quad (4a)$$

$$c = \mu_c^* + \gamma y \sigma_{cz}^* + \varepsilon_c. \quad (4b)$$

The variables ε_z and ε_c are normally distributed with means 0, variances σ_z^{2*} and σ_c^{2*} , covariance σ_{cz}^* , and are independent of y . Note that since sexual selection acts directly only on the male trait, the distribution of c changes solely as a correlated response to selection on z . The new means after sexual selection can now be obtained by taking expected values of (4):

$$\mu_z^{**} = \mu_z^* + \gamma \mu_y \sigma_z^{2*} \quad (5a)$$

$$\mu_c^{**} = \mu_c^* + \gamma \mu_y \sigma_{cz}^*. \quad (5b)$$

The new variances of z and c and the new covariance between c and z are also obtained from equation (4):

$$\sigma_z^{2**} = \gamma^2 \sigma_z^{4*} \sigma_y^2 + \sigma_z^{2*} \quad (6a)$$

$$\sigma_c^{2**} = \sigma_c^{2*} + \gamma^2 \sigma_y^2 (\sigma_{cz}^*)^2 \quad (6b)$$

$$\sigma_{cz}^{**} = \gamma^2 \sigma_y^2 \sigma_z^{2*} \sigma_{cz}^* + \sigma_{cz}^*. \quad (6c)$$

Both z and c remain normally distributed.

Fecundity selection on males

The number of offspring produced by a mated pair is assumed to depend on the characteristics of the male. We use the unlimited male fertility model of Kirkpatrick (1985), in which the fecundity of a mated pair is unaffected by the

number of matings in which the male participates. This simplification is not strictly appropriate for situations in which the male provides parental care, but qualitative results do not differ if fertility is made to depend also on the number of matings (Kirkpatrick, 1985). Fecundity selection is assumed to work in a similar way to viability selection (eqn 1). Fecundity is a Gaussian function of the male trait and increases exponentially with male condition:

$$w_f(c, z) = \exp\left(\alpha_f c - \frac{(z - \theta_f)^2}{2\omega_f^2}\right). \quad (7)$$

θ_f and ω_f^2 are the optimum and the width of the Gaussian curve relating fecundity to the male trait, and α_f is a positive coefficient translating male condition to male fecundity. The mean values for c and z after fecundity selection are (using Felsenstein, 1977):

$$\mu_z^{***} = \frac{\alpha_f \sigma_{cz}^{**} \omega_f^2 + \omega_f^2 \mu_z^{**} + \sigma_z^{2**} \theta_f}{\omega_f^2 + \sigma_z^{2**}} \quad (8a)$$

$$\mu_c^{***} = \mu_c^{**} + \alpha_f \sigma_c^{2**} - \frac{\sigma_{cz}^{**}}{\omega_f^2 + \sigma_z^{2**}} (\alpha_f \sigma_{cz}^{**} + \mu_z^{**} - \theta_f). \quad (8b)$$

Net selection on males over the whole life cycle

The net amounts of directional selection on the two male characters z and c over all three episodes of selection are defined as the selection differentials:

$$s_z = \mu_z^{***} - \mu_z \quad (9a)$$

$$s_c = \mu_c^{***} - \mu_c. \quad (9b)$$

These selection differentials can be written in terms of the means and variances at the beginning of a generation by substituting expressions (2), (5), (6) and (8) into (9). The results are two very long equations which are not reproduced here.

Selection on the female preference

The preference a female exhibits is assumed not to affect her viability nor her mating success. However, selection on the preference occurs because males of different phenotypes have different fecundities, and the preference of a female affects who she will mate with. Females with stronger preferences mate with more elaborate males, generating a phenotypic correlation between the preference and male character (Kirkpatrick, 1985). The covariance between the preference and the male character among the matings is calculated from equation (4):

$$\sigma_{yz}^{**} = \gamma \sigma_z^{2*} \sigma_y^2. \quad (10)$$

The female preference is also correlated with male condition, but this correlation is mediated through the male character (Fig. 1). Hence, the mean female preference after selection is obtained from the regression of y on z , and

from the change in mean z resulting from fecundity selection:

$$\mu_y^{***} = \mu_y + \frac{\sigma_{yz}^{**}}{\sigma_z^{2**}} (\mu_z^{***} - \mu_z^{**}). \quad (11)$$

The selection differential on females is:

$$s_y = \mu_y^{***} - \mu_y. \quad (12)$$

As in the case of the male, this differential can be written in terms of means and variances at the beginning of a generation.

Evolutionary dynamics

The change in the mean phenotype from one generation to the next is governed by selection, and by the genetic variances and covariances of the characters (Lande, 1979):

$$\Delta \bar{\mathbf{z}} = \frac{\mathbf{G}\boldsymbol{\beta}}{2}. \quad (13a)$$

$\Delta \bar{\mathbf{z}}$ is a vector whose three elements are the mean changes across one generation for the three characters c , z and y . \mathbf{G} is the genetic variance-covariance matrix for these three characters. For simplicity we assume the genetic variances and covariances to remain constant from generation to generation. The factor of 1/2 takes into account the sex-limited expression of the characters. We assume that the female preference and male characters are autosomally inherited, and that genetic variance for condition is absent. In reality, some genetic variance in condition will be present, maintained for example by directional mutation (Iwasa *et al.*, 1991). The consequences of allowing genetic variance in condition to be present do not alter the general arguments that follow, and will be discussed in a later section. The directional selection gradient, $\boldsymbol{\beta}$ (elements $\beta_c, \beta_z, \beta_y$), is obtained as

$$\boldsymbol{\beta} = \mathbf{P}^{-1} \mathbf{s} \quad (13b)$$

where \mathbf{P} is the phenotypic variance-covariance matrix at the start of each generation before any selection takes place, and \mathbf{s} is a vector whose elements are the three selection differentials for z , c and y as given by equations (9) and (12).

