

Honesty, perception and population divergence in sexually selected traits

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SUMMARY

We investigate the evolution of female preference for one and two male ornaments, to address two issues in sexual selection: (i) what factors affect the evolution of female preferences; and (ii) how do preferences diverge between isolated populations, leading to speciation? We assume that the male traits are costly indicators of male condition ('handicaps'), and that females benefit directly from a high-condition mate. We find that optimal female preference for a single male trait equals (benefit of condition) \times (detectability of male trait) \times (honesty of male trait)/(costliness of preference). With two male traits to choose from, females should prefer the one with greatest honesty \times detectability, and ignore the second. These results highlight the role of perception in the evolution of both male ornaments and female preferences, and provide a theoretical illustration of 'sensory drive'. They confirm that a less honest male trait can displace a more honest trait if its detectability is sufficiently high. Environmental differences can drive evolutionary divergence between populations in both the male trait and female preference. Even small differences between habitats in detectability of male traits can trigger dramatic change in the female preference. Finally, populations may drift apart in arbitrary directions if choice of different male traits yields equivalent benefits to females.

1. INTRODUCTION

The bright colours and extravagant displays that males use to attract females present at least two unsolved problems: (i) what mechanisms favour the evolution of female preferences? and (ii) how do female preferences and attractive male traits diverge between populations, ultimately generating new species? Considerable progress has been made towards answering the first question (Lande 1981; Hamilton & Zuk 1982; Heywood 1989; Kirkpatrick 1987; Grafen 1990; Kirkpatrick & Ryan 1991; Iwasa *et al.* 1991; Price *et al.* 1993). The Fisher runaway process provides an explanation for arbitrary female preferences and population differences (Lande 1981; Kirkpatrick 1982). Yet, many male traits can indicate male qualities of benefit to females (Reynolds & Gross 1990; Iwasa *et al.* 1991; Price *et al.* 1993), and this severely restricts the possibility of evolution and divergence via a runaway process (Kirkpatrick 1985). The present paper addresses how adaptive preferences for such male traits can evolve and diverge among populations.

We investigate female preferences for male traits of fixed honesty and detectability. By 'honesty' we mean the accuracy with which the value of a male's trait indicates his overall health and vigour (condition), which we assume is beneficial to the female. Male traits should rarely be perfect indicators of male condition, because of developmental errors (Price *et al.* 1993) and possible adaptive strategies (Dawkins & Guilford

1991). 'Detectability' is the accuracy with which females perceive differences among males, which depends on the environmental background. It has been argued that detectability should strongly determine which traits form the focus of female choice (Wiley 1991; Endler 1992; Marchetti 1993).

Our paper has two parts. First, we model the evolution of a preference for one male trait. We ask how the interaction between honesty and perception influences the evolution of the preference, and suggest how environments may influence these quantities. Second, we model the evolution of female preferences for two male traits. We investigate how preference for one trait may completely displace preference for a second, producing a turnover of attractive male traits. We ask how different environments may favour divergence in female preference. We also determine whether populations may drift apart along neutral lines, independently of environment.

We assume that females receive direct benefits (higher reproductive success) from mating with males in high condition (Heywood 1989; Reynolds & Gross 1990; Grafen 1990; Price *et al.* 1993), although our qualitative results would hold if benefits were indirect, enhancing offspring viability ('good genes' (Iwasa *et al.* 1991)). Countering this advantage is the cost of choice itself, which we model as a direct search cost (Kirkpatrick 1987; Pomiankowski 1987; Grafen 1990; Iwasa *et al.* 1991). For example, choice may be energetically expensive, delay breeding, and increase

exposure to predation. Elsewhere, we have considered the consequences of a second type of cost to the female, that derived from the phenotype of her mate, should his attractive trait draw predators to the nest or hamper paternal care of young (Kirkpatrick 1985; Price *et al.* 1993).

