

Models of speciation by sexual selection on polygenic traits

(mating preferences/sexual dimorphism/genetic correlation/runaway process)

RUSSELL LANDE

Department of Biophysics and Theoretical Biology, University of Chicago, Chicago, Illinois 60637

Communicated by James F. Crow, February 10, 1981

ABSTRACT The joint evolution of female mating preferences and secondary sexual characters of males is modeled for polygamous species in which males provide only genetic material to the next generation and females have many potential mates to choose among. Despite stabilizing natural selection on males, various types of mating preferences may create a runaway process in which the outcome of phenotypic evolution depends critically on the genetic variation parameters and initial conditions of a population. Even in the absence of genetic instability, rapid evolution can result from an interaction of natural and sexual selection with random genetic drift along lines of equilibria. The models elucidate genetic mechanisms that can initiate or contribute to rapid speciation by sexual isolation and divergence of secondary sexual characters.

The distinction between natural and sexual selection drawn by Darwin (1) is that natural selection arises from variance in individual survival (and fecundity), whereas sexual selection results from variance in mating success. Dimorphism of secondary sexual characters in higher animals is caused by two major factors: combat or competition between individuals of one sex (usually males) for mates and mating preferences exerted by the opposite sex (females) (1). The fitness of a trait with respect to mating success can override its value for survival, creating a kind of maladaptive evolution that may contribute to the extinction of a population (2–6). In contrast to intermale competition, which entails an obvious advantage of mating success for the winners, Darwin was unable to explain why in many species with polygamous systems of mating (where males are promiscuous and invest little or nothing but gametes in their offspring) females should prefer mates with extreme characters that are apparently useless or deleterious for survival, such as the extravagant plumage of some male birds and the exaggerated horns and tusks of certain male mammals (1, 7–9).

Fisher (2, 3) suggested an ingenious solution to Darwin's problem by outlining a genetic mechanism for the joint evolution of female mating preferences and secondary sexual characters of males. An essential feature of this mechanism is the genetic correlation between the sexes; that is, the extent to which variations in male and female traits are influenced by the same genes or segregating factors. Even if the genes affecting these characters are not mutually pleiotropic, a positive correlation between them will nevertheless arise in the population because of assortative mating created by genetic variance in mating preferences (where the more discriminating females mate with the more extreme males). The evolution of mating preferences may be self-reinforcing because, once started, females are selecting not only for more extreme males but also indirectly, through the genetic correlation, for a higher intensity of mating preferences. Fisher (3) stated that the result of this positive feedback could be a "runaway process," in which

a male trait and female preferences for it both increase geometrically or exponentially with time until finally checked by severe counterselection. This genetic mechanism could rapidly create a new species by sexual isolation and phenotypic divergence of a population from its closest relatives. It also could reinforce or accelerate other modes of speciation.

O'Donald (10) numerically confirmed the basic operation of Fisher's runaway process, using two-locus models, in which one locus with two alleles codes for variation in males and one di- or triallelic locus influences female mating preferences. He found that the rate and extent of evolution is enhanced when the most preferred genotype at the male character locus is recessive and that linkage can influence the dynamics. However, such models greatly restrict the evolution of a trait, which must cease with the fixation of an allele at the corresponding locus. For quantitative characters, it is generally more realistic to employ a polygenic model (11, 12) and to allow for the maintenance of genetic variability by mutation and recombination (13, 14).

Female mating preferences have been demonstrated in a variety of arthropods and vertebrates (7–9, 12), indicating that there is (or was) some genetic variation for them. A complete set of mating preference functions, which would specify for every female phenotype the sexual preference for each male phenotype, has not been measured for any population. Although for most species it may be difficult or impossible to obtain, such information is necessary to determine the course of evolution of male secondary sexual characters and female mating preferences. To clarify Fisher's mechanism for rapid speciation by sexual selection, I analyze here the joint evolution of male secondary sexual characters and different types of female mating preferences which have been discussed, often incorrectly, in the literature on sexual selection.

