Evolution, 55(1), 2001, pp. 25–32

MODELS OF SEXUAL SELECTION ON A QUANTITATIVE GENETIC TRAIT WHEN PREFERENCE IS ACQUIRED BY SEXUAL IMPRINTING

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Abstract.—The evolution of a quantitative genetic trait under stabilizing viability selection and sexual selection is modeled for a polygynous species in which female mating preferences are acquired by sexual imprinting on the parents and by exposure to the surviving population at large. Stabilizing viability selection acts equally on both sexes in the case of a sexually monomorphic trait and on males only in the case of a dimorphic trait. A genetically fixed sensory or perceptual bias defines the origin of the scale on which the trait is measured, and the possibility is incorporated that female preferences may deviate asymmetrically from the familiar—either toward or away from this origin. When viability selection is strong relative to sexual selection, the models predict that the mean trait value will evolve to the viability optimum. With intermediate ratios of the strength of viability to sexual selection, a stable equilibrium can occur on either side of this viability optimum, depending on the direction of asymmetry in female preferences. When viability selection is relatively weak and certain other conditions are also satisfied, runaway selection is predicted.

Key words.—Asymmetric mating preference, bivariate normal, quantitative genetic trait, sexual imprinting, weak selection approximation.

Received January 27, 2000. Accepted August 18, 2000.

Sexual preferences for mates exhibiting specific traits may develop in various ways. For example, they may be genetically fixed at birth (with random environmental modification), acquired by cultural transmission (as with mate-choice copying), or set by sexual imprinting. The evolutionary consequences for the preferred trait will depend on how the preference is determined.

Evidence for heritable variation in preferences is of two kinds (Kirkpatrick 1987; Bakker and Pomiankowski 1995). Correlated differences in male phenotype and female response have often been noted between populations of the same species and between related species in *Drosophila* (Tan 1946; Ehrman 1961; Kyriacou and Hall 1986), crickets (Hoy et al. 1977), butterflies (Grula and Taylor 1980), and frogs (Doherty and Gerhardt 1983; Ryan and Wilczynski 1988). These studies suggest that preferences can evolve and were genetically variable in the past (Bakker and Pomiankowski 1995). Direct demonstration of standing genetic variation for preference within a population would be more convincing. Possible examples are the artificial selection experiments on the preference for melanic males in the female ladybird beetle (Majerus et al. 1982; but see Ritchie 1992), and the genetic crosses of *D. melanogaster* strains differing in female mating propensities for *yellow* males (Heisler 1984).

Sexual preference may be acquired by cultural transmission, the social learning by one individual of a preference exhibited by another individual. Cultural transmission is likely to be a major determinant of mate choice in humans. Intriguing evidence comes, not from humans, but from small tropical fish, where the phenomenon is known as mate-choice copying (e.g., Dugatkin 1992; Schlupp et al. 1994). Mate-choice copying is said to occur when a female is more likely to choose a *specific* male after observing another female doing so. Unfortunately, the experiments do not always adequately control for confounding effects. Mate-choice copying has also been reported in birds (Hoglund et al. 1995; White and Galef 1999).

An alternative way in which a sexual preference may be acquired is by sexual imprinting (Lorenz 1935; Immelmann 1972), the phenomenon in which sexual preferences expressed later in life are acquired through exposure at a young age to other individuals, usually parents or siblings (Todd and Miller 1993). The classic example is the observation in many birds (e.g., fowl, ducks, geese, pigeons, doves, gulls, parrots, songbirds) that a cross-fostered individual prefers a mate of the same color as its foster parent(s) to one of its own color (for a review, see Laland 1994a). However, the rubric also covers negative imprinting on the properties of kin, which may occur in humans (Westermarck 1891; Wolf 1995) as well as birds and mammals (e.g., Bateson 1982; Yamazaki et al. 1988; Grant and Grant 1996). The current view is that sexual imprinting is taxonomically widespread among birds, but has a limited distribution among mammals (ten Cate and Vos 1999).

Sexual imprinting is apparently rather subtle, with experiments on zebra finches and Japanese quails suggesting that the preference is for mates differing somewhat from familiar individuals (Bateson 1982; ten Cate and Bateson 1988). Moreover, the ''choice is based on traits present in the rearing bird, in combination with a preference for what might be 'supernormal' characteristics'' (ten Cate and Bateson 1989, p. 357). These studies suggest that small quantitative distinctions are made by the sexually imprinted birds. Interestingly, Darwin (1871, p. 354) held a similar view on how a preference for a particular color of human skin might be formed. Thus, ''[t]he men of each race prefer what they are accustomed to; they cannot endure any great change; but they like variety, and admire each characteristic carried to a moderate extreme.''

Numerous models of sexual selection in polygynous species have been proposed to investigate the coevolution of a male secondary sexual trait and a female mating preference for such a trait (e.g., Lande 1981; Kirkpatrick 1982; Iwasa et al. 1991; Pomiankowski et al. 1991). Several models, the basic idea for which goes back to Darwin (1871) and Fisher (1958), have also been constructed to describe sexual selection in monogamous species (e.g., O'Donald 1980; Andersson 1986; Kirkpatrick et al. 1990; Ihara and Aoki 1999). These models all assume that the trait and the preference are both determined genetically.