2. THEORY: ONE PREFERENCE AND ONE MALE TRAIT

(a) Assumptions

We begin by considering a situation in which males differ by a single sexually selected trait z , and females vary in degree of preference y for the trait. Both z and y are heritable and not strongly genetically correlated, so they may evolve to their respective optima. Males also vary in overall health and vigour (condition, c) which is not heritable. Condition is equivalent to quality or true fitness in other models of the handicap, and higher condition is always advantageous. The three variables z , y , and c are normally distributed with phenotypic variances σ_z^2 , σ_y^2 and σ_c^2 . For simplicity these variances do not evolve from one generation to the next. Condition c and the trait z are positively correlated among males. The strength of the association between c and z is measured by their covariance (denoted $\sigma_{z,c}$), which is the honesty of the male trait. A low covariance means that numerous males are dishonest, having low condition but high z , or high condition but low z . A high covariance means that only males with high condition have large z . Differences between males in their condition are thus more strongly revealed by their trait z when this covariance is high. Honesty is fixed, and does not evolve (see Price *et al.* (1993) for a model of evolving trait honesty).

Mating is polygamous. Male mating success increases exponentially with increasing z , the rate of increase depending on the distribution of the preference y in the female population (figure 1*a*). Yet z is also a burden to males, directly reducing their survival (figure 1*a*). At equilibrium, the benefits to males of increased mating success must balance the survival costs. Males in high condition also have high 'fecundity'. Male fecundity refers to the direct effects a male has on the reproductive success of his mate, such as through territorial defence, paternal care, protection from harassment, and freedom from communicable disease. Male fecundity increases exponentially with c , other things being equal (figure 1*b*). Male survival also increases with c , but this has no qualitative effect on our conclusions, and we leave it out of the model.

A female chooses a male according to the value of her preference y : females with large y prefer males with high z , which leads to a correlation between y and z among mated pairs. Females are unable to detect c directly, but because c and z are correlated, females with large y tend to acquire mates in high condition, with positive effects on their fecundity (figure 2). However, female choice is costly, and choosy females (those with high y) pay a greater price than less choosy females. For simplicity we assume that females pay the cost of choice prior to mating (e.g. a survival cost). Without loss of generality, we set the natural selection

optima for both the male trait and the female preference equal to 0 in the absence of sexual selection.

(b) Fitness functions

With these assumptions, and using the relations shown in figures 1 and 2, we express fitness of

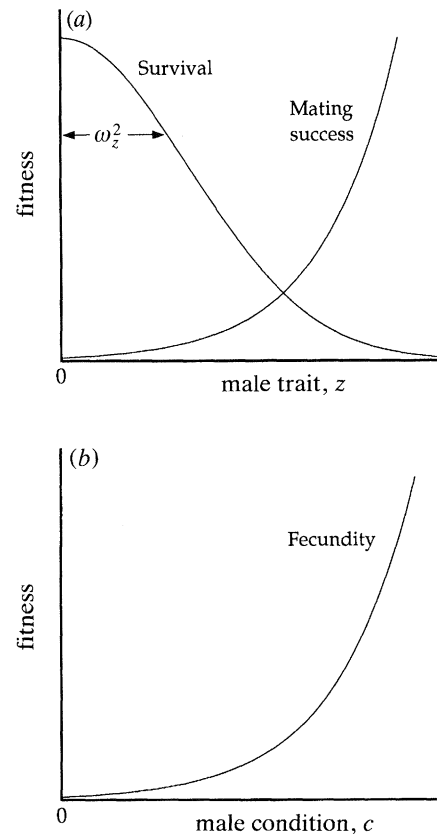


Figure 1. Selection on males. (a) Selection on the male trait z when male condition c is held constant. The bell-shaped (normal) curve indicates declining survival of males with increasing z ; ω_z^2 is the width or 'variance' of the normal curve (table 1). The exponential curve indicates sexual selection on z by a female of preference y ; the intensity of sexual selection is the rate of increase, γy . (b) Selection on male condition c when the male trait z is held constant; α is the rate of increased fecundity.

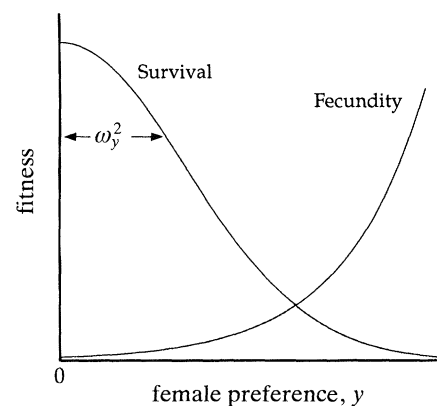


Figure 2. Selection on females. The normal curve indicates the cost of the preference: female survival (for example) declines at greater values of the preference, y ; ω_y^2 is the width or variance of the normal curve (table 1). The exponential curve indicates the increasing fecundity of females with increasing y , owing to the higher condition of chosen males.