QUANTITATIVE GENETIC MODELS

Evolution of the Mean Phenotypes. Consider for simplicity two sex-limited quantitative traits: a male character, z , and a female mating preference, y , each influenced by multiple autosomal genes and subject to environmental effects. On an appropriate scale of measurement, both traits are assumed to have normal distributions, $p(z)$ and $q(y)$, with means \bar{z} and \bar{y} and phenotypic variances σ^2 and τ^2 . For continuously varying characters, a logarithmic scale of measurement often renders the distributions approximately normal with variances roughly independent of the mean values (11). The additive genetic variances of the male and female traits are denoted as G and H , and the additive genetic covariance between them, B , is due to pleiotropy and nonrandom associations of alleles at different loci. In a population of autosomal genotypes, B is the covariance of additive genetic effects when in males with those when in females. These genetic variation parameters of a population can be estimated from phenotypic correlations between relatives or from artificial selection experiments (11, 12).

It is assumed that in each generation every female is inseminated

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U. S. C. §1734 solely to indicate this fact.

inated and that males do not help raise offspring or protect or provision their mate(s); hence, the expected number of progeny from a given female is independent of her mate choice. In any particular generation, female mating preferences do not change the mean fitness in a population but act only to redistribute fitness among the different male phenotypes. Thus, there is no selection directly on female mating preferences, which evolve only as a correlated response to selection on males. The direct response to one generation of selection on males and the correlated response in female mating preferences are

$$\Delta \bar{z} = \frac{1}{2}GS/\sigma^2 \quad \Delta \bar{y} = \frac{1}{2}BS/\sigma^2, \quad [1]$$

in which S is the selection differential on males, the difference between selected and unselected adults, and the factors of $\frac{1}{2}$ account for the sex-limited expression of both traits (6, 11).

Natural selection on males is assumed to act through differential viability, followed by sexual selection through differential mating success. Writing the viability of males with phenotype z as $w^*(z)$, the distribution of male phenotypes after natural selection is

$$p^*(z) = w^*(z)p(z)/\int w^*(z)p(z)dz. \quad [2]$$

Weak natural selection toward an optimal male phenotype, θ , can be approximated by a Gaussian function,

$$w^*(z) = e^{-(z - \theta)^2/2\omega^2}, \quad [3a]$$

in which ω indicates the range of male phenotypes around the optimum with high viability. After natural selection alone, the distribution of male phenotypes is normal with mean and variance

$$\bar{z}^* = (\bar{z}\omega^2 + \theta\sigma^2)/(\omega^2 + \sigma^2) \quad [3b]$$

$$\sigma^{2*} = \omega^2\sigma^2/(\omega^2 + \sigma^2). \quad [3c]$$

Denoting the relative preference of females with phenotype y for mating with males of phenotype z as $\psi(z|y)$, the frequency of matings of the different males with females of the given phenotype y is assumed to be proportional to this preference. The mating success of males with phenotype z relative to that of all surviving males in the population encountering females with phenotype y is then

$$\psi^*(z|y) = \psi(z|y)/\int p^*(z)\psi(z|y)dz. \quad [4]$$

The net relative fitness of males with phenotype z is the product of their viability and mating success averaged over the entire female population,

$$W(z) = w^*(z)\int q(y)\psi^*(z|y)dy. \quad [5]$$

Utilizing Eqs. 2, 4, and 5, the mean fitness in the population is

$$\bar{W} = \int p(z)W(z)dz = \int p(z)w^*(z)dz, \quad [6]$$

which is the same as under natural selection alone, as required by the assumptions. The selection differential on males can be computed as

$$S = \bar{W}^{-1}\int zp(z)W(z)dz - \bar{z} \\ = \int q(y)\int zp^*(z)\psi^*(z|y)dzdy - \bar{z}. \quad [7]$$

