THE DARWIN-FISHER THEORY OF SEXUAL SELECTION IN MONOGAMOUS BIRDS

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Abstract.—Males of monogamous birds often show secondary sexual traits that are conspicuous but considerably less extreme than those of polygynous species. We develop a quantitative-genetic model for the joint evolution of a male secondary sexual trait, a female mating preference, and female breeding date, following a theory proposed by Darwin and Fisher. Good nutritional condition is postulated to cause females to breed early and to have high fecundity. The most-preferred males are mated by early-breeding females and receive a sexual-selection advantage from those females' greater reproductive success. Results show that conspicuous male traits that decrease survival can evolve but suggest that the extent of maladaptive evolution is greatly limited relative to what is possible in a polygynous mating system for two reasons. First, in the absence of direct fitness effects of mate choice on the female, the equilibria for the male trait and female preference form a curve whose shape shows that the maximum possible strength of sexual selection on males (and hence the potential for maladaptive evolution) is constrained. Under certain conditions, a segment of the equilibrium curve may become unstable, leading to two alternative stable states for the male trait. Second, male parental care will often favor the evolution of mating preferences for less conspicuous males. We also find that sexual selection can appear in the absence of the nutritional effects emphasized by Darwin and Fisher. A review of the literature suggests that the assumptions of the Darwin-Fisher mechanism may often be met in monogamous birds and that other mechanisms may often reinforce it by producing additional components of sexual selection.

Among the most spectacular products of sexual selection are the extreme secondary sexual characters seen in the males of certain polygynous species such as peacocks. Darwin (1859, 1871) argued that these traits evolved because female mating preferences cause the more elaborate males to obtain more mates. Subsequent field and theoretical research has verified the elements of this hypothesis (reviewed by Kirkpatrick [1987]). Evidence of sexual selection is also seen in monogamous species. Males of many monogamous birds such as the New World warblers (family Parulidae) are brightly colored, while females are relatively cryptic (Darwin, 1871; Verner and Willson, 1969; Payne, 1984; Møller, 1986). Males of even closely related monogamous species are often strongly divergent in plumage and song, indicating that the secondary sexual characters are evolving rapidly. Naturalists have long been aware, however, that the male traits are typically less strongly developed in monogamous species than they are in polygynous ones.

The mechanism of sexual selection that Darwin postulated for polygynous species cannot apply in a species that is truly monogamous, since males with extreme traits do not obtain more matings than other males. Aware of this difficulty, Darwin (1871 Ch. 8) proposed a specific hypothesis for monogamous birds. He suggested that males with exaggerated traits receive a reproductive advantage by virtue of mating with females that are more fecund. Darwin's concept was elaborated by Fisher (1958 pp. 153–154), who made the ideas concrete by producing a numerical example of the mechanism. Our goal in this paper is to consider the theoretical and empirical validity of the Darwin-Fisher theory. The Darwin-Fisher mechanism may operate alone or in conjunction with other factors (such as biased

sex ratios, extra-pair copulations, etc.) that have been discussed more recently. We compare the empirical evidence for the Darwin-Fisher mechanism and its alternatives in the Discussion.

The Darwin-Fisher theory assumes that males come into breeding condition or arrive at the breeding grounds in advance of the females. The first females to come into breeding condition or to arrive at the breeding site choose mates from the full population of males. If females have preferences for certain males (for example, the brightest ones), then those males will be mated by the earliest females and be removed from the pool of unmated males. Females arriving later choose mates from a pool of males that is progressively more depleted of the brightest individuals, since those males have paired with earlier females. The dullest and least-preferred males are mated last. This process continues until all the females have arrived and every male has been mated.

Darwin and Fisher suggested that the earlier-breeding females have greater reproductive success. The greater success of these females is not, however, a result of their earlier breeding but, rather, a result of their superior health or nutritional condition. That is, the physiological effects of nutrition cause females in better condition both to breed earlier and to fledge more offspring (caused either by an increased number of eggs or greater success in rearing chicks). These effects can generate a persistent correlation between early breeding date and high reproductive success, even though breeding date itself is not under selection to evolve towards earlier dates (Fisher, 1958; Price et al., 1988). Since the most-preferred males are mated early, they will pair with females in good condition and, therefore, receive a reproductive advantage. This component of selection favors bright males even though they may be selected against at other points in the life cycle (by predation, for example).