Table 1. *Symbols and their meanings*

z, c, y	male trait, male condition, and female preference
α	benefit of male condition to his fecundity and to the fecundity of females mated to him
ω_z^2	1/costliness of male trait to his survival
ω_y^2	1/costliness of female preference to her survival
γ	detectability of male trait
$\sigma_{z,c}$	honesty of male trait

individuals over their lifetimes as functions of z, y and c . In the presence of females having a given preference y , male fitness $W_{M|y}$ is determined by the product of his survival, mating success and fecundity:

$$W_{M|y} = \exp[\alpha c - (z^2/2\omega_z^2) + (y\gamma z/\bar{W}_{M|y}^*)]. \quad (1)$$

Symbols and their interpretations are summarized in table 1: α is the fecundity advantage of male condition c ; ω_z^2 is the width of the survival function for z (figure 1*a*) and measures the costliness of z (a small value for ω_z^2 suggests that the male trait is very costly, in that a small increase in the trait leads to greatly reduced survival); γ is the intensity of sexual selection on the male trait by females of a given preference y (figure 1*a*). We interpret γ as the accuracy with which a female can perceive differences between males in z ($\gamma > 0$). If γ is large then, for a given y , small differences between males in z result in large differences in their mating success. Conversely, if γ is small, males varying in z will have similar mating success; this can be thought of as resulting from an inability of females to distinguish them; γ can also be thought of as a measure of the error rate made by females when choosing a mate (cf. Johnstone & Grafen 1992): it is inversely related to the average difference between the value of the male trait most preferred by females and the value they actually obtain. In this way, γ controls the strength of the covariance between y and z in mated pairs (see below).

Finally, $\bar{W}_{M|y}^*$ is the mean mating success of males in the presence of females of given preference y . It is computed as

$$\int_{-\infty}^{+\infty} \exp(\gamma y z) p(z)^* dz,$$

where $p(z)^*$ is the frequency distribution of z in the population after survival selection on males. $\bar{W}_{M|y}^*$ ensures that sexual selection on males depends on the frequency distribution of males available to females (Lande 1981).

Female fitness W_F depends simply on the cost of the preference and on the benefit obtained from the condition of the male with whom she mates:

$$W_F = \exp[-(y^2/2\omega_y^2) + (y\alpha\sigma_{y,c}^{**}/\sigma_y^{2*})]. \quad (2)$$

Here ω_y^2 is the width of the cost function on the preference (figure 2), and measures its costliness; female search costs increase steeply with increasing y when ω_y^2 is small, whereas costs are only mildly affected by increased y when ω_y^2 is large; α is the intensity of fecundity selection on male condition, and is the benefit to a female of mating with a male in high

condition; $\sigma_{y,c}^{**}$ is the covariance between female preference y and male condition c in mated pairs; it represents the success with which females having a strong preference obtain males in high condition, and it depends on both trait detectability γ and on the honesty $\sigma_{z,c}$ of the male trait; and σ_y^{2*} is the variance in y remaining after the search cost is paid (figure 2). The benefit from mating with a high-condition male is equivalent to fecundity selection directly on the female preference y ; the second term in the exponent of (2) describes such fecundity selection with the appropriate coefficients.

(c) *Equilibrium solution*

Here we present equilibrium mean values of the preference and male trait based on equations (1) and (2). These were calculated using the methods of Felsenstein (1977), as outlined by Price *et al.* (1993). The results are interpreted in the following Discussion.