One model of mating preferences is suggested by Stevens' (15) psychophysical law. Over a wide range of stimulus intensities in nearly every sensory modality in man, the perceived intensity is proportional to a power of the actual intensity. Measured values of human psychophysical exponents range from 0.5 for brightness of a point source of light to 3.5 for electric shock

to the fingers (15). It seems likely that in many higher animals, as in man, both sensory perceptions and emotional reactions of an individual often scale as power functions of quantities related to secondary sexual characters and mating displays. Such a mechanism may underlie the responses of many animals to supernormal stimuli (16). Thus, suppose that a quantitative character of males, ϕ , produces a perception and associated sexual preference, ψ , in a given female proportional to ϕ^y , where y is a constant pertaining to the particular female. If the male character is analyzed on a logarithmic scale, $z = \ln \phi$, as is often appropriate for statistical purposes, the psychophysical preferences of a given female can be written as

$$\psi(z|y) \propto e^{yz}. \quad [8a]$$

Individual females are assumed to differ in the degree of discrimination in mate choice, y .

Animal perceptions of some sensory modalities, such as color or the pitch of a sound, and matching constraints between the sexes may result in unimodal preferences. Such preferences could be either an absolute intrinsic property of each female or could be relative and scaled to the distribution of male phenotypes in a population.

Females who prefer most a particular value of a male character, regardless of its distribution in the population, are described by absolute preferences. An important class of absolute "preference" occurs where homologous or complementary characters of the sexes are under a matching constraint that determines the probability of successful mating. In many species, male and female morphology and sexual behaviors are mutually constrained in some way. A simple form of absolute preference is that for a given female the most preferred male phenotype is y with a tolerance of $\pm \nu$ or where the characters of mates are somehow constrained to be within about $\pm \nu$ of each other,

$$\psi(z|y) \propto e^{-(z - y)^2/2\nu^2}. \quad [8b]$$

Alternatively, if an individual female surveys the population of surviving males and chooses a mate from among them relative to the mean, with the highest preference for males of phenotype $\bar{z}^* + y$ but with a high preference for males having any phenotype within $\pm \nu$ of this value, she shows relative preferences that can be described by the Gaussian function

$$\psi(z|y) \propto e^{-[z - (\bar{z}^* + y)]^2/2\nu^2}. \quad [8c]$$

Because natural and sexual selection act independently on males, the total selection differential can be calculated as the sum of two corresponding parts. The change in the mean male phenotype due to natural selection within a generation is from Eq. 3b:

$$\bar{z}^* - \bar{z} = (\theta - \bar{z})\sigma^2/(\omega^2 + \sigma^2).$$

In the psychophysical model females of a given type y then choose mates with a mean phenotype that deviates from \bar{z}^* by an amount $\sigma^{2*}y$, whereas with unimodal preferences the analogous mean deviation from \bar{z}^* is

$$(y - \epsilon\bar{z}^*)\sigma^{2*}/(\nu^2 + \sigma^{2*}),$$

in which $\epsilon = 1$ for absolute preferences and $\epsilon = 0$ for relative preferences. Averaging these changes over the entire female population and adding the previous contribution from natural selection gives the general form of the total selection differential on males. The assumption that selection on the variance of males is weak ($\omega^2, \nu^2 \gg \sigma^2$) yields the approximation

$$\frac{S}{\sigma^2} = \frac{\bar{y}/\alpha - (1 + \epsilon/\alpha)\bar{z} + \theta}{\omega^2}, \quad [9]$$

in which, for the psychophysical model, $\alpha = 1/\omega^2$ and $\varepsilon = 0$, whereas with relative or absolute unimodal preferences, $\alpha \approx \nu^2/\omega^2$.