Fewer theoretical studies have addressed the evolution of traits subject to acquired sexual preferences, in spite of the growing recognition that this may be a fairly common phenomenon (Owens et al. 1999). Our understanding of the processes is correspondingly weak. Models in which preferences for color morphs are acquired by sexual imprinting have been investigated by O'Donald (1960), Kalmus and Maynard Smith (1966), Seiger (1967), and Laland (1994a). Models of sexual selection with cultural transmission (including mate-choice copying) of preference are considered by Richerson and Boyd (1989), Kirkpatrick and Dugatkin (1994), and Laland (1994b).

In this paper we formulate and analyze models of sexual selection on a quantitative genetic trait, where preference is acquired by sexual imprinting on the parental phenotypes. Other social influences are assumed to contribute in such a way that a preference may develop for the mean phenotype of the surviving population. Although preferences may be acquired by the young of both sexes, we assume that the females dominate pair formation, so that only the males are sexually selected (ten Cate 1988; Laland 1994a). We incorporate the possibility that (expressed) female preference may deviate asymmetrically from the familiar (ten Cate and Bateson 1988, 1989). Stabilizing viability selection is also assumed to occur—on females and males in the case of a sexually monomorphic trait and on males only in the case of a dimorphic trait. There is an important assumption, to be detailed below, regarding the origin of the scale on which the phenotypes are measured. We posit that socially isolated young would prefer, on average, a mate with a phenotypic value of zero.

Our models were motivated by Laland's (1994a) major gene model. Major gene models can suitably be applied to single-locus traits such as color morphs (e.g., Cooke and Mirsky 1972), which were the focus of classical studies on sexual imprinting. However, recent empirical work has shown that sexually imprinted birds may respond to finer phenotypic differences (Bateson 1982; ten Cate and Bateson 1988, 1989). Thus, it is of interest to investigate models that assume the quantitative genetic inheritance of the preferred trait and to compare their predictions with those derived from major gene models. When natural selection is strong relative to sexual selection, our models predict that the mean phenotype will evolve to the viability optimum. With intermediate ratios of the strength of natural to sexual selection, a stable equilibrium can occur on either side of this viability optimum, depending on the direction of asymmetry in female preference. When natural selection is relatively weak, runaway selection (Fisher 1958; Lande 1981) is predicted.

We briefly point out the relevance of our results to Darwin's evolutionary view on human skin color variation (Darwin 1871; see also Diamond 1992).

MODEL FOR A SEXUALLY MONOMORPHIC POPULATION

Associated with each individual are two continuously varying characters, z and y. Let z be a quantitative genetic trait, determined jointly by autosomal genes of small effect acting additively and the environment. Let y, which is measured on the same scale as z, be the parental image acquired by sexual imprinting on the trait values of the parents (see eq. 7). The trait has the same expression in both sexes, whereas the parental image is a property only of female mating behavior and is latent in males. Among juveniles who have imprinted on their parents but have not yet suffered mortality due to natural selection, the joint distribution of y and z is assumed to be bivariate normal. At this point in the life cycle, the mean and variance of y are $\bar{y}$ and τ^2, the mean and variance of z are $\bar{z}$ and σ^2, and the correlation between y and z is ρ. Throughout this paper, we adhere as closely as possible to the notation of Lande (1981), using the same symbols for analogous quantities.

Assume that stabilizing natural selection on trait value z is due to viability differences of the form

$$\exp\left\{\frac{-(z-\theta)^2}{2\omega^2}\right\} \tag{1}$$

and acts equally on both sexes. In both sexes, the optimal phenotype is θ, and the strength of natural selection is inversely proportional to ω^2. After natural selection alone, the joint distribution of y and z is bivariate normal with means, variances, and correlation

$$\bar{y}^* = \bar{y} + \frac{\rho\tau\sigma(\theta - \bar{z})}{\omega^2 + \sigma^2}, \tag{2a}$$

$$\bar{z}^* = \frac{\omega^2\bar{z} + \sigma^2\theta}{\omega^2 + \sigma^2}, \tag{2b}$$

$$\tau^{2*} = \frac{\tau^2[\omega^2 + (1-\rho^2)\sigma^2]}{\omega^2 + \sigma^2}, \tag{2c}$$

$$\sigma^{2*} = \frac{\omega^2\sigma^2}{\omega^2 + \sigma^2}, \quad \text{and} \tag{2d}$$

$$\rho^* = \frac{\omega\rho}{[\omega^2 + (1-\rho^2)\sigma^2]^{1/2}}. \tag{2e}$$

The sexual or mating preference of a female is a function of her parental image, y, and the mean trait value of the surviving population, $\bar{z}^*$. Specifically, we posit that she is most strongly attracted to a male of phenotype $ky + a\bar{z}^*$. Following Lande (1981), female relative preference for mating with a male of phenotype z is assumed to be

$$\psi(z\,|\,y) = \exp\left\{\frac{-(z - ky - a\bar{z}^*)^2}{2\nu^2}\right\}, \tag{3}$$

where the strength of sexual selection is inversely proportional to ν^2. We assume throughout that k and a are both nonnegative.

When $k > 0$ and $a = 0$ (a situation likely to apply to birds), there is variation in female sexual preference due to sexual imprinting. When $k = 0$ and $a > 0$, the same male phenotype is preferred by all females. In humans there is no evidence for imprinting that would warrant setting $k > 0$. In contrast, according to the central tendency hypothesis, women prefer men with an average phenotype, a claim that receives some support with regard to female preference for male height (Ellis 1992). Thus, possibly $k = 0$ and $a > 0$ in humans.