Mean female preference stops evolving when the benefits of mating with a male in high average condition are balanced by the increased costs of the preference. This equilibrium \hat{y} is achieved at

$$\hat{y} = \alpha\sigma_{y,c}^{**}\omega_y^2/\sigma_y^{2*} \quad (3a)$$

$$= \alpha\gamma\sigma_{z,c}[\omega_z^2/(\omega_z^2 + \sigma_z^2)]\omega_y^2. \quad (3b)$$

Unless selection on the male trait is severe, ω_z^2 is likely to be much larger than σ_z^2 , in which case (3*b*) simplifies to

$$\hat{y} \approx \alpha\gamma\sigma_{z,c}\omega_y^2. \quad (3c)$$

The equilibrium value of the male trait \hat{z} depends directly upon the mean value of the female preference:

$$\hat{z} = \omega_z^2\gamma\hat{y} - \alpha\sigma_{z,c}. \quad (4a)$$

Assuming that ω_z^2 is much greater than σ_z^2 ,

$$\hat{z} \approx \alpha\omega_z^2\omega_y^2\gamma^2\sigma_{z,c} - \alpha\sigma_{z,c}. \quad (4b)$$

The first term on the right-hand side of equations (4) is the main quantity of interest. The second term is a correction to \hat{z} to compensate for a correlated response in z to selection on male condition c (see Price *et al.* 1988).

3. THEORY: PREFERENCE FOR TWO MALE TRAITS

(a) *Two traits*

Results above show how evolution of a single female preference and male trait depends on both the detectability (γ) and honesty ($\sigma_{z,c}$) of the attractive trait. Here we ask how female preferences evolve when more than one trait indicates male condition. We consider two traits, z_1 and z_2 . Each is correlated with condition c and is subject to survival selection of the form illustrated in figure 1*a*. We assume that z_1 and z_2 are equally variable ($\sigma_{z_1}^2 = \sigma_{z_2}^2 = \sigma_z^2$), and that the genetic correlation between them is not strong, such that the two traits are free to evolve to their respective optima.

Incorporating two traits requires critical assumptions about how females compare males with more than one attractive trait. There is little evidence to guide us. We assume that for a given unit of search

(proportional to y) females allocate the fraction a towards z_1 , and the fraction $1-a$ towards z_2 . This is a simple allocation in which preferences for the two male traits essentially compete for units of search. More complicated allocations are imaginable, but our simple rule is a reasonable start. If $a = 1$ then females use z_1 alone and ignore z_2 . The reverse is true when $a = 0$. Between these extremes, females prefer a linear combination of the male traits determined by a .

Over their lifetimes, the fitness of males is then

$$W_{M|y} = \exp \left\{ \alpha c - \frac{z_1^2}{2\omega_{z_1}^2} + \frac{z_2^2}{2\omega_{z_2}^2} + \frac{y[a\gamma_1 z_1 + (1-a)\gamma_2 z_2]}{\bar{W}_{M|y}^*} \right\}. \quad (5)$$

This is similar to the one-trait case (equation (2)) except that both z_1 and z_2 experience survival selection (of widths $\omega_{z_1}^2$ and $\omega_{z_2}^2$) and sexual selection; γ_1 and γ_2 are the detectabilities of the two traits.

Female fitness W_F in the two-trait case is identical to (2), but the strength of the association between the preference y and male condition c is now determined from the honesties and detectabilities of both male traits. Assuming that survival selection on the males is relatively weak, $\sigma_{y,c}^{**} \approx [a\gamma_1 \sigma_{z_1,c} + (1-a)\gamma_2 \sigma_{z_2,c}] \sigma_y^{**}$. The equilibrium female preference is obtained from (3a), which for a given value of the allocation a yields $\hat{y} \approx \alpha[a\gamma_1 \sigma_{z_1,c} + (1-a)\gamma_2 \sigma_{z_2,c}] \omega_y^2$. (6)

The optimal allocation \hat{a} by females remains to be determined, assuming that it too can evolve under natural selection. It can be shown that in both the one- and two-trait cases, \hat{y} is that value of y maximizing female fitness (equation (2)). By a similar logic, a should also evolve to maximize (2), which occurs when a maximizes $\sigma_{y,c}^{**}$. Assuming relatively weak survival selection on the male trait

$$\hat{a} = \begin{cases} 1 & \text{if } \gamma_1 \sigma_{z_1,c} > \gamma_2 \sigma_{z_2,c}; \\ 0 & \text{if } \gamma_1 \sigma_{z_1,c} < \gamma_2 \sigma_{z_2,c}; \\ \text{arbitrary} & \text{if } \gamma_1 \sigma_{z_1,c} = \gamma_2 \sigma_{z_2,c}; \end{cases} \quad (7)$$

In the third case of (7), all values of a yield identical female fitness (i.e. a is neutral). This is the only case in which more than one female preference may coexist indefinitely.