The equilibria in each model of mate choice, from Eqs. 1 and 9 are all points on the line

$$\bar{y} = (\alpha + \varepsilon)\bar{z} - \alpha\theta. \quad [10]$$

For any mean value of the male character there is an average intensity of female sexual preference that will cancel the force of natural selection tending to restore the mean male phenotype to its optimum, θ . The slope of the line of equilibria, $\alpha + \varepsilon$, depends only on the selective forces impinging on the population, if these are weak.

Provided the genetic variances and covariance of the characters remain constant, deterministic evolution of the mean phenotypes occurs along lines of constant slope, $\Delta\bar{y}/\Delta\bar{z} = B/G$. The translation of coordinates

$$\bar{z} = \bar{z} - \theta/(1 + \varepsilon/\alpha), \quad \bar{y} = \bar{y} \quad [11a]$$

allows Eqs. 1 and 9 to be written in matrix form as

$$\Delta \begin{pmatrix} \bar{z} \\ \bar{y} \end{pmatrix} = \frac{1}{2\alpha\omega^2} \begin{pmatrix} -(\alpha + \varepsilon)G & G \\ -(\alpha + \varepsilon)B & B \end{pmatrix} \begin{pmatrix} \bar{z} \\ \bar{y} \end{pmatrix}. \quad [11b]$$

The eigenvalues of the matrix in Eq. 11b are $\lambda_0 = 0$, corresponding to lack of deterministic movement along the line of equilibria, and

$$\lambda = [B - (\alpha + \varepsilon)G]/(2\alpha\omega^2), \quad [12]$$

associated with the lines of motion. Thus, the mean phenotypes change geometrically with time at the rate of $(1 + \lambda)^t$. The general criterion for stability of the line of equilibria is $-2 < \lambda < 0$. Although it is possible with discrete generations for oscillations of period two generations to occur if $\lambda < -1$, under weak selection $|\lambda| \ll 1$, so that $(1 + \lambda)^t \approx e^{\lambda t}$. Then, if $\lambda < 0$ or equivalently $B/G < \alpha + \varepsilon$, the line of equilibria is stable; however, perturbations away from a certain point on the line will not generally return to the same point. If $\lambda > 0$ or $B/G > \alpha + \varepsilon$, the system is unstable and evolves away from the line of equilibria at a geometrically increasing rate, in a direction that may either exaggerate or diminish the male trait (Fig. 1). Under unimodal preferences, the condition for instability is more stringent with absolute ($\varepsilon = 1$) than with relative ($\varepsilon = 0$) mate choice.

Maintenance of Genetic Variance and Covariance. When the mating preferences of females are mediated by sensory and other nervous processes rather than by physical constraints and the male sexual trait is morphological, the sets of genes influ-

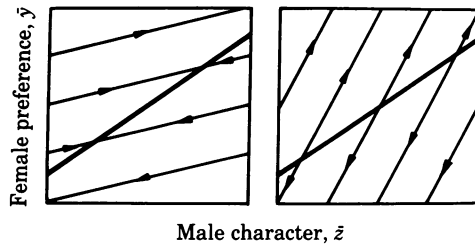


FIG. 1. The joint evolution of female mating preferences and a secondary sexual character of males. The male trait is under stabilizing natural selection and sexual selection by females. There is no selection directly on female mating preferences, which evolve as a genetically correlated response to selection on males, along lines of constant slope (with arrowheads). A (heavy) line of equilibria exists for the mean phenotypes that may be stable (Left) or unstable (Right), depending on the genetic variation parameters of the population.