Evolutionary equilibria

Evolutionary equilibria for the male secondary sexual character and female preference are obtained assuming that the characters remain heritable, and that the genetic correlation between them has an absolute value less than 1.0. This differs from some single locus models, in which the equilibrium reached is the result of exhaustion of additive genetic variance (e.g. Heywood, 1989). From (13a), equilibrium is attained when direct selection on the male secondary trait and female preference ceases, i.e. $\beta_z = \beta_y = 0$ (since c is not heritable, β_c need not be 0 at equilibrium). For the female preference this occurs when $s_y = 0$ which, from equations (11) and (12), is when

$$\mu_z^{***} - \mu_z^{**} = 0. \quad (14)$$

Setting $\beta_z = 0$, and using (2), (5), (6), (8) and (14) we obtain the following equilibria, which represent the means at the start of a new generation:

$$\hat{\mu}_z = \theta_f + \alpha_f \frac{\sigma_{cz}}{\sigma_z^2} \omega_f^2 - \sigma_{cz}(\alpha_v + \alpha_f) \quad (15a)$$

$$\gamma \hat{\mu}_v = \frac{\sigma_{cz} \alpha_f (\omega_f^2 + \omega_v^2)}{\sigma_z^2 \omega_v^2} + \frac{(\theta_f - \theta_v)}{\omega_v^2}. \quad (15b)$$

The third term on the right-hand side of (15a) represents the within-generation change in z as a result of its phenotypic correlation with male condition. Male condition is always under directional selection to increase (as measured by $\alpha_v + \alpha_f$). Because the mean value of the male trait z is pulled upward as a result of selection on condition, the equilibrium mean z at the start of the generation (prior to any selection) evolves to a lower value in compensation (see Price, Kirkpatrick & Arnold, 1988). The first two terms on the right-hand side of (15a) represent effects of fecundity selection. The equilibrium for the male trait is independent of the strength of viability selection acting on males, as noted also by Kirkpatrick (1985) (Kirkpatrick's (1985) equilibria in the absence of condition effects can be derived from eqns (15) by setting $\sigma_{cz} = 0$). The second term in equation (15a) arises because of the effect of condition on the evolution of the female preference, which causes the male trait to be displaced from its fecundity optimum. The effect of viability selection is to displace the mean male phenotype from the equilibrium point within each generation, and the female preference correspondingly evolves to a strength (as measured by the product $\gamma \hat{\mu}_v$) which counters this displacement (eqn 15b).

Note that equilibrium values of both the male trait and female preference will be greatly exaggerated when the cost to a female's fecundity of the male trait is slight (i.e. ω_f^2 large). Such situations may not be uncommon in nature. For example, ω_f^2 will be large if males do not help raise the young, since the male's trait cannot hinder him in this capacity. If females nevertheless gain directly by mating with a male in good condition (e.g. fewer contagious parasites), then female preference can evolve upward almost without bound.

An example of the approach to equilibrium from different starting trajectories is given in Fig. 2. Two stages are evident. In the first stage the evolution of the female preference may be largely dominated by correlated response to sexual selection on the male character, since the preference and male trait are expected to be genetically correlated (Lande, 1981; Kirkpatrick, 1986). These trajectories converge towards a line, which is identical in position to the line of equilibria in models which do not incorporate natural selection on female preferences (Lande, 1981; Kirkpatrick, 1986). Once close to the line, the preference evolves mainly in response to direct selection toward the single equilibrium point. These dynamics are described in greater detail by Heywood (1989).

Mean fecundity

One remarkable feature of sexual selection in which the benefits to a female derive from the condition of the mated male is that the average number of offspring raised by a female may actually decline as the male trait and female preference evolve. This effect is separate from a possible transient decline due to

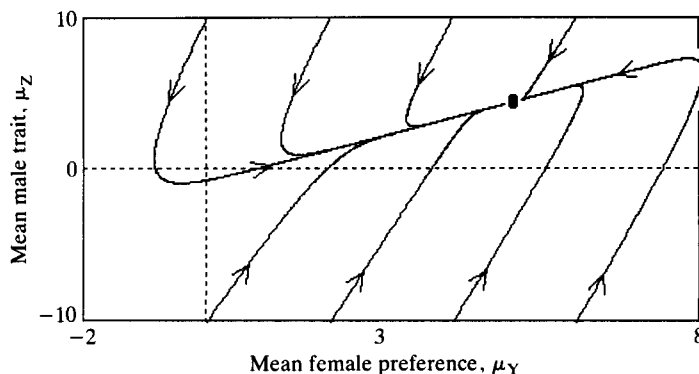


Figure 2. Joint evolution of the female preference and male trait when the male trait is correlated with condition, and both male condition and the male trait affect fecundity. The figure, obtained from iterating equations (6), (12) and (13) in the text, shows evolutionary trajectories from different starting conditions. Parameter values used are $\sigma_z^2 = \sigma_y^2 = \sigma_c^2 = 1$, $\sigma_{cz} = 0.5$, $\theta_v = \theta_f = 0$, $\omega_z^2 = \omega_f^2 = 20$, $\alpha_v = \alpha_f = 0.5$, $\gamma = 0.1$. The genetic correlation between the male trait and female preference is 0.1 and the heritability of each character 0.5, while condition is assumed non-heritable. Horizontal line shows the fecundity and viability optima for the male character, which in this example are both 0. At equilibrium (■) the male character is displaced from both its fecundity and viability optima. Vertical dotted line indicates mean female preference = 0, i.e. an absence of sexual selection. For illustrative purposes, very strong selection is depicted.

a strong correlated response to selection (Kirkpatrick, 1988) and, unlike models where condition is absent, mean female fecundity is not maximized at equilibrium. As the male trait evolves under sexual selection, its deleterious effects on fecundity will increase. However, average condition does not evolve, and so does not keep pace with the increasing value of the male trait through time, and mean fecundity evolves downward. While males in higher condition receive more of the matings as the mean preference increases in the population, this effect (which tends to increase mean fecundity) is often not sufficient to counteract the deleterious effect of the evolving male trait. The details of the process are described in Appendix 1.

A mean fitness surface is shown in Fig. 3, using the parameters of Fig. 2. In this example, mean fecundity at equilibrium is a factor of 1.8 lower than its value would be in the absence of any sexual selection. We have found a decline in mean fecundity under sexual selection to be the usual result when the fecundity and viability optima coincide. However, if the optimum values of the male trait differ between fecundity and viability, mean fecundity often increases under sexual selection. This is because, in the absence of sexual selection, the equilibrium value of the male trait lies between the fecundity and viability optima and sexual selection can shift the male trait closer to the fecundity optimum causing fecundity to rise.

