Evolution of Mating Preference and Sexual Dimorphism

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A quantitative genetic model of the joint evolution of female mating preferences and sexual dimorphism in homologous characters of the sexes is described for polygamous species with no male parental effort, such that mating preferences are selectively neutral and evolve only by indirect selection on genetically correlated characters. The male character and the homologous female character are each under stabilizing natural selection toward an optimum phenotype. At an evolutionary equilibrium the female character under natural selection is at its optimum, whereas there is a line of possible equilibria between female mating preferences and the male character. The line of equilibria may be stable or unstable, depending on the intensity of natural selection, the type of mating preferences, and the inheritance of the characters. Various mechanisms for maladaptive evolution of mating preferences and sexual dimorphism are discussed.

1. Introduction

The theory of sexual selection advanced by Darwin (1874) was intended to explain the common occurrence of striking secondary sexual characters which cannot easily be attributed to natural selection on viability or fecundity. Instead, he proposed that most of the extreme sexual dimorphism in animals is caused by sexual selection via combat or competition between males for access to mates, and by female mating preference. Fisher (1958, Ch. 6) described the evolution of sexual dimorphism in genetic terms and filled a major gap in Darwin's theory by suggesting a genetic mechanism for the evolution of female mating preferences in species where males contribute nothing but gametes to the next generation. Using models of quantitative (polygenic) characters, the evolution of sexual dimorphism under natural and sexual selection, and the evolution of female mating preferences for a male sex-limited trait, have each been analyzed separately by Lande (1980a, 1981) and Kirkpatrick (1985). In the present paper we model the simultaneous evolution of sexual dimorphism and female mating preferences.

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Darwin (1874) observed that closely related species of higher animals often differ most in the secondary sexual characters of adult males, whereas adult females and juveniles of both sexes resemble each other more closely among the species. He also noted that adult females frequently express in rudimentary form the exaggerated characters of males of their species, a phenomenon which he called the "transference" of the character between the sexes, since he felt that such traits evolved by sexual selection on males and were useless or even deleterious to females. The mechanism for this "transference" involves a genetic correlation between homologous characters in the sexes caused by pleiotropic effects of genes which act similarly in males and females (Fisher, 1958; Lande, 1980*a*). The typically high genetic correlation between homlogous male and female characters implies that strong sexual selection on males will produce not only a direct response in the male character(s), but also an indirect (correlated) response in the homologous female character(s), as has been observed several times in artificial selection experiments (e.g. Harrison, 1953; Korkman, 1957; Frankham, 1968*a,b*; Eisen & Hanrahan, 1972). There is evidence from *Drosophila* that sexual dimorphism in quantitative traits is produced mostly by autosomal genes which are expressed differently in males and females, with some contribution from sex-linked genes (Bird & Schaffer, 1972; Val, 1977; Templeton, 1977; Carson & Lande, 1984).

In polygamous species with no male parental expenditure, Fisher's mechanism for the origin and evolution of female mating preferences for extreme male characters involves a positive feedback in the evolution of these two traits. This feedback depends on a genetic correlation between the sexual preference of females and the secondary sexual characters of males created by genetic variation in mating preferences. Even when separate genetic and developmental systems control these characters, the tendency for females with more extreme sexual preferences to mate with males possessing more extreme characters produces a genetic correlation between these characters in the population through assortative mating and the linkage disequilibrium (nonrandom association of alleles at genetic loci affecting different traits) that it creates. Then when females mate on average with males that deviate from the mean phenotype in the male population, they are selecting not only for more extreme male characters, but also indirectly for more extreme mating preferences. Fisher suggested that female sexual preferences may initially be adaptive, originating by indirect natural selection (genetic hitchhiking) on male characters. But once mating preferences have been established they may become sufficiently strong to override natural selection for a male phenotype that is optimal for survival, producing

an unstable runaway process leading to exaggerated secondary sexual characters.