Several lines of evidence now support the Darwin-Fisher hypothesis. First, good nutrition in females has been shown to cause early breeding and high reproductive success in a number of species (reviewed by Price et al. [1988]). Second, differential male mating success has been observed in many monogamous species, particularly with respect to song and plumage variation (Howard, 1974; Catchpole, 1980; O'Donald, 1980a, 1983; Proctor-Gray and Holmes, 1981; Payne, 1982; Järvi, 1983; Flood, 1984; Price, 1984; Searcy and Andersson, 1986; Grant and Grant, 1987; Møller, 1988). Two of these studies identified sexual selection occurring on males in the way that Darwin envisaged. Møller (1988) showed that male swallows with artificially elongated tail streamers paired up early and fledged more than twice the number of young than those with artificially shortened tail streamers, which paired up late. O'Donald (1980a, 1983) showed that early-breeding Arctic Skua females preferentially mate with dark-phase males and also have higher reproductive success.

O'Donald (1972, 1980b, 1980c) has developed single-locus genetic models describing the evolution of male characters under the Darwin-Fisher mechanism for different female preference functions and has fit these models to his data on the Arctic Skua. He simplified the analysis by assuming that neither the date of breeding nor female preference evolves and found that the mechanism can cause a male trait to evolve away from its survival optimum under the influence of sexual selection.

Here we develop a quantitative-genetic model of the Darwin-Fisher theory that considers the simultaneous evolution of the male trait, the female mating preference, and date in the season on which the female breeds. Our results support the arguments made by Darwin and Fisher that the mechanism can lead to the evolution of extreme male sexual characters such as bright plumage even if this reduces male survival. There is, however, a constraint on the strength of sexual selection, because variation in male reproductive success is limited by the variation in female fecundity. This restricts the amount of maladaptive evolution of the male trait that is likely to occur in monogamous mating systems, as compared to polygynous systems. In the absence of direct selection on mating preferences, the equilibria for the male trait and female mating preference form a continuous curve. Under some conditions, a segment of the curve may become unstable, causing the male trait

to evolve rapidly between two alternative states. Direct selection on preferences, which may often result from male parental care, can favor preferences for less conspicuous males and further limit the potential for the evolution of extreme male characters. The model shows that sexual selection can appear in the absence of the nutritional effects emphasized by Darwin and Fisher.

The Model

Ecological and Behavioral Assumptions.—The hypothesis suggested by Darwin and Fisher involves three traits: a male secondary sexual trait (such as plumage brightness or song), a female mating preference for that trait, and female breeding date. The phenotypic value for the male trait is denoted z. The trait is assumed to have a normal (Gaussian) distribution among males at the beginning of each generation, with mean $\bar{z}$ and variance σ_z^2. We suppose that the male trait influences the probability of survival to adulthood, which is maximized at $z = \theta_z$. For example, a certain amount of yellow carotenoid in the plumage might be needed to produce a cryptic green coloration. Less pigment renders males brown, and more pigment renders males orange; both of these colors might be conspicuous to predators. The survival to adulthood of males with phenotype z, $W_m^*(z)$, falls off as the value of z deviates from θ_z in proportion to a Gaussian curve of width (or "variance") ω_z^2, and so larger values of ω_z^2 imply weaker natural selection. We will in fact assume that the strength of stabilizing selection acting on the male trait is weak (i.e., $\omega_z^2 \gg \sigma_z^2$).

Females choose mates on the basis of the male secondary sexual trait. The female mating preferences are assumed to affect only the probability of choosing different types of males, so that variation in the preference does not cause variation in female survival or fecundity. Factors such as parental care in many monogamous birds, however, may cause a female's mate choice to influence her reproductive success. We will consider the consequences of this type of direct fitness effects in the Discussion; for now, we consider the simplest null model with no direct fitness effects of the preference and assume that other factors were responsible for the establishment of a preference in the population (see Kirkpatrick, 1987). The mating-preference phenotype of a female is denoted y, while its mean and variance in the population are $\bar{y}$ and σ_y^2, respectively. We will assume that females follow the "psychophysical" preference rule introduced by Lande (1981). The relative mating preference of a y female for a z male, denoted $\psi(z|y)$, is an exponential function of the degree of expression of the male trait and the strength of the female's preference:

$$\psi(z|y) \propto \exp(zy). \tag{1}$$

Thus, a positive value of y corresponds to a female preference for males with large values of z, a negative value corresponds to a preference for smaller values of z, and a value of 0 indicates that the female does not discriminate between males with different trait phenotypes. Variation among females in their preferences selects for increased variance in the male trait; we assume that this effect is weak by requiring that $\sigma_z^2\sigma_y^2 \ll 1$.

The third trait in the model is female breeding date, denoted b. A critical assumption made by Darwin and Fisher is that the times at which females come into breeding condition and choose mates are spread out over a period of the season, so that the most-preferred male phenotypes tend to be mated early. Following Fisher's (1958) numerical example, we consider a female's breeding-date phenotype to be determined by the sum of three components: x, an additive genetic component; n, a nonheritable component attributable to the female's nutritional condition; and e, a nonheritable component caused by other environmental sources and genetic dominance. A female's breeding date can thus be written

$$b = x - n + e. \tag{2}$$

The nutritional effect n is subtracted rather than added because increased levels of nutrition result in earlier breeding. Genes affecting the mating preference and breeding date are expressed only in females. Variation in the three components (x, n, and e) cause females to breed on different dates. The variance of the nutritional effect among females is denoted σ_n^2, while the overall

mean and variance of breeding date are denoted $\bar{b}$ and σ_b^2, respectively.