encing the two characters are not expected to be mutually pleiotropic. This case is of special interest in assessing the magnitude of genetic covariance between the characters that can be produced purely by the assortative mating that necessarily results from variance in mating preferences. Enumerating the loci as $1, \dots, m$ for the male trait and $m + 1, \dots, n$ for the female preference, any linkage map with positive recombination rates between loci is allowed, $0 < r_{ij} \leq 1/2$ for $i \neq j$, and $r_{ii} = 0$. With the assumption that all of the genetic variation is additive, the covariance between the effects of alleles at loci i and j from the same gamete is denoted as C_{ij} , whereas the covariance of allelic effects within individuals but from different gametes (due to nonrandom mating) is written as C'_{ij} . By defining

$$C_{iz} = \sum_{j=1}^m (C_{ij} + C'_{ij}) \quad C_{iy} = \sum_{j=m+1}^n (C_{ij} + C'_{ij}), \quad [13a]$$

the genetic variances and covariance of the characters are

$$G = 2 \sum_{i=1}^m C_{iz}, \quad H = 2 \sum_{i=m+1}^n C_{iy}, \quad [13b]$$

$$B = 2 \sum_{i=m+1}^n C_{iz} = 2 \sum_{i=1}^m C_{iy}.$$

Male and female traits are assumed to have normally distributed environmental effects with variances E and F and no genotype-environment interaction or correlation, so that the phenotypic variances are respectively

$$\sigma^2 = G + E \quad \tau^2 = H + F. \quad [14]$$

In a model of mutation with a wide range of possible allelic effects at each locus and the same rate and distribution of mutational changes for all alleles at a given locus i , mutation creates a constant input of new genetic variance each generation, u_i , but does not alter the covariances between loci (13, 14). By assuming that mutation produces no net directional force on the mean phenotypes, the dynamics of the variances and covariances of allelic effects can be derived (17) as

$$\Delta C_{ij} = -r_{ij}(C_{ij} - C'_{ij}) - \frac{1}{2}kC_{iz}C_{jz}/\sigma^2 + \delta_{ij}u_i + D_{ij}, \quad [15]$$

in which $\delta_{ij} = 1$ if $i = j$, and zero otherwise. k is the proportional reduction in the phenotypic variance of males caused by selection within a particular generation, and the factor of $1/2$ accounts for sex-limited expression of the selected trait. D_{ij} represents the disruptive influence of sex-limited selection (due to different intensities of directional selection on the sexes); this vanishes when the mean phenotypes are at an equilibrium ($S = 0$) and is negligible under sufficiently weak directional selection, near the line of equilibria, hence D_{ij} is ignored in subsequent calculations.

The diagonal Eqs. 15 with $i = j$ have a unique admissible equilibrium solution, provided $k > 0$,

$$C_{iz} = \sqrt{2u_i\sigma^2/k}. \quad [16a]$$

Although this does not completely solve the system, in conjunction with the definitions in Eq. 13b it does determine the critical genetic parameter that governs the stability of the mean phenotypes near the line of equilibria,

$$B/G = \sum_{i=m+1}^n \sqrt{u_i} / \sum_{i=1}^m \sqrt{u_i}. \quad [16b]$$

This parameter does not depend on the linkage map of the genes or on the form of natural or sexual selection on males; it depends

only on the relative mutability of genes affecting female mating preferences and the male trait.

Variance in female mating preferences exerts a disruptive effect on the male trait, which, if sufficiently large, may overcome the stabilizing influence of natural selection, so that $k < 0$. Under weak selection on the variance of males ($\omega^2, \nu^2 \gg \sigma^2$), it can be shown that existence of the equilibrium in Eq. 16 a and b requires in the psychophysical model that $\tau^2 < \omega^2$ and, with relative or absolute unimodal preferences, that $\tau^2 < \nu^2(1 + \nu^2/\omega^2)$. Numerical analysis of the complete dynamical system (not given here) confirmed that these equations specify a unique locally stable equilibrium of genetic variability.

Random Genetic Drift in Mating Preferences. In a finite population, random genetic drift in female mating preferences produces random selective forces on males, which in turn affect mating preferences through the genetic correlation between the traits. When the line of equilibria created by genetic variance in mating preferences is unstable, random genetic drift could trigger a runaway process of sexual selection. Even when the line of equilibria is stable, evolution along it can occur rapidly through the interaction of random genetic drift with natural and sexual selection because populations starting from the same point may drift to different sides of the line of equilibria and be selected in opposing directions (Fig. 1).