Explicit genetic models of Fisher's runaway process of sexual selection postulate that in polygamous species with no male parental effort, female mating preferences are selectively neutral and can evolve only by indirect selection on genetically correlated characters, or by random genetic drift (Lande, 1981; Kirkpatrick, 1982). Even under stabilizing natural selection toward an optimum male phenotype there is a line of possible equilibria for a male trait and female mating preference for it, along which indeterminate evolution can occur by random genetic drift.

It might be supposed that the existence of a female character homologous to the male character (and also under stabilizing natural selection) could prevent a runaway process or eliminate the indeterminacy in the line of equilibria by collapsing the line to a single equilibrium point. Here we show that the addition of such a female character to the model does not alter the line of equilibria involving a male character and female mating preferences for it. Furthermore, runaway sexual selection, similar to that described by Fisher, can still occur. When there is no genetic pleiotropy between female mating preference and the other characters, and all of the genetic correlation between them is created by assortative mating and linkage disequilibrium, the condition for instability is identical to that in the simpler two-character model with a male sex-limited trait (Lande, 1981).

2. The Model

The general model concerns homologous quantitative characters of males and females, z_m and z_f, and a female mating preference, y, based on the male character. We assume that the characters are polygenic (with autosomal inheritance), and that scales of measurement can be found for the characters such that they are normally distributed in the population, with phenotypic and genetic variances and covariances that remain constant during the evolution of the mean phenotypes. Most commonly, a logarithmic transformation of the original measurements renders the pattern of variability nearly constant (Wright, 1968, Chs 10, 11; Falconer, 1981, Ch. 18). Polygenic mutation and recombination are assumed to maintain genetic variation in each trait, despite natural selection toward optimal values of the homologous male and female characters (Lande, 1975, 1980b, 1981; Bulmer, 1980, Chs 9, 10; Turelli, 1984).

Postulating that genotypic and environmental effects on the characters are independent and additive on the chosen scales of measurement, the

total phenotypic variance in the ith character P_{ii}, can be partitioned into additive genetic variance, G_{ii}, plus environmental (and non-additive genetic) variance, E_{ii} (Falconer, 1981). The phenotypic covariance between the female characters, P_{fy}, can be partitioned similarly into additive genetic covariance, G_{fy}, plus environmental (and nonadditive genetic) covariance, E_{fy} (Falconer, 1981). Additive genetic covariances between characters expressed in males and females can be defined and measured from phenotypic correlation between related individuals of opposite sex, or from artificial selection experiments (Griffing, 1966a,b; Bohidar, 1964; James, 1972; Falconer, 1981). Since selection is assumed to act on each sex separately, there is no need to define a phenotypic covariance between characters expressed in individuals of opposite sex.

Supposing for simplicity that generations are discrete and non-overlapping, the change per generation in the mean phenotypes is given by

$$
\begin{pmatrix} \Delta \bar{z}_m \\ \Delta \bar{z}_f \\ \Delta \bar{y} \end{pmatrix} = \frac{1}{2} \begin{pmatrix} G_{mm} & G_{mf} & G_{my} \\ G_{fm} & G_{ff} & G_{fy} \\ G_{ym} & G_{yf} & G_{yy} \end{pmatrix} \begin{pmatrix} \beta_m \\ \beta_f \\ \beta_y \end{pmatrix} \tag{1}
$$

where β_i is the force of directional selection acting directly on the ith character, and the factor of $\frac{1}{2}$ accounts for the sex-limited expression of the characters (Lande, 1980a; Lande & Arnold, 1983). The additive genetic variance-covariance matrix in this equation is symmetric and is assumed to be positive definite (with real, positive eigenvalues).