The origin of the scale on which the phenotype, and thus the preference, is measured is not arbitrary as in models of sexual selection where the preference is genetically determined. It is assumed to correspond to the male phenotype that would be preferred on average by a female who has been raised in social isolation; for such a female $k = a = 0$. For example, the population may be monomorphic for a genetically fixed sensory bias (Ryan et al. 1990). There are no known instances in amphibians where this bias is overridden (Ryan et al. 1990), but a study on mate choice in cichlid fish suggests the presence of both a foster-parental effect and a bias for the ''primitive'' color (Barlow et al. 1990). The asymmetrical preference for increased contrast in zebra finches and Japanese quails may also be the result of a perceptual bias (ten Cate and Bateson 1988, 1989).

Henceforth, we assume that a genetically fixed sensory bias defines the origin. Therefore, relative to this origin, k and a are each a measure of both the strength and asymmetry of socially acquired preference. An imprinted female prefers a male whose phenotype is more extreme than the parental image if $k > 1$ and less extreme if $k < 1$. Similarly, exposure to the surviving population at large results in a preference for a male trait value that is more ($a > 1$) or less ($a < 1$) extreme than the population mean. Equation (3) implies that the dynamics of $\bar{z}$ are determined mainly by the sum $k + a$ rather than k and a individually. Thus, there is a centripetal force that draws $\bar{z}$ toward the origin when $k + a < 1$ and a disruptive force that destabilizes the origin when $k + a > 1$ (see below).

It will subsequently be convenient to distinguish the quantitative trait values in surviving females and males by writing z_f and z_m. Further, we denote the joint distribution of y and z_f by $f^*(y, z_f)$ and the distribution of z_m by $p^*(z_m)$. Thus, $f^*(y, z_f)$ is bivariate normal with parameters (2a–e) and $p^*(z_m)$ is univariate normal with parameters (2b) and (2d). The proportion of females with parental image y that mate with males of phenotype z_m is

$$p^*(z_m)\psi^*(z_m \mid y) = \frac{p^*(z_m)\psi(z_m \mid y)}{\int p^*(z_m)\psi(z_m \mid y)\, dz_m}. \tag{4}$$

Thus, the joint distribution of trait values in mated pairs, where a male may pair with more than one female, is

$$m(z_f, z_m) = \int f^*(y, z_f) p^*(z_m)\psi^*(z_m \mid y)\, dy. \tag{5}$$

It can be shown that $m(z_f, z_m)$ is bivariate normal and that

$$\bar{z}_f = \bar{z}^*, \tag{6a}$$

$$\bar{z}_m = \frac{\nu^2 \bar{z}^* + \sigma^{2*}(k\bar{y}^* + a\bar{z}^*)}{\nu^2 + \sigma^{2*}}, \tag{6b}$$

$$\sigma_f^2 = \sigma^{2*}, \tag{6c}$$

$$\sigma_m^2 = \frac{\sigma^{2*}[\tau^{2*}\sigma^{2*}k^2 + \nu^2(\nu^2 + \sigma^{2*})]}{(\nu^2 + \sigma^{2*})^2}, \quad \text{and} \tag{6d}$$

$$\mu = \rho^* \left\{ \frac{\tau^{2*}\sigma^{2*}k^2}{\tau^{2*}\sigma^{2*}k^2 + \nu^2(\nu^2 + \sigma^{2*})} \right\}^{1/2}, \tag{6e}$$

where the quantities σ_f^2 and σ_m^2 are the phenotypic variances in females and males who have paired, and μ is the phenotypic correlation between mates. Note from equations (6a) and (6c) that the mean and variance of the trait value among females who have paired is the same as among all surviving females. This result is consistent with our assumption that all females mate equally. In contrast, the mean and variance among males have changed (eqs. 6b, 6d), reflecting the assumption that some males participate in a disproportionate number of matings. Note also that sexual selection induces assortative mating for trait values (eq. 6e).

By assumption, each (surviving) female produces the same number of offspring. (Female choosiness entails no cost, and the chosen male contributes nothing that might affect female fertility and nothing beyond his genes that might affect offspring survival.) However, reproductive success for a (surviving) male is directly proportional to the number of matings he obtains.

When the parents have trait values z_f (female parent) and z_m (male parent), we posit the parental image acquired by the (female) offspring by sexual imprinting to be

$$y' = b_f z_f + b_m z_m + e_y, \tag{7}$$

where b_f and b_m are the maternal and paternal effects ($b_f + b_m = 1$) and e_y is the error term (Cavalli-Sforza and Feldman 1981, p. 275). The error term is assumed to be normally distributed with mean zero and variance s_y^2 and represents the possibility that imprinting may be imperfect.

The quantitative genetic trait in the offspring of these parents is

$$z' = \bar{z} + h^2\left[\frac{z_f + z_m}{2} - \bar{z}\right] + e_z, \tag{8}$$

where $\bar{z}$ is the mean of the parental generation before natural and sexual selection, h^2 is the heritability, and e_z is the error term (Falconer 1989, p. 189). The assumption that the heritability can be regarded as a parameter of the model rather than a variable (e.g., Lande 1981), which we adopt, is shown in the Appendix to hold approximately under weak selection. The error term e_z represents perturbations due to segregation, random mutation, recombination, and random environment. (It also includes the residual associated with the reverse path from phenotype to genotype in the parental generation.) The error term is assumed to be normally distributed with mean zero and variance s_z^2.