If the effective size of a population, N_e (5), is not very small and remains nearly constant through time, the probability distribution of genetic variation parameters will have negligible dispersion around its expected value (18); then G , B and H can be approximated as constants. Although the effective population size changes with the degree of polygamy (5) as the intensity of sexual selection evolves, for weak selection, N_e should be nearly constant over a wide range of mean phenotypes. Under these conditions, phenotypic evolution can be analyzed by using the theory of Gaussian diffusion processes (19). The vector of mean phenotypes in a population of effective size N_e has a variance-covariance matrix due to genetic sampling (each generation) of

$$\mathbf{V} = \frac{1}{N_e} \begin{pmatrix} G & B \\ B & H \end{pmatrix}, \quad [17]$$

which is unaltered by the translation of coordinates in Eq. 11a. Starting from a specified point, the joint probability distribution of the mean phenotypes is approximately Gaussian, with expectation obeying a continuous time version of Eq. 11b. The dispersion matrix of the mean phenotypes (in either the original or translated coordinates) is initially null, $\mathbf{D}(0) = \mathbf{0}$, and satisfies (19)

$$\frac{d\mathbf{D}}{dt} = \mathbf{M}\mathbf{D} + \mathbf{D}\mathbf{M}^T + \mathbf{V}, \quad [18]$$

in which \mathbf{M} is the matrix in Eq. 11b and \mathbf{M}^T is its transpose. The general solution

$$\mathbf{D}(t) = \int_0^t e^{\mathbf{M}(t-\xi)} \mathbf{V} e^{\mathbf{M}^T(t-\xi)} d\xi \quad [19]$$

can be evaluated by expanding the matrix exponentials in power series. Noting from Eqs. 11 and 12 that $\mathbf{M}^2 = \lambda\mathbf{M}$, summing the series and integrating shows that when the line of equilibria is asymptotically stable ($-1 < \lambda < 0$), the ultimate rate of dispersion along the line for $t \gg -\lambda^{-1}$ is

$$\mathbf{D}(t) \approx \text{constant matrix} + \frac{H(1-\gamma^2)t}{N_e(\alpha+\epsilon-B/G)^2} \begin{pmatrix} 1 & \alpha+\epsilon \\ \alpha+\epsilon & (\alpha+\epsilon)^2 \end{pmatrix}, \quad [20]$$

in which $\gamma = B/\sqrt{GH}$ is the additive genetic correlation between the sexes. In spite of stabilizing natural selection on males, random genetic drift in female mating preferences produces a diversification of male phenotypes among populations that may be quite rapid.

DISCUSSION

In polygamous species where males are promiscuous, providing only genetic material to the next generation, and females have many potential mates, there is no selection directly on female mating preferences. Nevertheless, female sexual preferences can evolve in response to selection on genetically correlated traits, such as secondary sexual characters of males. A male character under stabilizing natural selection toward a phenotype that is optimal with respect to survival may evolve to a markedly suboptimal phenotype by sexual selection acting through mating success. For a population with additive genetic variance in both female mating preference and a male sexual trait, a selective constraint on the male trait alone implies a line of possible equilibria for the mean phenotypes. Regardless of how much the average male deviates from the optimum phenotype under natural selection, there is an intensity of sexual selection that will bring the system into balance (Fig. 1). In the models of psychophysical, absolute, and relative mating preferences, the slope of the line of equilibria depends essentially on the selective forces acting on the population. The evolutionary stability of the line of equilibria is determined by the ratio B/G , the additive genetic covariance between male and female traits divided by the additive genetic variance in the male character. If this genetic regression slope exceeds the slope of the line of equilibria, the line is unstable (Eq. 12).