Correlation between the male trait and condition

How do male traits that are correlated with condition arise in the first place? In many cases, male traits are automatically associated with condition prior to any evolution by sexual selection. For example, it may be more difficult for an individual bird in poor condition to grow as long a tail as would be optimal for survival or fecundity because of nutritional limitations. However, sexual

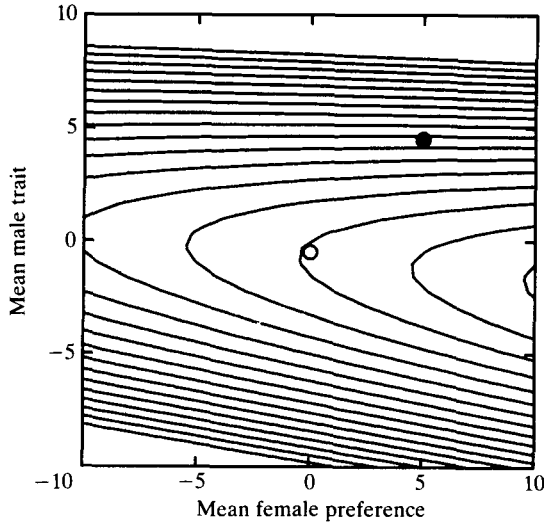


Figure 3. Plot of log mean fecundity (contours) against mean female preference and mean male trait, for the parameters of Fig. 2, based on the expression for $h(u)$ in Appendix 1. Contours are spaced 0.25 units apart. The surface of mean fecundity is a ridge whose height increases as μ_z decreases and μ_y increases. Filled circle (●) marks the equilibrium under sexual selection ($\hat{\mu}_z = 4.5$, $\hat{\mu}_y = 5.0$) and the open circle (○) represents the equilibrium in the absence of sexual selection ($\mu_z = -0.48$, $\mu_y = 0$). In the absence of sexual selection, the male trait is still displaced from the natural selection optimum (0,0), because it is selected upwards each generation through its correlation with condition. The effect is described in more detail by Price *et al.* (1988). In this example, mean fecundity in the absence of sexual selection is $1.8\times$ higher than it is at the equilibrium with sexual selection.

selection, once begun, will itself often favour both the evolution and strengthening of a correlation between the male trait and condition (i.e. sexual selection favours plasticity in the male trait whereby the degree of exaggeration

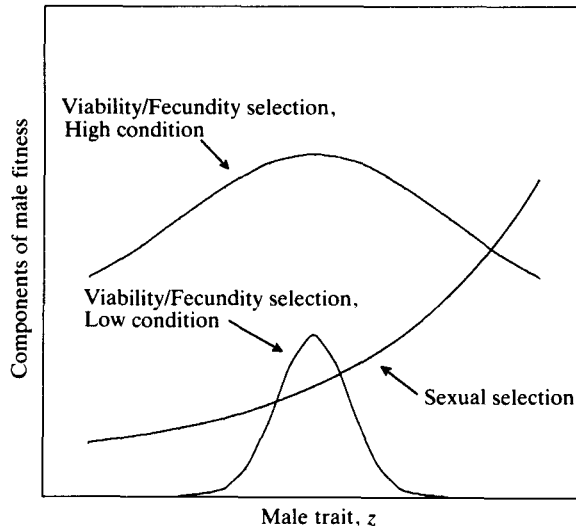


Figure 4. Males in lower condition experience proportionately greater natural selection on their secondary sexual character toward the viability and fecundity optima than males in high condition. All males experience the same intensity sexual selection. The result is that the male character is optimally developed to different degrees for males in different condition (Nur & Hasson, 1984).

of the trait in an individual male is dependent on his condition). The plasticity is expected to evolve whenever the loss in viability or fecundity stemming from a given exaggerated value of the male trait is less for a male in good condition than for a male in poor condition (e.g. Parker, 1983; Nur & Hasson, 1984). Typically, males in lower condition will suffer higher costs for a given deviation from the viability and fecundity optima (Fig. 4). To model condition-dependent selection on the male trait we can modify equations (1) and (7):

$$w_v(c, z) = \exp\left(\alpha_v c - \frac{(z - \theta_v)^2}{2c\omega_v^2}\right) \quad (17a)$$

$$w_f(c, z) = \exp\left(\alpha_f c - \frac{(z - \theta_f)^2}{2c\omega_f^2}\right), \quad (17b)$$

and add the restriction that $c > 0$.

The equations (17) differ from the earlier versions by the incorporation of condition (c) in the denominator of the Gaussian part of the selection function, indicating that selection on the male trait towards the optimum θ_v (or θ_f) is stronger for males in low condition than males in high condition. We did not include this term in the original model because the distributions of the characters become non-normal as a result of selection and it is impossible to obtain analytical solutions. We have numerically investigated dynamics and equilibria using equations (17) and found that when σ_c^2 is not large, evolution of the means μ_z and μ_y are closely predicted by use of approximate selection functions in which μ_c is substituted for c in the Gaussian (right-hand) part of equations (17). In this case, the equilibrium solutions are those shown in (15), substituting $\mu_c \omega_v^2$ for ω_v^2 .

Using equations (17) we can determine the optimal value of the male trait as a function of male condition. The total fitness function for males over the whole life cycle is found as the product of $w_m(c, z)$, $w_v(c, z)$ and $w_f(c, z)$ (eqns 3 and 17). Differentiating this product with respect to z , and setting the derivative equal to zero we obtained an expression for the optimal value of z as a function of condition. The full expression was complex and difficult to interpret, and so we took an approximation, assuming that σ_y^2 is small (this is equivalent to setting $w_m(c, z) \cong \exp(\gamma\mu_y z)$), to yield:

$$z_{\text{opt}} = \frac{\omega_f^2 \omega_v^2 \gamma \mu_y}{\omega_f^2 + \omega_v^2} c + \frac{\theta_f \omega_v^2 + \theta_v \omega_f^2}{\omega_f^2 + \omega_v^2}. \quad (18)$$

Thus, males are under selection to produce a different degree of elaboration of the male trait in proportion to their condition c . This predicts a plastic response in the degree to which the secondary sexual character is expressed, with males in lower condition developing less elaborate characters (see also Andersson (1982), Parker (1983) and Grafen (1990b) for similar results using different functional forms). The evolution of the plastic response depends on selection (i.e. the extent to which the cost of a given deviation in the male trait from its fecundity and viability optima depends on condition, and the strength of the female preference) and will also depend on genetic variability in plasticity (Via & Lande, 1985).