Equilibrium values for the male trait are

$$\hat{z}_1 = \omega_{z_1}^2 a \gamma_1 \hat{y} - \alpha \sigma_{z_1,c} \quad (8a)$$

$$\hat{z}_2 = \omega_{z_2}^2 (1-a) \gamma_2 \hat{y} - \alpha \sigma_{z_2,c}. \quad (8b)$$

4. HONESTY, PERCEPTION AND THE EVOLUTION OF FEMALE PREFERENCE

The optimal level of female preference for a single male trait can be expressed in words (equation (3c)). Mean female preference should equal (benefit of condition) \times (detectability of male trait) \times (honesty of male trait) / (costliness of preference).

This result demonstrates that the handicap mechanism of sexual selection works when females receive direct benefits, in agreement with earlier theory (Heywood 1989; Grafen 1990; Price *et al.* 1993). Female preference may evolve even when the male condition indicator is not completely honest (Johnstone & Grafen 1992); however, greater honesty favours a stronger

preference. Honesty of the male trait may be favoured to increase once the trait is preferred by females (Nur & Hasson 1984; Price *et al.* 1993).

Preference should be greatest when the detectability of the male trait is high. Search costs to females underly perception's effect. To intuit this, consider that strength of preference is proportional to time spent looking for a mate, and that each male encountered takes time to inspect. At any level of preference, a lower detectability of the male trait increases the female's inspection time per male (and may also increase the travel time between males), reducing the number of males that can be assessed per unit time. This in turn lowers the average condition of the best male encountered. If time is not costly, then females should merely spend more of it looking for additional males. But if time is expensive, lower benefits from a given level of preference will be outweighed by the costs, causing the preference to evolve to lower levels. As with honesty, detectability of a preferred male trait may be favoured to increase (Hasson 1989).

Detectability is likely to be a property of both the female sensory apparatus and the background against which the male trait is displayed. Its role exemplifies the phenomenon of 'sensory drive' in which sensory perception directs evolutionary change (Ryan *et al.* 1990; Endler 1992; Marchetti 1993). Ryan (1990) argued that female perception bias would guide the evolution of male ornaments. Our model confirms this, and extends perception's role to the evolution of the female preference itself.

With two (or more) male traits, females should prefer only the one having the highest detectability \times honesty, which is that trait revealing the greatest 'effective' amount of condition. The male trait preferred by females may be the less honest of the two if its detectability is sufficiently high (Guilford & Dawkins 1991).

Our prediction that females should prefer one male trait is at variance with the observation that species commonly possess many secondary sexual traits (Burley 1981; Zuk *et al.* 1990; Gibson *et al.* 1991; Reynolds & Gross 1992; Møller & Pomiankowski 1993). Possible mechanisms to maintain a diversity of preferences include: (i) all male traits are equally effective indicators of condition (similar detectability \times honesty), and preference is arbitrary (the third case of equation (7)); (ii) detectability \times honesty of male traits may vary temporally, and females adopt different preferences on different occasions (Zuk *et al.* 1990; Gibson *et al.* 1991); (iii) females may prefer different traits at different distances from the male, according to detectability; for example, male calls may be used at long distance, male display at short distance (McDonald 1989); (iv) different traits indicate different attributes of male condition (e.g. ectoparasites against endoparasites (Hamilton 1989; Zuk *et al.* 1990); and (v) female search costs are reduced when choice is based on a combination of male traits rather than on just one; this latter possibility could be modelled by altering the form of the allocation in equation (5) to allow simultaneous inspection of multiple male traits. A final possibility is that most

preferences are without adaptive consequences for females, and do not currently signal condition (Møller & Pomiankowski 1993).

5. POPULATION DIVERGENCE IN SEXUALLY SELECTED TRAITS

Our theory predicts a single equilibrium value for the female preference as determined by the parameters (i.e. benefit of condition, detectability, honesty of the male traits, and costliness of the preference). Hence, separate populations are expected to diverge in female preference whenever environmental differences affect these parameters.