Polygenic mutation, recombination, and assortative mating can maintain the additive genetic variance and covariance of the traits nearly constant in spite of selection tending to deplete genetic variation. Genetic covariance between characters in a population is attributable to pleiotropy and nonrandom associations of alleles at loci affecting the traits. Homologous characters of the two sexes, such as body size, usually show similar patterns of variation and a high genetic correlation probably due to pleiotropy (6). Female mating preferences operating through nervous and other sensory processes are not expected to be mutually pleiotropic with male morphological characters. However, even in the absence of pleiotropy, a positive genetic correlation between female sexual preferences and the secondary sexual characters of males inevitably results from assortative mating due to genetic variance in mating preferences.

In the present models, if there is no pleiotropy of genes influencing female mating preferences and male sexual traits, the critical genetic parameter governing the evolutionary stability of the mean phenotypes, B/G , is completely determined by the relative mutability of genes affecting the two traits. For the mutation process studied here (Eq. 15; refs. 13 and 14), this ratio is independent of the linkage map of the genes and the forms of natural and sexual selection (Eq. 16b).

The expectation of a genetic correlation between female mating preferences and the male characters on which mate choice is based can be experimentally tested. Breeding and selection experiments can be used to estimate the additive genetic variances and covariances of quantitative characters in a population. But these techniques generally cannot distinguish pleiotropy from nonrandom association of alleles at tightly linked loci (11).

As stated by Fisher, during the unstable phase, the rates of evolution of a male trait and female mating preferences for it both increase with time geometrically or approximately exponentially, at least near the line of equilibria. Thus, the rates of

evolution may become quite rapid, especially when the preding statement applies to characters measured for statistical purposes on a logarithmic scale. These results contrast with the conclusions from simple two-locus models (10).

In Fisher's account, a runaway process must eventually be stopped by severe counterselection against extreme males or against the most discriminating females because of their difficulty in finding a suitable mate. The model of stabilizing natural selection with a Gaussian fitness function (Eq. 3a) produces a linear restoring force on the mean male phenotype toward its optimum. But some intensities of natural selection can be overcome by the evolution of sexual preference, which in the present models produces a linear perturbing force (Eq. 9). This implies that a nonlinear force from natural selection is necessary to finally stabilize runaway sexual selection or, equivalently, that the viability of individual males must decrease faster than a Gaussian curve as the mean male phenotype departs from its optimum.

Despite his generally gradualistic view of evolution, Fisher (3) believed that striking secondary sexual characters often evolved in sudden bursts, followed by long periods of comparative stability. He discussed runaway sexual selection as a mechanism for rapid speciation by premating reproductive isolation and divergence of quantitative characters. The exponential nature of the instability means that the process could be explosive or virtually instantaneous on a geological time scale.

Fisher (3) alluded to the indeterminacy involved in unstable systems, where small perturbations can produce large effects, but suggested that the initial direction of runaway evolution in female mating preferences and male traits is determined by natural selection or intermale combat. Instability also implies that fluctuating selection and random genetic drift may be important sources of nonadaptive diversity in taxa undergoing rapid speciation. Even in the absence of genetic instability, there may be rapid indeterminate evolution by random genetic drift interacting with natural and sexual selection along lines of equilibria (Eq. 20). In species with complex morphology and behavior, the diversity of possible outcomes could be enormous, with a hyperplane rather than a line of equilibria. The male traits most likely to become exaggerated by such mechanisms are those under weak natural selection and subject to relatively large variance in female sexual preferences, such as some behavioral and morphological elements of courtship and mating.

Male characters can be diminished as well as enhanced by female sexual preferences. A bias in the direction of evolution toward conspicuous male traits is inevitable during the origin of a new character. Furthermore, unlike the highly polygamous mating systems often associated with exaggerated male traits, evolution toward diminished development tends to restore random mating as the population passes a lower threshold for the development of the trait in males or its detection by females. Fisher (2) noted that, for species in which individuals have limited time and ability to assess potential mates, the expression of strong mating preferences for one trait may decrease the opportunity for sexual selection on other traits; thus, the evolution of new secondary sexual characters and associated mating preferences may contribute to the decline of old ones (see also ref. 7).