Stabilizing natural selection on the homologous characters of the sexes is approximated by Gaussian fitness functions with optimum phenotypes θ_m and θ_f and widths ω_m and ω_f. Thus the expected fitness of females with phenotype z_f is

$$
W_f(z_f) = c \exp \{-(z_f - \theta_f)^2 / 2\omega_f^2\}
$$

where c is an arbitrary (positive) constant, and similarly for natural selection on males. This produces a force of directional selection on the mean phenotype of the female character z_f which increases linearly with increasing deviation of the mean phenotype from its optimum (Lande, 1980a, 1981)

$$
\beta_f = -(\bar{z}_f - \theta_f)/(\omega_f^2 + P_{ff}) \simeq -(\bar{z}_f - \theta_f)/\omega_f^2 \tag{2a}
$$

in which we have assumed that natural selection on the phenotypic variance is weak, $\omega_f^2 \gg P_{ff}$. A similar assumption, $\omega_m^2 \gg P_{mm}$, yields an analogous formula for the force of natural selection on males, but sexual selection must also be taken into account in calculating β_m.

In our model the system of mating is polygamous, in that males may mate repeatedly without reducing their fertility per mating, and we assume that every female surviving to sexual maturity eventually mates, regardless of her mating preference. If males contribute nothing but genetic material to their offspring, and do not protect or provision their mates, then the number of progeny produced by any female is independent of her mate choice and female mating preference is a selectively neutral trait

$$\beta_y = 0 \tag{2b}$$

which can evolve deterministically only by indirect selection on genetically correlated characters. The genetic quality of the offspring, in terms of viability and mating success, is not included in the fitness of the parents but is accounted for during selection in the next generation. This fitness definition follows the standard practice in quantitative genetics of separating phenotypic selection from inheritance and the genetic response to selection (Falconer, 1981).

The sexual preference for males with phenotype z_m by females with preference phenotype y is denoted as $\psi(z_m|y)$. The frequency of matings between females of phenotype y and males of phenotype z_m is assumed to be proportional both to the intensity of female preference and the frequency of males with that phenotype. In any population one of the following types of female mating preferences is assumed to exist (Lande, 1981). Females with an absolute preference have a most preferred male phenotype y with a tolerance of $\pm\nu$, regardless of the distribution of male phenotypes, which is described by the Gaussian function

$$\psi(z_m|y) = \exp\{-(z_m - y)^2/2\nu^2\}.$$

Females with a relative preference have a most preferred male phenotype which deviates by an amount y from the mean of surviving males, $\bar{z}_m^*$, with a tolerance of $\pm\nu$, which is described by the Gaussian function

$$\psi(z_m|y) = \exp\{-[z_m - (\bar{z}_m^* + y)]^2/2\nu^2\}.$$

Psychophysical mating preferences are open-ended and take the exponential form

$$\psi(z_m|y) = k\exp\{z_m y\}$$

where k is an arbitrary (positive) constant. With absolute or relative unimodal preferences we assume that sexual selection on the variance of the male character is weak, $\nu^2 \gg P_{mm}$.

Calculation of the total force of selection on the male character then proceeds as in Lande (1981), except that natural selection on the female

character z_f can alter the distribution of female mating preferences within a generation if they are phenotypically correlated ($P_{fy} \neq 0$), changing the mean mating preference from $\bar{y}$ to $\bar{y}^*$, so that

$$\beta_m = [\bar{y}^*/\alpha - (1 + \varepsilon/\alpha)\bar{z}_m + \theta_m]/\omega_m^2 \tag{2c}$$

approximately. With psychophysical preferences $\alpha = 1/\omega_m^2$ and $\varepsilon = 0$, whereas with unimodal preferences $\alpha \simeq \nu^2/\omega_m^2$, and depending on whether these are absolute or relative $\varepsilon = 1$ or 0 respectively. The mean mating preference of females after natural selection on z_f can be obtained from the phenotypic response to multivariate selection within a generation (Lande & Arnold, 1983, eqn 6c), and using (2b)

$$\bar{y}^* = \bar{y} + P_{yf}\beta_f \tag{2d}$$

where β_f is given by equation (2a). This completes the specification of the model. We now proceed to analyze its equilibrium properties and evolutionary dynamics.