The expression (18) additionally allows us to predict the ultimate effect of sexual selection on the phenotypic variance of the male trait and its covariance with condition. To do this we assume that the variance among males in their

condition is fixed, and that the optimal value of the male trait as a function of condition (eqn 18) is eventually attained. The male trait at any point in its evolution has three components: an underlying additive genetic component, g , a component linearly attributable to condition (bc) (where b scales the effect of condition on the character) and a random environmental component, e :

$$z = bc + g + e. \quad (19)$$

If the optimal plasticity of the male trait is reached, then b attains the value $(\omega_f^2 \omega_v^2 \gamma \mu_y) / (\omega_f^2 + \omega_v^2)$ (from eqn 18). At this point, the variance in z and the covariance between c and z , are

$$\sigma_z^2 = \left(\frac{\omega_f^2 \omega_v^2 \gamma \mu_y}{\omega_f^2 + \omega_v^2} \right)^2 \sigma_c^2 + e_z^2 + g_z^2 \quad (20a)$$

$$\sigma_{cz} = \frac{\omega_f^2 \omega_v^2 \gamma \mu_y}{\omega_f^2 + \omega_v^2} \sigma_c^2, \quad (20b)$$

where e_z^2 is residual environmental variance in z , and g_z^2 is the genetic variance in z . One key result is that the equilibrium variance in the male trait and its covariance with condition both increase with an increase in the strength of the female preference. In addition, when fecundity or viability selection are weak, the variance in the male character can become very large.

The first term of (20a) is the variance in the male character attributable to condition. Grafen (1990b) defined a 'Fisher index' as the ratio of the portion of the variance in a character not attributable to condition to the total phenotypic variance in the character, i.e. as $(g_z^2 + e_z^2) / \sigma_z^2$. This will approximate the heritability of the trait when e_z^2 is small and condition is non-heritable (Grafen, 1990b). For moderately weak selection on the male trait (ω_f^2 and ω_v^2 large) the condition term dominates the variance (eqn 20a), the Fisher index is small, and variation in the male trait is greatly increased over that expected in the absence of any sexual selection. Thus, we expect condition indicators to be often highly variable.

Equation (20) indicates that the mean female preference in the population need not be large in order to favour a large increase in the variance of the male trait and its covariance with condition. Note also that the variance in the male character increases with the square of the intensity of sexual selection, whereas the covariance between the character and condition increases only linearly with the intensity of sexual selection. The result is that, as the male trait becomes more condition-dependent, the slope of the regression of condition on the male character decreases. This will cause the equilibrium values for both the female preference and the male trait to decline as a consequence (eqn 15).

It is somewhat surprising that as the male trait becomes more condition-dependent, selection on the female preference and male trait should weaken, with the result that both decline. However, as the variability of the male trait rises, a lesser preference is needed to yield a male in good condition than before. Indeed, it can be shown that the mean condition of mated males at equilibrium is (using 5 and 15):

$$\hat{\mu}_c^{**} = \frac{\sigma_{cz}^2 \alpha_f}{\sigma_z^2} + \alpha_v \sigma_c^2 + \mu_c \quad (21)$$

which, since σ_{cv}^2 and σ_z^2 rise at the same rate, does not decline as the male trait becomes more condition-dependent.

As a result of sexual selection, many characters may come under further selection to be condition indicators. The important conclusion from this section is that the sign of the covariance which is generated between the male character and condition depends only on the direction of the average preference, μ_v (eqn 20b). Thus, a small initial displacement of the male character (and preferences for that character) from the viability/fecundity optimum could potentially lead to rapid evolution of female preferences in different populations in different directions, with the direction depending on the sign of the initial displacement.

Correlation between the male trait and components of fitness

The observation of a correlation between a male sexually selected trait and one or more components of fitness has been used to test alternative models of sexual selection in nature (see Kirkpatrick & Ryan (1991) for a review of the various models). For example, Møller (1991a) demonstrated a positive correlation between a male swallow's tail length and his viability, and concluded that this association was a powerful force favouring the evolution of female preferences. This need not be the case. A correlation between the male trait and viability depends on both the direct effects of the trait on viability (which may be negative) and also on the positive effects of condition on viability (Zeh & Zeh, 1988). In our model, where the female preferences have evolved as a result of fecundity effects, the net correlation between the male character and viability is positive whenever $(\alpha_v \sigma_{cz})/\sigma_z^2 > (\mu_z - \theta_v)/\omega_v^2$ (from eqn 2). Even if $\mu_z - \theta_v > 0$ (indicating that the direct effect of the male trait on viability is negative), this can be obscured by the positive correlation between the male trait and condition. Thus, the male trait can be positively correlated with viability (and need not be correlated with fecundity) even when the female preference has evolved in direct response to the fecundity effects of the male. We demonstrate this numerically in Fig. 5.

The expected correlation between the male trait and fecundity of mated pairs depends on whether the trait itself has a direct deleterious effect on fecundity. If fecundity is unaffected by the male trait (e.g. when there is no parental care), a positive correlation between the male trait and fecundity may persist indefinitely, since both are correlated with condition. In such cases the observation of a correlation between the male trait and his contributions to fecundity is a strong test of the hypothesis that female preference has evolved by direct natural selection. In contrast, when the male trait has a direct negative effect on fecundity, then at equilibrium the male trait is expected to be uncorrelated with fecundity, because the positive effects of male condition on fecundity are balanced by the deleterious effects of his trait (Fig. 5). In these cases, tests of the hypothesis that the female preference has evolved by direct natural selection will require that the direct benefits from condition (e.g. few parasites) are distinguished from the direct costs of the correlated trait (e.g. poorer assistance at the nest).

Note that condition indicators will be positively correlated with a male's total fitness (the product of viability, mating success, and fecundity) even at

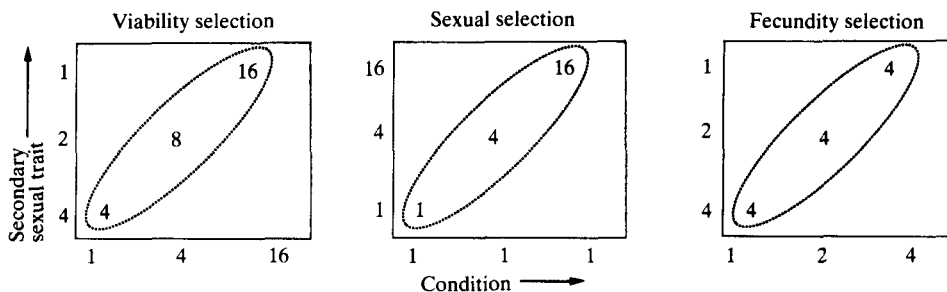


Figure 5. A numerical example of a pattern of selection on the male in an equilibrium situation. Numbers on the margins represent the fitness effects of condition (with the secondary sexual trait held constant) and the trait (with condition held constant). Numbers within the figure represent the net fitness at each life stage. Net fitness was obtained by multiplying the fitnesses attributable to the trait and to condition; other schemes such as additivity could as easily be employed. Dotted line encircles male phenotypes present in the population and show that condition and the male character are correlated. The two conditions for equilibrium are: no correlation between the male trait and fecundity and no net directional selection on the trait when condition is held constant (Fig. 6). Both conditions are met in this example. The correlation between the male trait and each component of fitness is indicated within the ellipses. In this example the trait is correlated with both viability and mating success at equilibrium.