The joint distribution of y' and z' is bivariate normal with means, variances, and correlation

$$\bar{y}' = b_f \bar{z}_f + b_m \bar{z}_m, \tag{9a}$$

$$\bar{z}' = \bar{z} + h^2 \left[\frac{\bar{z}_f + \bar{z}_m}{2} - \bar{z} \right], \tag{9b}$$

$$(\tau^2)' = b_f^2 \sigma_f^2 + 2 b_f b_m \mu \sigma_f \sigma_m + b_m^2 \sigma_m^2 + s_y^2, \tag{9c}$$

$$(\sigma^2)' = \frac{h^4(\sigma_f^2 + 2\mu\sigma_f\sigma_m + \sigma_m^2)}{4} + s_z^2, \quad \text{and} \tag{9d}$$

$$\rho' = \frac{h^2(b_f\sigma_f^2 + \mu\sigma_f\sigma_m + b_m\sigma_m^2)}{2\tau'\sigma'}. \tag{9e}$$

Thus, we have come full circle. From the moments in one generation, after viability selection (eqs. 2a–e), sexual selection (eqs. 6a–e), sexual imprinting on the parental phenotypes, and reproduction (eqs. 9a–e), we have the moments of the next generation. Under the assumption of bivariate normality—either of the parental image and trait value in the same individual or of the trait values in mated pairs—the recursions (2), (6), and (9) give a consistent and complete description of the model. The five basic variables are $\bar{y}$, $\bar{z}$, τ^2, σ^2, and ρ. The 10 parameters are, in order of appearance, θ, ω^2, k, a, ν^2, b_f, b_m ($= 1 - b_f$), h^2, s_y^2, and s_z^2.

It is clear that the recursions in the variances and the correlation are closed and can be investigated independently of the dynamics of the means. Numerical work shows that, for a given set of parameter values, the variances and the correlation rapidly (within a few generations) approach a unique and finite equilibrium, where the realized heritability (eq. A2) also rapidly approaches a constant value. We subsequently assume that both natural and sexual selection are weak, that is, both ω^2 and ν^2 are large. Then, as discussed in the Appendix, the nominal heritability, h^2 approximates the realized heritability.

RECURSIONS IN THE MEAN PARENTAL IMAGE, $\bar{y}$, AND THE MEAN TRAIT VALUE, $\bar{z}$

Set $\beta = \rho\tau/\sigma$, $\delta = \sigma^2/(\omega^2 + \sigma^2)$, and $\epsilon = \sigma^{2*}/(\nu^2 + \sigma^{2*})$. Here, β is the regression of parental image on trait value in the same individual, and δ and ϵ are small by the weak selection assumption. From equations (2), (6), and (9) the recursions in the mean parental image and the mean trait value are

$$\begin{aligned} \bar{y}' = {} & \theta\delta[1 + b_m(k\beta - 1 + a)\epsilon] + b_m k\epsilon\bar{y} \\ & + \{1 - b_m(1 - a)\epsilon - \delta[1 + b_m(k\beta - 1 + a)\epsilon]\}\bar{z} \end{aligned} \tag{10a}$$

and

$$\begin{aligned} \bar{z}' = {} & \frac{h^2}{2}\theta\delta[2 + (k\beta - 1 + a)\epsilon] + \frac{h^2}{2}k\epsilon\bar{y} \\ & + \left\{1 - \frac{h^2}{2}\langle(1 - a)\epsilon + \delta[2 + (k\beta - 1 + a)\epsilon]\rangle\right\}\bar{z}. \end{aligned} \tag{10b}$$

With β, δ, ϵ, and h^2 assumed to be constant, equations (10a) and (10b) are linear in $\bar{y}$ and $\bar{z}$ and the equilibrium and its stability properties can be determined.

We have approximately

$$\hat{\bar{y}} = \hat{\bar{z}} = \frac{2\theta\alpha}{2\alpha + 1 - k - a}, \tag{11}$$

where $\alpha = \nu^2/\omega^2$ is a measure of the strength of natural selection relative to sexual selection (Lande 1981), and we have ignored the small terms in ϵ and $\delta = \epsilon\alpha/(1 - \epsilon)$. The equilibrium is unique except in the degenerate case of $\omega^2 \to \infty$ and $k + a = 1$ and is stable if (the denominator) $2\alpha + 1 - k - a > 0$ and unstable if $2\alpha + 1 - k - a < 0$. At this level of approximation, parameter b_m has no effect. Moreover, because the equilibrium (11) and its stability depend on the sum $k + a$ and not on k and a individually, sexual imprinting (k) and exposure to the population (a) at large have formally interchangeable effects.

When $\theta = 0$, the viability optimum coincides with the origin of the phenotypic scale. In this case, the equilibrium of the mean trait value, $\hat{\bar{z}}$, also lies at the origin, and is stable if $2\alpha + 1 - k - a > 0$ and unstable if $2\alpha + 1 - k - a < 0$. Recall that the origin of the phenotypic scale is defined as the default preference, corresponding to a weak sensory bias. There is no reason to expect the sensory bias to be tuned to the viability optimum of the trait, because by assumption the trait played no role in the evolution of the sensory bias. Therefore, let us assume that $\theta \neq 0$, and without loss of generality set $\theta > 0$.