Equilibria. Since by assumption the additive genetic variance–covariance matrix in equation (1) is not singular, at an evolutionary equilibrium there must be no directional selection on any of the characters, $\beta_m = \beta_f = \beta_y = 0$. This implies from (2a) that the mean phenotype of females is at its optimum under natural selection

$$\bar{z}_f = \theta_f. \tag{3a}$$

From (2b), (2c), and (2d) there is a line of possible equilibria for the male character and female mating preferences

$$\bar{y} = (\alpha + \varepsilon)\bar{z}_m - \alpha\theta_m. \tag{3b}$$

This is the same line of equilibria which appeared in the two-character model of sexual selection on a male sex-limited trait (Lande, 1981). Regardless of how much the mean male phenotype deviates from its optimum, there is an intensity of female mating preference which can exactly counteract the force of natural selection, and because there is no selection directly on mating preferences, this balance can be achieved in an infinite number of possible ways. The balance between natural and sexual selection on the male character is not influenced by the existence of an homologous female character, provided that this is at its optimum under natural selection, as in (3a). The position and slope of the line of equilibria depends only on the form and intensity of natural and sexual selection acting on the male character.

Stability analysis. With the translation of coordinates

$$\tilde{y} = \bar{y}, \qquad \tilde{z}_f = \bar{z}_f - \theta_f$$

$$\tilde{z}_m = \bar{z}_m - \theta_m/(1 + \varepsilon/\alpha)$$

the dynamical equations for the mean phenotypes can be written in matrix form as $\Delta\tilde{z} = M\tilde{z}$ where $\tilde{z}$ is a column vector of the elements $\tilde{z}_m$, $\tilde{z}_f$, $\tilde{y}$, and M is the matrix

$$\frac{1}{2\alpha\omega_m^2}\begin{pmatrix} -(\alpha + \varepsilon)G_{mm} & -(\alpha G_{fm}\omega_m^2 + G_{mm}P_{fy})/\omega_f^2 & G_{mm} \\ -(\alpha + \varepsilon)G_{mf} & -(\alpha G_{ff}\omega_m^2 + G_{mf}P_{fy})\omega_f^2 & G_{mf} \\ -(\alpha + \varepsilon)G_{my} & -(\alpha G_{fy}\omega_m^2 + G_{my}P_{fy})/\omega_f^2 & G_{my} \end{pmatrix}.$$

The determinant of this matrix is zero since the first and third columns are proportional, hence at least one of the eigenvalues is zero, $\lambda_0 = 0$, corresponding to lack of motion along the line of equilibria. The other two eigenvalues are of the form

$$\lambda_\pm = (C \pm \sqrt{C^2 - 4A})/2$$

where

$$A = [(\alpha + \varepsilon)(G_{mm}G_{ff} - G_{mf}^2) - G_{ff}G_{my} + G_{mf}G_{fy}]/4\alpha\omega_m^2\omega_f^2$$

and

$$C = [G_{my} - (\alpha + \varepsilon)G_{mm} - (\alpha G_{ff}\omega_m^2 + G_{mf}P_{fy})/\omega_f^2]/2\alpha\omega_m^2.$$

Under the assumption of weak selection on the phenotypic variances of the homologous male and female traits, λ_+ and λ_- are both small in magnitude compared to unity, hence deviations of the mean phenotypes from the line of equilibria grow at the rate $(1 + \lambda)^t \simeq e^{\lambda t}$ in the direction of the eigenvector corresponding to a particular eigenvalue, and the dynamic system can be approximated in continuous time using $d\tilde{z}/dt$ instead of $\Delta\tilde{z}$. Thus the necessary and sufficient conditions for asymptotic stability of the line of equilibria are approximately that the real parts of λ_+ and λ_- are both negative, or equivalently that $A = \lambda_+\lambda_- > 0$ and $C = \lambda_+ + \lambda_- < 0$. Evidently, the line of equilibria can be either stable or unstable, depending on the additive genetic variances and covariances of the characters, the intensity of natural selection, and the type of female mating preferences. Evolutionary oscillations will occur if $C^2 < 4A$.