equilibrium (Fig. 6). This is because the male trait and total fitness both remain correlated with condition. Condition indicators are examples of heritable characters which appear to be under directional selection but do not evolve because the appearance of selection arises as a consequence of the phenotypic correlation between the trait and condition (see Price *et al.* (1988) and Alatalo, Gustafsson & Lundberg (1990) for other examples).

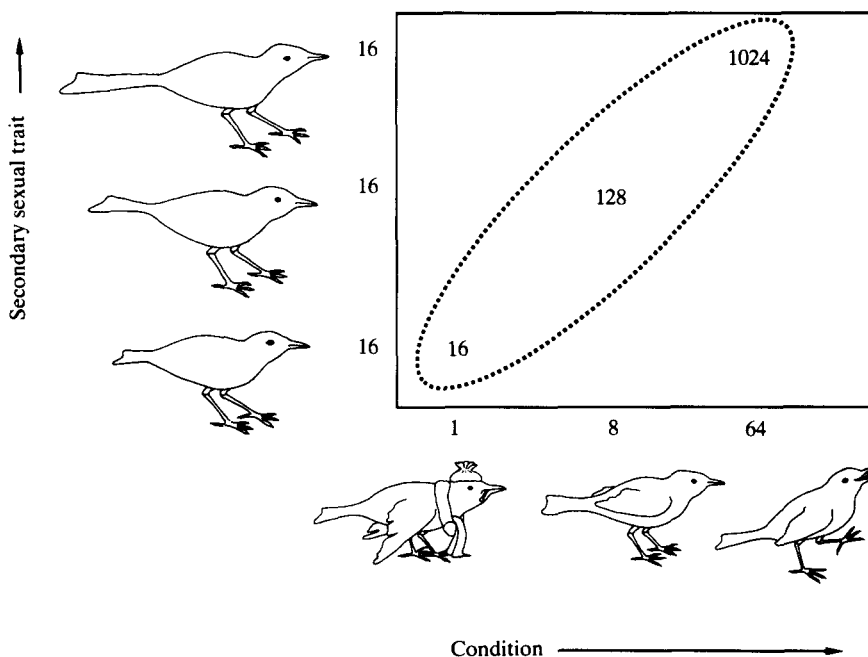


Figure 6. Total fitness across all three life-history stages is the product of the fitnesses at each life history stage (from Fig. 5). The male trait is positively correlated with total fitness at equilibrium.

DISCUSSION

In this paper we have emphasized the effects of natural selection on the evolution of female preferences acting through variation in male condition. As argued by Heywood (1989) and Reynolds & Gross (1990), females are likely to experience direct consequences of male condition in most mating systems, even if it is just by the occasional transfer of venereal disease. For example, transmission of infectious diseases from male to female in the satin bowerbird (Borgia & Collis, 1990), and male protection of females from harassment by other males in ducks (Holmberg, Edsman & Klint, 1989) have been proposed as important effects of male condition on females in species without parental care. The explicit model we have used to obtain analytical results has been one of unlimited polygamy. The essential conclusions are more general (Fig. 1) and should also be applicable to monogamous systems (Grafen, 1990a). In monogamy the intensity of sexual selection is limited (Kirkpatrick, Price & Arnold, 1990), but exaggeration can still be extreme if viability and fecundity selection on the male character are not strong.

Our model also assumes that the expression of male traits is plastic, and that they serve as indicators of male condition (Andersson, 1982). Problems in measuring condition and in identifying targets of sexual selection have made it difficult to demonstrate unequivocally that the expression of traits preferred by females is correlated with male condition. Nevertheless, most secondary sexual traits are phenotypically plastic and seem to be condition dependent (often called handicaps) (McComb, 1991; Hill, 1991). Examples in birds include plumage colouration (Lyon & Montgomerie, 1986; Hill, 1990, 1991), courtship intensity (Simmons, 1988; Hoelzer, 1989), song repertoires (Searcy & Andersson, 1986; Catchpole, 1987) and tail-length (Alatalo *et al.*, 1988; Barnard, 1991; Møller, 1991b). Indeed, there are few examples of male traits apparently subject to sexual selection that are not condition dependent. Plumage colouration in the Arctic skua (O'Donald, 1983) and in the yellow warbler (Studd & Robertson, 1985) are possibilities, but in neither case is there strong evidence that the plumage colour is a direct target of sexual selection (Baker & Parker, 1979; Studd & Robertson, 1985).

We distinguish two sorts of condition indicators on the basis of the magnitude of their deleterious effects on female fitness. In the first kind, effects of the male trait on female fitness are negligible. For example, the elaborate plumages of many lek-mating species probably have no adverse effects on the female at all, when the males provide no parental care and do not attend the nest. As a result, any direct effects of condition (however small) indicated by these characters should result in continual selection on the female preferences to increase. In this case we should expect preferences to become very strong, as noted by Heywood (1989). The intensity of sexual selection will increase as a result, but it will be checked because there are limits on the number of females an individual male can mate with (e.g. Kirkpatrick *et al.*, 1990). Nevertheless, the male character will be greatly exaggerated.

One sexually selected trait that has received detailed study is display of the male sage grouse. The sage grouse is polygamous and the male provides no parental care. Many secondary sexual traits are highly exaggerated. Strut rate and 'inter-pop interval' are two main targets of female choice (Gibson, Bradbury

& Vehrencamp, 1991). Display rate is highly variable among males (some apparently do not display at all), and displaying is highly energy consuming (Vehrencamp, Bradbury & Gibson, 1989). Although displaying at high rates for long periods of time is very costly to males, display rate and viability are not negatively correlated, presumably because display rate is positively correlated with male condition (Vehrencamp *et al.*, 1989). Thus, display rate has all the attributes of a condition indicator of the first type.