It is necessary to distinguish the three cases $k + a = 1$, $k + a > 1$, and $k + a < 1$. They correspond, roughly speaking, to a female preference for the same, a more extreme, or a less extreme male phenotype, relative to the origin, than what is familiar. When $k + a = 1$, we again have $\hat{\bar{z}} = \theta$, which is stable because $2\alpha > 0$. In Figure 1 we plot $\hat{\bar{z}}/\theta$ against α for the remaining two cases $k + a > 1$ (Fig. 1a) and $k + a < 1$ (including the case $k + a = 0$; Fig. 1b). Note from equation (11) that the curves approximate hyperbolae and that positive equilibria are stable, whereas negative equilibria are unstable.

For both $k + a > 1$ and $k + a < 1$, $\hat{\bar{z}}$ approaches θ as α increases and the equilibria are stable. This result is intuitively reasonable, as we expect the mean trait value to be stabilized near the viability optimum when natural selection is strong relative to sexual selection. When $k + a > 1$ and $\alpha > (k + a - 1)/2$, $\hat{\bar{z}}$ is always greater than θ and stable, and as α decreases within this range the equilibrium values can become indefinitely large. When $k + a > 1$ and $\alpha < (k + a - 1)/2$, $\hat{\bar{z}}$ is negative and unstable, so that runaway selection is predicted. When $k + a < 1$, $\hat{\bar{z}}$ is always smaller than θ and stable, and decreases monotonically toward zero as α decreases.

In summary, the equilibrium of the mean trait value, $\hat{\bar{z}}$, varies with the strength of natural selection relative to sexual selection, α, when $\theta \neq 0$ and $k + a \neq 1$. Otherwise, $\hat{\bar{z}} = \theta$ for all α.

MODEL FOR A SEXUALLY DIMORPHIC POPULATION

Let the expression of the quantitative genetic trait be limited to males. Thus, only the males are subject to stabilizing natural selection, and the joint distribution of the parental image and the (latent) trait in females does not change. Therefore, the means, variances, and correlation of trait values in mated pairs are

$$\bar{z}_f = \bar{z}, \tag{12a}$$

$$\bar{z}_m = \frac{\nu^2\bar{z}^* + \sigma^{2*}(k\bar{y} + a\bar{z}^*)}{\nu^2 + \sigma^{2*}}, \tag{12b}$$

$$\sigma_f^2 = \sigma^2, \tag{12c}$$

$$\sigma_m^2 = \frac{\sigma^{2*}[\tau^2\sigma^{2*}k^2 + \nu^2(\nu^2 + \sigma^{2*})]}{(\nu^2 + \sigma^{2*})^2}, \quad \text{and} \tag{12d}$$

$$\mu = \rho\left\{\frac{\tau^2\sigma^{2*}k^2}{\tau^2\sigma^{2*}k^2 + \nu^2(\nu^2 + \sigma^{2*})}\right\}^{1/2}, \tag{12e}$$

where $\bar{z}^*$ and σ^{2*} are given by equations (2b) and (2d). Because the young females imprint on the father, $b_f = 0$ and $b_m = 1$. This requires the presence of the father as in monogamous birds where one male provides care. Thus, the means, variances, and correlation of the parental image and trait value in the new generation are

$$\bar{y}' = \bar{z}_m, \tag{13a}$$

$$\bar{z}' = \bar{z} + \frac{h^2(\bar{z}_m - \bar{z})}{2}, \tag{13b}$$

$$(\tau^2)' = \sigma_m^2 + s_y^2, \tag{13c}$$

$$(\sigma^2)' = \frac{h^4(\sigma_f^2 + 2\mu\sigma_f\sigma_m + \sigma_m^2)}{4} + s_z^2, \quad \text{and} \tag{13d}$$

$$\rho' = \frac{h^2(\mu\sigma_f\sigma_m + \sigma_m^2)}{2\tau'\sigma'}. \tag{13e}$$

As before, by assuming constancy of $\beta = \rho\tau/\sigma$, $\delta = \sigma^2/(\omega^2 + \sigma^2)$, $\epsilon = \sigma^{2*}/(\nu^2 + \sigma^{2*})$, and h^2, and that δ and ϵ are small, we obtain approximately

$$\hat{\bar{y}} = \hat{\bar{z}} = \frac{\theta\alpha}{\alpha + 1 - k - a}. \tag{14}$$

Equation (14) differs from equation (11) only in that α replaces 2α. The equilibrium is stable when the denominator is positive and unstable when it is negative.

DISCUSSION

The evolutionary consequences of sexual selection for a quantitative genetic trait under stabilizing viability selection were investigated for a polygynous species in which female mating preferences are acquired by sexual imprinting on the parents (eq. 7, analogous to vertical cultural transmission). Females may also in various ways develop a preference for the mean phenotype of the surviving population (analogous to horizontal cultural transmission). The relative contributions of sexual imprinting and these other social influences are measured by the parameters k and a. In imprinting birds, $k > 0$ and $a = 0$ are likely. The situation for humans may possibly be described as $k = 0$ (no sexual imprinting) and $a > 0$ (central tendency). The resulting preference is symmetrical if $k + a = 1$ and asymmetrical if $k + a \neq 1$ (sensu ten Cate and Bateson 1988, 1989). A genetically fixed sensory bias is assumed such that a socially isolated female would prefer a male whose trait value is zero—this defines the origin of the phenotypic scale.