A female's reproductive success is affected by her nutritional condition and the date on which she breeds. We assume that the fitness component of each female that is directly attributable to her nutritional state is an exponential function of n. Simultaneously, female reproductive success is directly affected by breeding date. Weather, predation, and other environmental factors are assumed to favor the date θ_b in the season, and cause breeding success to fall off on either side of this date in proportion to a Gaussian curve of width (or "variance") ω_b^2. The strength of stabilizing selection on breeding date is assumed to be weak ($\omega_b^2 \gg \sigma_b^2$). The fitness of a female in nutritional state n that breeds on date b is therefore

$$W_f(n,b) \propto \exp\left[\alpha n - \frac{(\theta_b - b)^2}{2\omega_b^2}\right] \quad (3)$$

where α is a constant for the population determined by the strength of the physiological effect of nutrition on female fecundity (see Price et al., 1988). We consider nonsymmetric forms for the breeding-date distribution and the breeding-date fitness function later in the paper.

Genetic Assumptions. — We assume that the additive genetic components of the male trait, female mating preference, and female breeding date are multivariate normally distributed in the population at the outset of each generation, as can result from polygenic inheritance (see Bulmer, 1985 Ch. 8). The additive genetic variances for these three characters are written g_z^2, g_y^2, and g_b^2, respectively, while the additive genetic covariance between traits i and j is written g_{ij}. We treat the genetic variances and covariances as parameters in our model and do not attempt to predict their evolution based on more fundamental genetic variables. (Our model for the evolution of the mean phenotypes could, however, be extended by including a submodel for the evolution of the genetic variances and covariances.) Results from earlier models of sexual selection (O'Donald, 1980c; Lande, 1981; Kirkpatrick, 1982) suggest that female mate choice will tend to produce a positive additive genetic covariance between the preference and the male trait (g_{zy}). Mate choice will likewise tend to produce a genetic covariance between breeding date and the male trait (g_{zb}); this covariance will be negative if females on average prefer larger values of the male trait and will be positive if they prefer smaller values of the male trait. These two genetic covariances will tend to generate a genetic covariance between the preference and breeding date (g_{yb}) of the same sign as g_{zb}, although the strength of this effect will generally be weak.

Following standard quantitative-genetic theory (Falconer, 1981 Ch. 7–8; Bulmer, 1985 Ch. 4, 8), the environmental components of the three traits (including the nutritional component of female breeding date) are assumed to be independent of the additive genetic components and multivariate normally distributed with means of zero. Therefore, the phenotypic distribution of the male trait is normal, and the multivariate distribution in females of the mating preference, nutrition, and breeding date, denoted $p_f(y, n, b)$, is multivariate normal. Inheritance is autosomal, and generations are nonoverlapping.

Evolutionary Dynamics. — It follows from these assumptions that the per-generation changes in the phenotypic means of the three traits are

$$\Delta\bar{z} = \frac{g_z^2}{2\sigma_z^2} s_z + \frac{g_{zb}}{2g_b^2} s_x \quad (4a)$$

$$\Delta\bar{y} = \frac{g_{zy}}{2\sigma_z^2} s_z + \frac{g_{yb}}{2g_b^2} s_x \quad (4b)$$

$$\Delta\bar{b} = \frac{g_{zb}}{2\sigma_z^2} s_z + \frac{1}{2} s_x \quad (4c)$$

where s_z is the selection differential for the male trait (the difference in the phenotypic means between selected and newborn males) and s_x is the genetic selection differential for breeding date (the difference in the mean value of x between selected and newborn females). Each of the equations consists of two terms, the first representing the evolutionary change resulting from selection on the male trait, the second resulting from selection on breeding date. The factors of ½

appear because each trait is sex-limited in its expression.

The selection differentials s_x and s_z can be determined from the ecological assumptions outlined above. The derivations are presented in the Appendix. The genetic selection differential on breeding date is

$$s_x \approx \frac{(\theta_b + \alpha\sigma_n^2 - \bar{b})g_b^2}{\omega_b^2} . \qquad (5)$$

Unfortunately, we are unable to determine the general analytic solution for the selection differential for the male trait. We can, however, calculate it numerically for particular cases of interest using the formulas developed in the Appendix. Additionally, we can show that the selection differential in the limiting case, as female preferences become infinitely strong, is

$$s_z \approx \frac{(\theta_z - \bar{z})\sigma_z^2}{\omega_z^2} + \frac{\sigma_b\sigma_z(\bar{b} - \theta_b)}{\omega_b^2}$$
$$+ \frac{\alpha\sigma_n^2\sigma_z}{\sigma_b} \qquad (6)$$

as derived in the Appendix. Equations (4)–(6) and numerical calculations are the basis of the conclusions that we present below.