The absence of parental care may be as important as polygamy in accounting for the extreme development of male characters in lekking species. We predict that the secondary sexual characters will be the most exaggerated and ornate in those systems in which (1) male condition positively affects a female's fecundity and viability, but (2) the male traits that indicate male condition have no negative effects themselves on fecundity or viability of females. This contrasts with other explanations for exaggerated male traits which assume condition effects are absent, and predict that the most favourable situation for exaggeration is the absence of any direct effects on female fecundity.

Many condition indicators may have negligible deleterious effects on female fecundity, even in species in which the male provides parental care. For example, Price (1984) argued that territory size was a condition indicator. Though defending a territory is costly to a male, territorial defence and associated costs may be greatly diminished by the time the female is raising young, when she is receiving benefits from male parental care. Lyon & Montgomerie (1986) suggested that the degree of acquisition of adult plumage by individual birds may also be a condition indicator. The cost to a male possessing adult plumage (attacks from other males) may also have largely disappeared by the time females are receiving material benefits (Price, 1984). Female preferences for such traits may thus be under persistent directional selection.

In the second kind of condition indicator, the male trait has a direct deleterious effect on female fecundity. In such cases an equilibrium is reached when the negative effects of the male trait on female fecundity match the positive effects of high condition. An example of this type of equilibrium is shown in Figs 5 and 6. Interestingly, the mean fecundity of individuals is not generally maximized at such an equilibrium (Appendix 1). The evolution of condition indicators therefore provides an excellent example of how selection can lead to a decline in population mean fitness, and in some cases this might contribute to extinction of populations. Grafen (1990b) gives a numerical illustration of the process in a similar model. Such a decline in mean fecundity as the male trait and female preference evolve does not appear in models of sexual selection without condition effects. Indeed, in these other models, female mean fecundity is maximized at equilibrium (Kirkpatrick, 1985).

A possible example of a condition indicator which directly affects fecundity is tail length in the male swallow. Tail length is a phenotypically plastic trait, and tail growth is negatively correlated with parasite load, which affects condition (Møller, 1990). Manipulation experiments have been used to show that females prefer to mate with males having a long tail (Møller, 1988), and that a long tail probably negatively affects a male's viability, fecundity, and future mating success (Møller, 1989a). The benefit to a female from mating with a male in high condition (e.g. avoiding parasites) may be balanced by the deleterious effect of a long tail on her fecundity (e.g. reduced paternal care), although this remains to

be demonstrated. Tail ornaments appear to be condition indicators in a diversity of avian groups (Alatalo *et al.*, 1988; Barnard, 1991). Alatalo *et al.* (1988) showed that these ornaments are highly variable within populations of several species, as would be expected of characters correlated with condition. They also showed that ornament size is highly correlated with body size among individual males, which is not expected of a condition indicator unless condition is correlated with body size.

The correlation between the male trait and condition may arise in two ways. First, a male trait may be correlated with condition prior to becoming the target of female choice. For example, male sage grouse in low condition are unlikely to be able to display vigorously, whether or not display vigour is under sexual selection. In addition, many traits may be correlated with condition if condition is correlated with body size. Female preferences that subsequently arise for such traits will then be favoured by natural selection. Second, the male trait may not be correlated with condition initially, but if it should become the target of sexual selection for any reason, then a correlation with condition is expected to evolve subsequently. The scenario is as follows. As some sexual selection arises due to increase in a preference (e.g. by genetic drift), the male character is displaced from the male viability/fecundity optima. If males in different condition suffer different decrements in fitness due to this displacement, selection will cause the evolution of a correlation between condition and the character. The correlation will be positive or negative, depending on the direction of the sexual selection. Consider, for example, carotenoid in plumage which makes birds a cryptic green; higher levels make the birds a more conspicuous yellow and lower levels make the bird a more conspicuous brown (Kirkpatrick *et al.*, 1990). If female preference arises for yellow, there will be selection favouring a positive correlation between condition and carotenoid content. However, should a female preference arise for brown instead, then there will be selection favouring the evolution of a negative correlation between condition and carotenoid content. The preference will then be further selected to increase in the direction in which it first became established. Many female preferences that arise by chance may be biased in their directionality (Endler, 1992), and many male characters may have prior correlations with condition (a high carotenoid diet is difficult to maintain, for example (Endler, 1983; Hill, 1990, 1991)). However, the scenario we have outlined provides at least the possibility that two alternative preference states may exist, yielding some degree of arbitrariness in which one is achieved.

Interestingly, sexual selection on male traits to become better indicators of condition should also result in their becoming variable. Even with weak sexual selection male traits may become very variable, and this has an effect of weakening the selection pressures on the female preference to further increase. Thus, among male traits which directly affect fecundity, we expect extreme exaggeration to be confined to those which are somehow constrained in their variability. Note that if the male traits have no negative effect on fecundity, extreme exaggeration is always eventually expected.

The presence of condition indicators is probably widespread, and they may often be associated with fecundity. For simplicity we have assumed that condition is not heritable, but this is almost certainly not the case. How do our conclusions change when the assumption of non-heritable condition is relaxed?

Female preferences should now evolve upward not only as a direct result of a correlation between male condition and the number of offspring produced, but also indirectly as a result of higher offspring condition, and hence viability. We expect the direct and indirect forces to complement each other. Indeed, the effects of heritable and non-heritable condition can both lead to the evolution of male condition indicators, even if choice itself is costly (Pomiankowski, 1987; Grafen, 1990b; Iwasa *et al.*, 1991; this paper). The relative importance of direct and indirect natural selection on female preferences in nature will depend on the magnitude of the heritable and non-heritable components, the magnitude of the effects of condition on viability and on many other factors. Manipulative experiments of both condition and secondary sexual traits should prove to be a very fruitful avenue of research, enabling us to distinguish these forces as well as tackle other problems concerning the evolution of female preferences and male secondary sexual traits.