We wish to concentrate on the important case in which there are no pleiotropic genetic effects between female mating preferences and either of the homologous characters expressed in males and females. This is likely to occur when mating preferences are sensory and/or psychological and

the homologous traits of the sexes are morphological, so that the genetic covariance G_{my} is positive and due entirely to assortative mating and linkage disequilibrium created by genetic variance in mating preferences. We also suppose that the genetic covariance between homologous male and female characters is caused mainly by pleiotropy. In this situation the additive genetic correlation between the female characters y and z_f, defined as $\gamma_{fy} = G_{fy}/\sqrt{G_{ff}G_{yy}}$, can be traced through a causal pathway of genetic correlation between y and z_m created by assortative mating, and the genetic correlation between z_m and z_f created by pleiotropy. Because there is no other source of additive genetic correlation between y and z_f in this situation, from the rules of path analysis (Wright, 1968, Ch. 13) $\gamma_{fy} = \gamma_{fm}\gamma_{my}$ or in covariance form

$$G_{fy} = G_{fm}G_{my}/G_{mm}. \tag{4a}$$

In addition we assume that the phenotypic correlation between the female characters has the same sign as the additive genetic correlation between them, so that

$$G_{mf}P_{fy} \geq 0. \tag{4b}$$

Substituting (4a) into the dynamical equations it can be seen that along any evolutionary trajectory $\Delta\bar{y}/\Delta\bar{z}_m = G_{my}/G_{mm}$. The ratio of the additive genetic covariance of the male trait and female mating preference to the additive genetic variance in the male trait is equivalent to the additive genetic regression of female mating preferences on the male character in the population. The slope of the lines of motion for $\bar{y}$ and $\bar{z}_m$ is the same as in the absence of natural selection on z_f (as in the two-character model of Lande, 1981) because under the condition (4a) the ratio of the correlated responses in $\bar{y}$ and $\bar{z}_m$ to selection on z_f is the same as the ratio of responses when mating preferences evolve only as a correlated response to selection on the male character. Again employing (4a) in the expression for A produces

$$A = (\alpha + \varepsilon - G_{my}/G_{mm})(G_{mm}G_{ff} - G_{mf}^2)/4\alpha\omega_m^2\omega_f^2.$$

From the assumption that the additive genetic variance-covariance matrix of the characters is positive definite, $G_{mm}G_{ff} - G_{mf}^2 > 0$ and the condition $A < 0$ is satisfied if $G_{my}/G_{mm} < \alpha + \varepsilon$. Then from (4b) the condition $C > 0$ is also fulfilled. Therefore in the situation given by (4a) and (4b) the line of equilibria is unstable if and only if

$$G_{my}/G_{mm} > \alpha + \varepsilon \tag{5}$$

that is, the slope of the lines of motion for female mating preference and the male character must exceed the slope of the line of equilibria. This condition for an unstable (runaway) process of sexual selection does not depend on the intensity of natural selection on the female character homologous to the male character. Condition (5) is identical to that in the simpler two-trait model with a sex-limited male character and a female mating preference (Lande, 1981). One difference that can be noted, however, is that in the present model evolutionary instability will generally involve all three characters moving away from their equilibria at a rate which increases geometrically, or approximately exponentially, with time.

If, as is often the case, the additive genetic correlation between the homologous male and female characters is high (near one), then G_{mf}^2 approaches $G_{mm}G_{ff}$, A approaches zero, and assuming C is not near zero $(4A \ll C^2)$ the nonzero eigenvalues are approximately

$$\lambda_+ \simeq C - A/C, \qquad \lambda_- \simeq A/C.$$

In this case it can be shown that if the homologous characters of the sexes have similar patterns of variation and are under comparable intensities of stabilizing natural selection, the largest eigenvalue corresponds to rapid evolution of female mating preferences and the male character, and the homologous female character evolves to an extent nearly equal that of the male character. The smaller of the two nonzero eigenvalues then corresponds to the relatively slow evolution of sexual dimorphism, described by Fisher (1958, Ch. 6) and modelled by Lande (1980a). When the line of equilibria is stable the rapid phase of evolution is followed by relatively slow divergence of homologous male and female characters until the mean phenotype of females achieves its optimum under natural selection, $\bar{z}_f = \theta_f$, and natural and sexual selection on the male character are in balance. It can also be noted that increasing the strength of stabilizing natural selection on z_f (decreasing ω_f^2) decreases λ_+. Thus when the line of equilibria is unstable, natural selection on z_f decreases the rate of the runaway process.