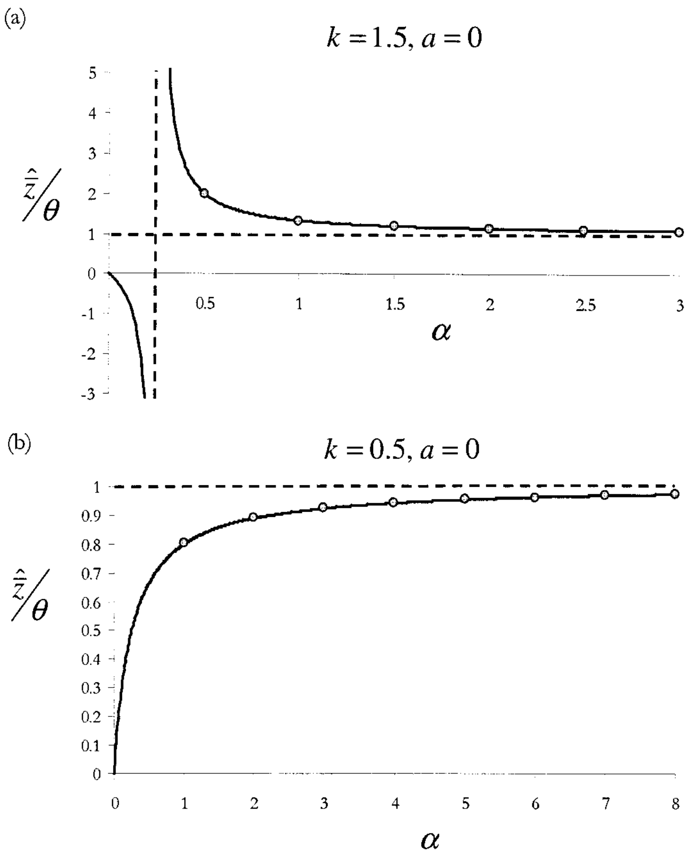

FIG. 1. (a) The function $\hat{\bar{z}}/\theta = 2\alpha/(2\alpha + 1 - k - a)$ when $k = 1.5$, $a = 0$. The vertical asymptote occurs at the value $\alpha = (k + a - 1)/2 = 0.25$. As $\alpha \to \infty$, we see $\hat{\bar{z}}/\theta \to 1$ (or $\hat{\bar{z}} \to \theta$). To the right of the vertical asymptote, $2\alpha + 1 - k - a > 0$ and $\hat{\bar{z}}$ is stable. To the left of the asymptote, $2\alpha + 1 - k - a < 0$ and $\hat{\bar{z}}$ is unstable. When $k + a > 1$, the function $\hat{\bar{z}}/\theta$ has the same general shape as in the case shown here. The plotted points represent $\hat{\bar{z}}/\theta$ values obtained from numerical iteration of the moment recursions until successive $\hat{\bar{z}}/\theta$ values differed by less than 10^{-10} (the parameter values used are $k = 1.5$, $a = 0$, $b_f = 0.2$, $b_m = 0.8$, $h^2 = 0.1$, $s_y^2 = s_z^2 = 0.5$, $\theta = 1$, and $\omega^2 = 10$). The parameter ν^2 was varied to produce different α values. Note again that there was no stable equilibrium for α values to the left of the vertical asymptote (the phenotypic mean diverged in this region and no points are plotted). To the right of the vertical asymptote the numerical results agree with the analytical approximation quite well. (b) The function $\hat{\bar{z}}/\theta$ when $k = 0.5$, $a = 0$. As $\alpha \to \infty$, we see $\hat{\bar{z}} \to \theta$. For all $\alpha \geq 0$, $2\alpha + 1 - k - a > 0$ and $\hat{\bar{z}}$ is stable. When $k + a < 1$, the function $\hat{\bar{z}}/\theta$ has the same general shape as in the case shown here. Again the plotted points represent $\hat{\bar{z}}/\theta$ values obtained from numerical iteration (using the same parameters as in [a] with the exception of $k = 0.5$). The fit between the numerical and analytical results is quite good.

The equilibrium of the mean trait value, $\hat{\bar{z}}$, is an isolated point (eq. 11 or 14) (our principal findings apply to sexually monomorphic and dimorphic traits alike) rather than a line of neutral equilibria as in Lande's (1981) model. When $k + a = 1$, this point coincides with the viability optimum of the trait, θ, and is (globally) stable. In contrast, when $k + a \neq 1$, the equilibrium is displaced away from θ. We first note that this result is reminiscent of the theoretical observations of Pomiankowski et al. (1991) and Iwasa et al. (1991), who incorporated costly female choice and biased mutation into their quantitative models of sexual selection. The assumption $k + a \neq 1$ implies an asymmetry, or bias, in female preference—not to be confused with the sensory bias that defines the origin—analogous to the bias in mutation. Second, an asymmetrical preference is a necessary condition for sexual selection to effect a change in the mean phenotype. Thus, ten Cate and Bateson (1988, p. 1356) are correct in suggesting that ''the key to the understanding of the potential role of sexual imprinting in the evolution of conspicuous characteristics lies in the observed shift towards slightly novel partners.''