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APPENDIX 1

Mean fecundity often declines

In this section we show that mean fecundity is not maximized by sexual selection. Let p^{**} denote the joint density of a mated pair's male condition and male trait. That is, p^{**} is bivariate normal with means μ_c^{**} and μ_z^{**} , variances σ_c^{2**} and σ_z^{2**} , and covariance σ_{cz}^{**} . Using calculations similar to those of Felsenstein (1977), one can show that the mean fecundity is

$$\begin{aligned} \bar{w}_f &= \int_{c,z} w_f(c, z) p^{**}(c, z) dc dz \\ &= \frac{\exp\left(\frac{1}{2}\left(\alpha_f^2 \sigma_c^{2**} + \frac{2\alpha_f \theta_f \sigma_{cz}^{**} - \theta_f^2 - \alpha_f (\sigma_{cz}^{**})^2}{\sigma_z^{2**} + \omega_f^2} + 2\lambda^t \mu^{**} - \mu^{**t} H \mu^{**}\right)\right)}{\det(\mathbf{I} + \mathbf{B}\Sigma^{**})} \end{aligned} \quad (22)$$

where \mathbf{I} is the 2 by 2 identity matrix, Σ^{**} is the 2 by 2 covariance matrix of male condition and the male trait in mated pairs,

$$\mathbf{B} = \begin{pmatrix} 0 & 0 \\ 0 & 1/\omega_f^2 \end{pmatrix},$$

$$\mu^{**} = \begin{pmatrix} \mu_c^{**} \\ \mu_z^{**} \end{pmatrix},$$

$$\mathbf{H} = \Sigma^{**^{-1}} - \Sigma^{**^{-1}}(\Sigma^{**^{-1}} + \mathbf{B})^{-1}\Sigma^{**^{-1}}$$

$$= \begin{pmatrix} 0 & 0 \\ 0 & \frac{1}{(\omega_f^2 + \sigma_z^{2**})} \end{pmatrix},$$

$$\lambda = \Sigma^{**^{-1}}(\Sigma^{**^{-1}} + \mathbf{B})^{-1} \begin{pmatrix} \alpha_f \\ \theta_f/\omega_f^2 \end{pmatrix}$$

$$= \begin{pmatrix} \alpha_f \\ (\theta_f - \alpha_f \sigma_{cz}^{**})/(\omega_f^2 + \sigma_z^{2**}) \end{pmatrix},$$

and t indicates transpose. Using equations (2) and (5), we can write μ^{**} in terms of the means, μ_c , μ_z and μ_y , and the variances and covariances of male condition and the male trait at the start of a new generation. For ease of exposition we will

assume that $\mu_c = 0$; its exact value does not affect the results.

$$\begin{aligned}\mu_c^{**} &= \frac{\sigma_{cz}}{\omega_v^2 + \sigma_z^2} (\gamma\mu_y\omega_v^2 - \mu_z) + \alpha_v\sigma_c^2 + \frac{\theta_v\sigma_{cz} - \alpha_v(\sigma_{cz})^2}{\omega_v^2 + \sigma_z^2} \\ \mu_z^{**} &= \frac{\omega_v^2}{\omega_v^2 + \sigma_z^2} (\mu_z + \gamma\mu_y\sigma_z^2) + \frac{\alpha_v\omega_v^2\sigma_{cz} + \theta_v\sigma_z^2}{\omega_v^2 + \sigma_z^2},\end{aligned}\tag{23}$$

which can be written in matrix notation

$$\mu^{**} = D\mu + \rho$$

where $\mu = (\mu_z, \mu_y)^t$.

Substituting this expression in \bar{w}_f yields

$$\begin{aligned}\bar{w}_f &= \left(\frac{1}{\det(I + B\Sigma^{**})} \right) \exp \left(\frac{1}{2} (2(\lambda - H\rho)^t D\mu - (D\mu)^t H(D\mu)) \right) \\ &\quad \times \exp \left(\frac{1}{2} \left(\alpha_f^2 \sigma_c^{2**} + \frac{2\alpha_f\theta_f\sigma_{cz}^{**} - \theta_f^2 + \alpha_f^2(\sigma_{cz}^{**})^2}{\omega_f^2 + \sigma_z^{2**}} + 2\lambda^t\rho - \rho^t H\rho \right) \right).\end{aligned}$$

The only part of \bar{w}_f that depends upon the means at the start of a new generation is the first exponential, and thus the behaviour of mean fecundity as a function of μ can be studied via

$$h(\mu) = 2(\lambda - H\rho)^t D\mu - (D\mu)^t H(D\mu).$$

For instance, the ratio of mean fecundities at two alternative values of μ ($\mu = \mu_1$ and $\mu = \mu_2$) is $\exp((h(\mu_1) - h(\mu_2))/2)$. Also, \bar{w}_f is maximized if and only if h is maximized. Note that the ratio of mean fecundities cannot strictly be used if one wishes to compare mean fecundities when sexual selection is present with its absence. If there is random mating (i.e. no sexual selection), the variances and covariances do not change as a result of mating. Therefore, in the absence of sexual selection, the expression for \bar{w}_f should be written with single *s on the variance and covariance terms, and the full expressions for \bar{w}_f (cf. $h(\mu)$) need to be evaluated and compared. However, a comparison based on expressions $h(\mu)$ provides a close approximation if the variance in female preference is assumed small.

Since D is invertible when $\sigma_{cz} \neq 0$ (note also that γ is > 0), we can study h in the transformed coordinates $\tilde{\mu} = D\mu$. To show that h has no maximum, we need only show that

$$\tilde{h}(\tilde{\mu}) = 2(\lambda - H\rho)^t \tilde{\mu} - \tilde{\mu}^t H\tilde{\mu}$$

has no maximum. This is proved by writing $\tilde{\mu} = (\tilde{\mu}_c, \tilde{\mu}_z)^t$ and

$$\tilde{h}(\tilde{\mu}) = 2\alpha_f\tilde{\mu}_c + 2 \left(\frac{\theta_f - \alpha_f\sigma_{cz}^{**}}{\omega_f^2 + \sigma_z^{2**}} - \frac{\alpha_v\omega_v^2\sigma_{cz} + \theta_v\sigma_z^2}{(\omega_f^2 + \sigma_z^{2**})(\omega_v^2 + \sigma_z^2)} \right) \tilde{\mu}_z - (\omega_f^2 + \sigma_z^{2**})^{-1} \tilde{\mu}_z^2.$$

For any fixed value of $\tilde{\mu}_z$, we can make \tilde{h} arbitrarily large by making $\tilde{\mu}_c$ arbitrarily large. Translating this statement into one involving the original μ coordinate, for any fixed value of $\mu_z + \gamma\mu_y\sigma_z^2$, we can make mean fecundity arbitrarily large by taking an arbitrarily large value of $\sigma_{cz}(\gamma\mu_y\omega_v^2 - \mu_z)$. By considering (20), we see that fixing $\mu_z + \gamma\mu_y\sigma_z^2$ fixes μ_c^{**} , the mean trait of the