3. Discussion

Our model of the simultaneous evolution of sexual dimorphism and female mating preferences concerns polygamous species in which there is no male parental effort, and males may mate repeatedly without diminishing their fertility per mating. It is assumed that in each generation every surviving female mates, and the number of offspring she raises does not depend on her mate choice, which is then a selectively neutral character. Female mating preference is based on a morphological or behavioral character of males,

which is assumed to be under stabilizing natural selection toward an intermediate optimum phenotype. A homologous character of females is also assumed to be under stabilizing natural selection toward a potentially different optimum phenotype. Heritable variation for sexual dimorphism is postulated to allow evolutionary divergence between the homologous characters of the sexes.

We find that in general at an evolutionary equilibrium the female character under stabilizing natural selection always has its mean phenotype at the optimum (3a), and there is a line of possible equilibria between the male character and female mating preferences (3b). The position and slope of the line of equilibria depends only on the form and intensity of natural and sexual selection on the male character and is independent of natural selection on the homologous female character, or its inheritance. This line of equilibria is the same as that occurring in a similar model of the evolution of female mating preferences and a male sex-limited trait (Lande, 1981).

The stability of the line of equilibria depends in general on the type of female mating preference, the intensity of stabilizing natural selection on the homologous male and female traits, and the inheritance of the characters. A situation of special interest is where female mating preferences and the other characters are determined by different sets of genes, e.g. if mating preferences are perceptual and/or psychological and the other characters are morphological. In this case the genetic correlation between the male trait and female mating preference is attributable entirely to assortative mating and linkage disequilibrium created by genetic variance in mating preferences (Lande, 1981; Kirkpatrick, 1982). Then the condition for instability of the line of equilibria is that the additive genetic regression coefficient of female mating preference on the male character exceeds the slope of the line of equilibria (5). The condition for instability in this situation is identical to that for runaway evolution of female sexual preference and a male sex-limited trait (Lande, 1981). In the present model when the line of equilibria is unstable, all three characters will evolve away from their equilibria at a geometrically, or approximately exponentially, increasing rate.

In the commonly observed situation where homologous male and female characters have similar patterns of variation and are highly correlated genetically, deterministic evolution generally has a rapid phase where the homologous characters of the sexes evolve almost equally in conjunction with female mating preferences, and a relatively slow phase corresponding to the evolution of sexual dimorphism (cf. Fisher, 1958; Lande, 1980a). When the line of equilibria is stable, the rapid phase of evolution will cease when the sum of forces of natural selection on the homologous male and

female traits nearly balances the force of sexual selection on the male character; sexual dimorphism will then increase on a comparatively slow timescale until the mean phenotype of females reaches its naturally selected optimum, and natural and sexual selective forces are in balance on the male character. When the line of equilibria is unstable, natural selection on the female trait homologous to the male character slows the rate of runaway sexual selection, but does not alter the condition for its occurrence.

Following Fisher (1958) we suppose that a process of runaway sexual selection, driven by positive feedback in the evolution of mating preferences, may be halted by strong natural selection against extreme expression of the homologous male and female characters (if individual fitness decreases faster than a Gaussian function, used in the present model), or by selection directly against females with extreme mating preferences because of their inability to find a suitable mate. However, in this model, runaway sexual selection could also cause the population to become extinct, since the mean fitness of both sexes under natural selection (i.e. viability) would be continually decreasing. Eventual extinction of the population would not require that all of the individuals suddenly fail to survive or mate, but simply that the demographic growth rate of the population become negative ($dN/dt <$ 0) so that the individuals on average cannot replace themselves in subsequent generations.