Although in the present models selection is limited to males and mate choice is restricted to females, genetic instability of mating preferences and sexual dimorphism may occur in a wider set of circumstances. With the addition of a constraint by stabilizing natural selection directly on female mating preferences, caused by variation in male parental behavior or mating delays incurred by the most discriminating females, there would be a qualitative change in the dynamics described here. Instead of a line of equilibria for the mean phenotypes there would exist an equilibrium point where the mean fitness of females is maximized but that of males is not (6). However, by continuity with the present limiting case, this equilibrium point could still be genetically unstable. Natural selection on mating preferences also creates the possibility of evolutionary oscillations.

These models help to explain the classical observations of Darwin (1) and others (7–9) that closely related species of higher animals often differ most in the characters of adult males, in a substantially nonadaptive or random pattern, whereas females resemble one another more strongly. Sexual isolation is frequently a major reproductive barrier between closely related animal species (20). Studies of natural and experimental populations of Hawaiian *Drosophila* (21) suggest that, in small geographically isolated populations, random genetic drift in female mating preferences may initiate rapid speciation by sexual isolation and evolution of sexual dimorphism.

I thank S. J. Arnold, J. J. Bull, J. F. Crow, M. J. West-Eberhard, E. G. Leigh, Jr., M. J. Ryan, and the reviewers for helpful criticisms. This work was supported by National Science Foundation Grant DEB-7909804 and the Andrew W. Mellon Foundation.

1. Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex* (Murray, London).
2. Fisher, R. A. (1915) *Eugen. Rev.* 7, 184–192.
3. Fisher, R. A. (1930) *The Genetical Theory of Natural Selection* (Clarendon, Oxford); (1958) (Dover, New York), Rev. Ed., pp. 135–162.
4. Haldane, J. B. S. (1932) *The Causes of Evolution* (Harper and Row, New York), pp. 119–124.
5. Wright, S. (1969) *Evolution and the Genetics of Populations. Vol. 2. The Theory of Gene Frequencies* (Univ. of Chicago, Chicago).
6. Lande, R. (1980) *Evolution* 34, 292–305.
7. Gilliard, E. T. (1969) *Birds of Paradise and Bower Birds* (Natural History, New York).
8. Geist, V. (1971) *Mountain Sheep* (Univ. of Chicago, Chicago).
9. Brown, J. L. (1975) *The Evolution of Behavior* (Norton, New York), pp. 151–185.
10. O'Donald, P. (1980) *Genetic Models of Sexual Selection* (Cambridge Univ. Press, Cambridge).
11. Falconer, D. S. (1960) *Introduction to Quantitative Genetics* (Ronald, New York).
12. Ehrman, L. & Parsons, P. A. (1976) *The Genetics of Behavior* (Sinauer, Sunderland, MA).
13. Kimura, M. (1965) *Proc. Natl. Acad. Sci. USA* 54, 731–736.
14. Lande, R. (1975) *Genet. Res.* 26, 221–235.
15. Stevens, S. S. (1975) *Psychophysics* (Wiley, New York).
16. Alcock, J. (1975) *Animal Behavior* (Sinauer, Sunderland, MA), pp. 158–160.
17. Lande, R. (1977) *Genetics* 86, 485–498.
18. Avery, P. J. & Hill, W. G. (1977) *Genet. Res.* 29, 193–213.
19. Lande, R. (1980) *Am. Nat.* 116, 463–479.
20. Dobzhansky, Th. (1970) *Genetics of the Evolutionary Process* (Columbia, New York), pp. 319–325.
21. Carson, H. L. (1978) in *Ecological Genetics: The Interface*, ed. Brussard, P. F. (Springer, New York), pp. 93–107.