TABLE 1. Traits, selection pressures and notation in some recent models of sexual selection

| Author | Male secondary sexual trait | | Male condition | | Female preference | |
|----------------------------|-----------------------------|-------------------------------|----------------|-------------------------------|-------------------|-------------------------------|
| | Notation | Direct selection ¹ | Notation | Direct selection ¹ | Notation | Direct selection ¹ |
| Lande (1981) | z | v, m | — | — | y | — |
| Kirkpatrick (1985) | z | v, m, f | — | — | y | f^2 |
| Kirkpatrick (1986) | h | v, m | v | v | ρ | — |
| Heywood (1989) | H + E | v, m | E | v, f | P | f^3 |
| Grafen (1990b) | a | v, m | q | v, f | D | f^4 |
| Iwasa <i>et al.</i> (1991) | t | v, m | v | v | ρ | f^5 |
| Present study | z | v, m, f | c | v, f | y | f^* |

¹ v , Trait directly affects viability; m , trait directly affects mating success; f , trait directly affects post-mating fecundity and/or female viability. ² Fecundity selection on the female preference arises only through its phenotypic correlation with the male trait which itself directly affects fecundity. ³ Fecundity selection arises through the phenotypic correlation with the male trait, but only because the male trait is correlated with condition. ⁴ Fecundity selection on the female preference arises directly (as a 'time in the breeding season effect'), and also through the phenotypic correlation with male condition (*via* the male trait). ⁵ Fecundity selection on the female preference arises directly through the preference, as a cost of being choosy (see also Kirkpatrick, 1987). * The present study combines (2) and (3) above.

mated males. Increasing σ_{cz} ($\gamma\mu_y\omega_v^2 - \mu_z$) increases μ_c^{**} , the mean condition of the mated males, and thus increases mean fecundity. In other words, mean fecundity is large when μ_c^{**} is large, provided that μ_z^{**} is neither too large nor too small. This occurs (assuming that $\sigma_{cz} > 0$) when $\mu_y \gg 0$ and $\mu_z \ll 0$, such that females mate with extreme males in extremely high condition.

In Fig. 3 we have illustrated a mean fecundity surface (actually $h(u)$) as a function of the mean male trait and female preference. In this example, mean fecundity at equilibrium is substantially lower than it would be in the absence of any sexual selection.

APPENDIX 2

Relationship of this study to previous theoretical studies

There have been many models of sexual selection over the past decade. In this appendix we contrast the results of some of these models with the one presented here (Table 1). Early models (Lande, 1981; Kirkpatrick, 1982) came up with two appealing results. First, preferences can evolve rapidly and in different directions through a combination of genetic drift and correlated response to selection on the male trait. Second, there are an effectively infinite number of possible equilibrium points. These models could thus account for both the striking differences seen among species, and the apparently arbitrary nature of many preferences (as reflected in the adornments of the males). The two features incorporated here—direct fitness effects and male condition indicators—have been added to the models, although usually separately (Table 1). In this case, both the number of alternative equilibria and presumably the possibilities for genetic drift are reduced. If these features are widespread, the cause of apparently arbitrary sexually-selected differences among species requires new explanations.

Direct fitness effects have been added to the models in two ways. Either the

female suffers a cost as a result of her preference (choosy females have to search more; Kirkpatrick, 1987; Pomiankowski, 1987; Iwasa *et al.*, 1991) or the female's fitness is affected by the male she mates with (Kirkpatrick, 1985; Heywood, 1989). This latter type of selection, which is the kind we have considered here, arises because of the phenotypic correlation between the female preference and the male trait. Kirkpatrick (1985) argues that this type of selection may be quite weak. However, differences among males in their potential effects on females is more evident in natural populations than a correlation between search cost and choosiness among females. There may also be costs to choosing, and the effect of adding such costs to our model needs to be explored. One result will be that female preferences and male fecundity will remain correlated at equilibrium (cf. Fig. 5). General costs of female choice in a lekking species have been recently discussed by Phillips (1990), who argued that they were balanced by general benefits (reduced predation risk).

Two other researchers have jointly modelled condition indicators with direct natural selection on the female preference (Heywood, 1989; Grafen, 1990b). Their conclusions are similar to ours, in that an increase in the female preference is favoured. In their one and two-locus models there was no fecundity cost to the male trait, although Grafen (1990a) recognizes this possibility. In both cases the male condition indicator allele becomes fixed in the population. Both Heywood and Grafen noted a second equilibrium at which the male trait is fixed for the non-showy non-indicator type and female preference is absent. This appears to arise in Grafen's model because of the presence of direct search costs to the choosier females. Heywood's result arises because in his model the evolution of female preferences at low frequency is governed largely by the genetic correlation between the preferences and the male trait. Viability selection on the male trait outweighs sexual selection and the frequency of the male character becomes very low and essentially fixed. This second equilibrium is not seen in quantitative genetic models in which genetic variance is assumed to be present (and constant) in both male trait and female preference whatever their mean. Thus, a correlated response to selection of the female preferences is eventually countered by forces of direct selection (see the trajectories in Fig. 2). It has been argued that quantitative genetic models are less realistic than the two-locus models in which variances also evolve. However, we regard the decline of the variance to zero to be unrealistic, and current evidence indicates that heritability is generally present in male traits (Møller, 1989b, 1991b; Grant, 1991; Hill, 1991), such that optima are reached as a result of a balance of selective forces, and not through the exhaustion of additive genetic variance.

Throughout the paper we have downplayed the importance of the genetic correlation between the male trait and female preference, because it has no influence on equilibrium positions, although it does influence the directions and rate of approach to equilibrium (Fig. 2). The genetic correlation could be important to the equilibrium in some situations, since theoretically the equilibrium can be unstable (Kirkpatrick, 1985), and the female preference will then evolve in maladaptive directions as a correlated response to selection on the male trait. In 'good genes' models, the female preference evolves as a correlated response to heritable variation in condition (Iwasa *et al.*, 1991). We expect this latter effect to augment that which we have described here.

Finally, we note that in a model of monogamous sexual selection, Kirkpatrick

et al. (1990) considered the effect of female condition on the evolution of the male secondary sexual trait. In their model the date on which a female breeds is a female secondary sexual trait, and they used the phrase 'variance in nutritional state' for that portion of the variance in breeding date attributable to effects of female condition. Males were assumed not to actively choose females. However, since female condition affects male fecundity, condition indicators should arise in females and male preferences for these indicators spread; male choice is one explanation for the presence of many elaborated traits in females (Kirkpatrick *et al.*, 1990).