The equilibrium value also depends on the parameter α, which is a measure of the strength of natural selection relative to sexual selection. Figure 1 plots $\hat{\bar{z}}$ against α for the two cases $k + a > 1$ (Fig. 1a) and $k + a < 1$ (Fig. 1b), where it is permissible to set $\theta > 0$. In both cases $\hat{\bar{z}}$ approaches θ as α increases, and the equilibria are stable—the mean trait value is stabilized near the viability optimum when natural selection is strong relative to sexual selection. When $k + a > 1$ and $\alpha > (k + a - 1)/2$, $\hat{\bar{z}}$ is always greater than θ and stable, and as α decreases within this range the equilibrium values can become indefinitely large. When $k + a > 1$ and $\alpha < (k + a - 1)/2$, $\hat{\bar{z}}$ is negative and unstable, so that runaway is predicted. When $k + a < 1$, $\hat{\bar{z}}$ is always smaller than θ and stable, and decreases monotonically toward zero as α decreases.

Previous theoretical studies of the evolutionary consequences of sexual imprinting have all assumed single-locus traits such as color morphs (Kalmus and Maynard Smith 1966; Seiger 1967; Laland 1994a). Laland's analysis is most general, so we compare our model with his (model 1). With regard to the assumptions, weak selection is a necessary component of a quantitative genetic model. Otherwise, marked discrepancies may be observed between the nominal and realized heritabilities, rendering the model inconsistent. In contrast, it is possible to posit strong selection in a major gene model, as Laland (1994a) does in the numerical examples that appear as figures in his paper (selection coefficients of the order of 0.1 and two- to fourfold differences in the mating preference strength). In the models of Kalmus and Maynard Smith (1966) and Seiger (1967), sexual selection is even stronger in that the mating preferences for a particular phenotype are typically assumed to be absolute. In addition, our models require us to assume that a socially isolated female would prefer a specific male phenotype over mating at random.

There are three major differences in the results. First, our quantitative genetic model predicts at most one stable equilibrium, whereas two stable equilibria can occur in Laland's major gene model. Second, the mean trait value evolves to the viability optimum in our model when female preference is not biased ($k + a = 1$), but the less viable homozygote may be fixed in Laland's model even when mating preference is symmetrical. Third, runaway is predicted by our model when $k + a > 1$ and α is small.

But these differences are perhaps more apparent than real. For example, when the mating preference is symmetrical, Laland finds that a viability reducing trait is unlikely to invade, which is congruent with our prediction that $\hat{\bar{z}} = \theta$ and is stable. However, ''some types of asymmetrical mating preference can drag a less viable trait from low frequency to fixation'' in Laland's (1994a, p. 482) model. Again, this observation agrees with our result that $\hat{\bar{z}}$ may deviate from the viability optimum, θ, when the mating preferences are asymmetrical. Furthermore, spread of a viability-reducing trait from a low frequency to fixation is analogous to runaway selection.

Although runaway selection is a possible outcome, the conditions for its occurrence may not be realized. It requires that females prefer males that deviate from what is familiar in the direction away from the sensory bias ($k + a > 1$), which is contrary to what ten Cate and Bateson (1988, 1989) apparently have in mind ($k < 1$ and $a = 0$ so that $k + a < 1$). Moreover, $k + a > 1$ is also a necessary condition for the indefinitely large equilibrium values illustrated in Figure 1a. Thus, when mating preferences are acquired by sexual imprinting, it does not seem likely that the sexually selected trait will undergo a major evolutionary change.

Finally, a word on the relevance of our theoretical results for an understanding of human skin color variation. Most anthropological hypotheses that attempt to explain the inverse correlation between pigmentation and latitude among indigenous peoples share the assumption that dark skin is adaptive at low latitudes, whereas light skin is adaptive at high latitudes (e.g., the vitamin D hypothesis; Murray 1934; Loomis 1967). Recent findings reinforce the prevailing view that dark skin is a rigidly maintained adaptation to the strong ultraviolet radiation at low latitudes (Robins 1991; Rana et al. 1999; Harding et al. 2000). However, they also suggest that light skin may *not* be positively selected at high latitudes as is usually claimed (Harding et al. 2000). In fact, there may be ubiquitous natural selection against light skin that shows a latitudinal gradient in intensity (Ihara and Aoki 1999). Then, if we are also prepared to accept that asymmetrical mating preferences for skin color are formed as a result of becoming accustomed to the persons around us (Darwin 1871), the observed latitudinal gradient in skin color is readily explained using our model. That is, the gradient in skin color follows the gradient in the strength of natural selection relative to sexual selection, α (Fig. 1b).

ACKNOWLEDGMENTS

We are grateful to K. Laland for numerous helpful suggestions on an earlier draft. Thanks are also due to Y. Ihara and the anonymous reviewers for comments. This research was supported in part by National Institutes of Health grant GM-28016.