This and previous models (Lande, 1981; Kirkpatrick, 1982, 1985) refute the widespread notion that mating preferences will always evolve to maximize the genetic quality of the offspring (e.g. Trivers, 1972; Mayr, 1972; Barash, 1977; Borgia, 1979; Thornhill & Alcock, 1983). In these models of polygamous species, where males contribute nothing but gametes to the next generation, female mating preferences are selectively neutral because the number of progeny produced by a female does not depend on her choice of mates. These models employ the standard definition of fitness used in evolutionary analysis of populations with discrete, nonoverlapping generations, that is, the expected fitness of an individual phenotype (or genotype) is equal to its viability (probability of survival to sexual maturity) times its fecundity (number of offspring produced) (Crow & Kimura, 1970, p. 5; Prout, 1965, 1969). The common practice of counting the survival and mating success of the offspring as part of the parents' fitness confounds selection within a generation and inheritance across generations, which must be separated in order to make a precise evolutionary model (see Arnold, 1983).

We do not wish to deny that mating preferences may commonly be adaptive (i.e. acting in the same direction as natural selection on particular male characters), if not optimal. As noted by Fisher (1958, p. 151-2), female

mating preferences often may originate by indirect natural selection on male characters, and initially may be adaptive in reinforcing natural selection; this has been confirmed theoretically by Heisler (1984). But once established in a population, mating preference becomes a selective force in its own right, capable in some situations of opposing and overcoming natural selection, and leading to maladaptive evolution (Fisher, 1958). It remains a major empirical question to determine whether in species with extreme sexual dimorphism female mate choice acts in the same direction as other selective forces such as natural selection and intermale combat. This question can be approached by measuring phenotypic selective forces within a generation in a population, in the field or laboratory, without studying the inheritance of the characters (Lande & Arnold, 1983).

Quantitative genetic models help to explain an important observation of Darwin (1874) which has hardly been addressed by other models of sexual selection: closely related species of animals often differ most in male secondary sexual characters. In polygamous species with no male parental effort, an infinite number of possible equilibria exist between selectively neutral female mating preferences and male characters, because no matter how much the male characters deviate from the optimum under natural selection, an opposing force of female mate choice can be strong enough to exactly balance the force of natural selection on the male traits. When the line of equilibria in the present model is unstable, small differences in the initial composition of different populations can quickly produce a large divergence between populations. Even when the line of equilibria is stable, rapid diversification between populations in male secondary sexual characters can result from the interaction of natural and sexual selection with random genetic drift, especially when populations sizes are small or are often reduced to low numbers, because a population perturbed away from the line of equilibria will not generally return to the same point on the line.

In the present model the line of equilibria arises because by assumption there are three dimensions for genetic evolution of the mean phenotypes, but only two independent selective constraints (on the homologous male and female characters). In general, the dimensionality of the equilibrium set is equal to the number of genetic degrees of freedom for evolution, minus the number of linearly independent selective constraints on the genetically independent characters; hence there is a line of equilibria in the present model where mating preferences are not directly selected. If female mating preferences were under direct natural selection toward an optimal mate choice, such as when the male character affects male parental behavior which in turn influences the number of offspring produced by the pair, this adds a new selective constraint on the system which is linearly independent

of the previous constraints, and there would be an equilibrium point. At this equilibrium point the mean mating preference would be at its optimum under natural selection, although the equilibrium point may still be genetically unstable. Kirkpatrick (1985) reached similar conclusions based on a two-character model of the evolution of female mating preferences and a male sex-limited character, with stabilizing natural selection on both traits. Kirkpatrick has also noted that even if the equilibrium point is stable, female mating preferences evolve to optimize (maximize) the mean fitness of females in terms of the number of progeny produced, by choosing mates with the best paternal behavior, rather than by mating with males that carry the best genes for the survival or mating success of their offspring.

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