Perception (detectability) of the male trait is likely to be one of the largest differences between environments, favouring divergence in preferences as suggested by Endler (1992). Interestingly, the male trait is more sensitive than the female preference to such differences. This is because the intensity of sexual selection on the male trait depends directly on detectability as well as indirectly through the effects of this parameter on the evolution of female preference (equation (4)). The expected result is a curvilinear relation between the equilibrium male trait and female preference across environments (figure 3).

With two traits, even small environmental differences in detectability can trigger dramatic changes. For example, consider two male traits of equal honesty. In one habitat one has higher detectability than the other, but the rank order of detectabilities is reversed in a second habitat. By our mechanism, the first trait should be exclusively preferred in the first habitat, whereas females in the second habitat should prefer only the second trait.

Another parameter likely to differ between environments is the intensity of natural selection against the male ornament. However, this factor affects mainly evolution of the male trait (equation (4)) and affects the evolution of the female preference only weakly

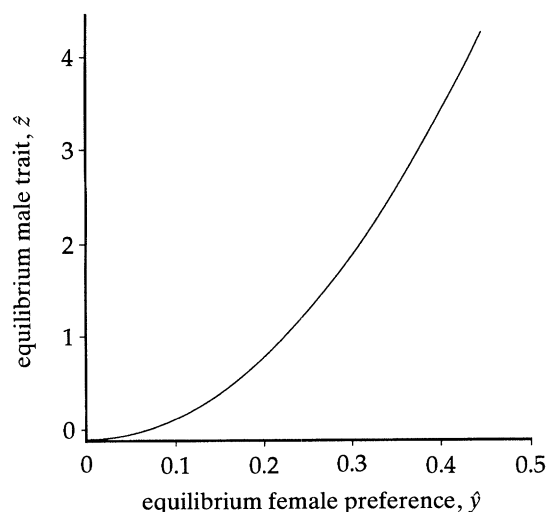


Figure 3. Predicted line of variation among populations in the equilibrium female preference and male trait caused solely by environmental differences in the detectability γ of the male trait; γ was varied from 0 at lower left to 1 at upper right. Other parameter settings: $\omega_z^2 = \omega_y^2 = 10$; $\alpha = 0.1$; $\sigma_{z,c} = 0.5$; $\sigma_z^2 = 1$.

(equation (3)). Hence even large between-population differences in expression of the male trait should often be accompanied by little or no change in the female preference. This finding makes it especially important to measure the female preference directly, and not just the male trait, when assessing population divergence (Houde & Endler 1990).

Our model leaves open the possibility of neutral population divergence in female preference, when choice of alternative male traits yields equivalent benefits. Equivalent male traits are probably common, and may include alternative phrases in insect song, or alternative choreographies of bird display.

6. SEXUAL SELECTION AND SPECIATION

Sexual selection would be implicated in speciation if it could be shown that isolated populations diverge in mate preferences, such that when the two forms eventually are brought into contact they no longer prefer one another as mates. The fact that many closely related species differ greatly in secondary sexual characteristics (Darwin 1871; West-Eberhard 1983) does not by itself implicate sexual selection in speciation for two reasons. First, as shown above, female preferences are expected to vary between populations much less than male traits. However, some studies have demonstrated divergence in female preferences as well as male traits (see, for example, McPhail 1969; Houde & Endler 1990; Baker & Baker 1990). Second, the female preferences may have diverged long after post-mating isolation (and hence speciation) was completed. Hence, the most telling examples of sexual selection's potential role in speciation are those in which closely related species show divergent mate preferences but comparatively little post-mating isolation (Coyne & Orr 1989; Schluter & McPhail 1992; Grant & Grant 1992).

This paper describes several adaptive mechanisms that would lead to population divergence in female preferences, and hence ultimately speciation. Other postulated mechanisms for the evolution of female preference can have similar consequences. These include neutral divergence via the Fisher process (Lande 1981; Kirkpatrick 1982), and correlated evolution in response to natural selection in other traits (Kirkpatrick & Ryan 1991). These alternative mechanisms for population divergence have not yet been tested, and the problem is likely to be a fruitful area of research.

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