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Corresponding Editor: M. Morgan

APPENDIX

Weak Selection Approximation

The following numerical check was done to verify that the nominal heritability, h^2, and the realized heritability, h_r^2 (see below), are approximately equal. For the moment, assume no sex differences in the distribution of trait values and pure assortative mating for phenotype (i.e., no viability or fertility selection). We continue to use the symbols σ^2 and μ for the phenotypic variance and the phenotypic correlation between mates. Then, if we view equation (8) as a regression of offspring on midparent values, the coefficient of determination is $h^4(1 + \mu)/2$ and the residual variance is

$$s_z^2 = \left[1 - \frac{h^4(1 + \mu)}{2}\right]\sigma^2. \qquad \text{(A1)}$$

In our model of sexual selection, the relation (A1) will not hold exactly, inasmuch as there is viability selection on both sexes and fertility selection on males. However, we can formally solve equation (A1) for h^2 to obtain the realized heritability, which is defined as

$$h_r^2 = \left[\frac{2\left(1 - \frac{s_z^2}{\sigma^2}\right)}{1 + \mu}\right]^{1/2}. \qquad \text{(A2)}$$

The adequacy of the approximation of h_r^2 in equation (A2) to h^2 is evaluated by substituting the equilibrium values of σ^2 and μ, which are attained within a few generations.

We assume that both natural and sexual selection are weak. Thus, ω^2 and ν^2 are large; more specifically the ratios s_z^2/ω^2 and s_y^2/ν^2 are small. Under these assumptions numerical work shows that the agreement between h^2 and h_r^2 is good. We regard the approximation inherent in equation (8) as acceptable, if the difference between h^2 and h_r^2 is less than $(0.1)h^2$, and h_r^2 does not exceed one. Figure A1 illustrates the regions in the parameter space of ω^2 and ν^2 where these conditions are satisfied. Although large values of ω^2 and ν^2 generally correspond to good heritability approximations, in some cases h^2 will approximate h_r^2 for smaller values of ω^2 and ν^2 provided that they are approximately equal (e.g., Fig. A1a). These considerations suggest that we are justified in studying the dynamics of the means, assuming constancy of the variances, correlation, and heritability.

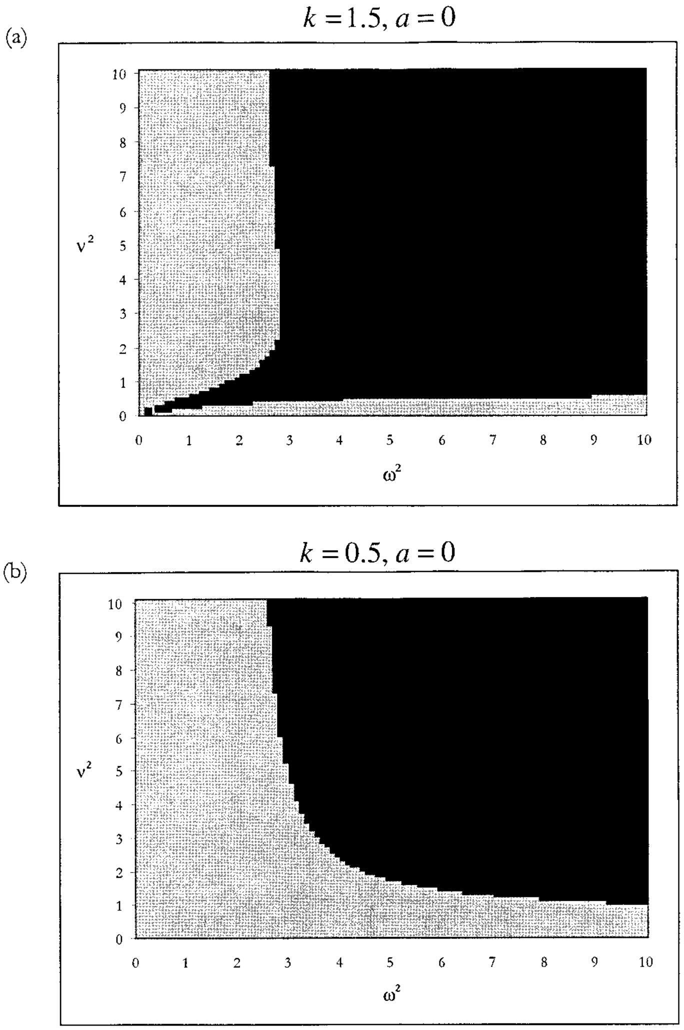

FIG. A1. Depicted are the regions where the realized heritability (h_r^2) is approximated well by the nominal heritability (h^2). In black are the points in the (ω^2, ν^2) plane for which $|h^2 - h_r^2| < (0.1)\, h^2$ (the approximation is acceptable). In gray are the points where $|h^2 - h_r^2| \geq (0.1)\, h^2$ (the approximation is unacceptable). The parameter values used here are $b_f = 0.2$, $b_m = 0.8$, $h^2 = 0.5$, $s_y^2 = s_z^2 = 0.5$. Several different parameter values were investigated, but the results did not differ qualitatively from those presented here. (a) The regions with $k = 1.5$, $a = 0$. (b) The regions with $k = 0.5$, $a = 0$. For both (a) and (b), we numerically iterated the second moment recursions given in equations (2c–e), (6c–e), and (9c–e) to find the equilibrium values of the phenotypic variance (σ^2) and the phenotypic correlation between mates (μ). Then, the realized heritability was calculated by equation (A2). This was done for every (ω^2, ν^2) pair where both ω^2 and ν^2 ranged from 0.1 to 10 by increments of 0.1.