Evolutionary Equilibria.—Given heritable variation for all three traits (i.e., nonzero additive genetic variances) and a genetic correlation between x and z that is less than one in magnitude, Equations (4a)–(4c) show that an evolutionary equilibrium can be reached only when the selection differentials s_x and s_z are zero.

Equation (5) therefore implies that the equilibrium for the mean breeding date is

$$\hat{b} \approx \theta_b + \alpha\sigma_n^2 \qquad (7)$$

(Price et al., 1988). At equilibrium, the mean breeding date is not the optimal breeding date θ_b, but is displaced to later in the season. The discrepancy between the optimal breeding date and the mean breeding date is $\alpha\sigma_n^2$, which reflects the strength of the effect of nutritional variation on female breeding date. Although the average female breeds at a date later than is optimal, females in good nutritional condition breed earlier than average and have higher fecundity. Consequently, the average offspring

hatch on the optimal date. In a previous theoretical study (Price et al., 1988), we found that there will be heritable variation for breeding date at this equilibrium despite the persistence of a correlation between breeding date and female reproductive success, with earlier breeding females having higher fecundity (as pointed out by Fisher [1958]). This correlation seems to imply that directional selection favors earlier breeding, but it is actually caused by the nonheritable variation in nutritional state, which both accelerates breeding and increases fecundity. At equilibrium, a genetic predisposition to breed earlier or later than the mean will, on average, decrease a female's reproductive success (see Price et al., 1988).

An evolutionary equilibrium for the male trait requires that the selection differential s_z equals zero. We have numerically calculated the equilibrium value for the mean of the male trait with a variety of parameter values, including different values of the mean female mating preference, using the method described in the Appendix. In the limiting case of infinitely strong mating preferences for large values of z and assuming weak stabilizing selection on breeding date, Equations (6) and (7) show that the equilibrium for the mean of the male trait is

$$\hat{z} \approx \theta_z + \frac{\alpha\sigma_n^2\omega_z^2}{\sigma_b\sigma_z} . \qquad (8)$$

Equations (6) and (8) indicate that the male trait will be most exaggerated at equilibrium when natural selection on the trait is weak (ω_z^2 large), when the male trait is relatively stereotyped within the population (σ_z small), when much of the variation in breeding date is caused by variation in female nutritional variation (σ_n^2/σ_b large), and when nutrition has a large effect on fecundity (α large).

The major result from numerical analysis (see Appendix) is that there is an equilibrium value of the mean male trait corresponding to each possible value of the mean female mating preference. This produces an infinite set of equilibrium combinations for the trait and preference that fall along a curve, shown in Figure 1. If the population comes to rest at any point along this curve, none of the evolutionary forces specified thus far in the model will cause the population
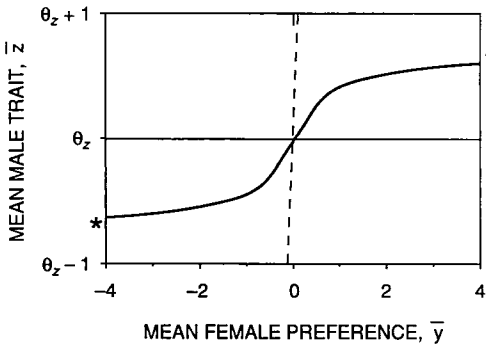
FIG. 1. Equilibrium mean male phenotype as a function of the equilibrium mean female preference (solid curve). Parameter values are $\sigma_b^2 = \sigma_z^2 = 1.0$, $\sigma_y^2 = 0.1$, $\sigma_n^2 = 0.25$, $g_{yb} = 0$, $\alpha = 0.25$, $\omega_z^2 = \omega_b^2 = 10.0$. Equilibria for the male trait when preferences are infinitely strong are indicated by the stars. The dashed line is the curve of equilibria under polygyny with the same parameters but no variation in nutrition (from Lande [1981]). The survival optimum for the male trait is indicated by the horizontal line.

FIG. 2. Curves of equilibria for different values of α, the effect of nutrition on female fecundity. All other parameters are as in Figure 1. A value of $\alpha = 0.1$ produces a 22% difference in fecundity between females lying two standard deviations above and below the mean of the distribution of nutritional values; $\alpha = 0.25$ produces a 66% difference.

to evolve further. The mean of the male trait lies at the point that maximizes male survival when $\hat{y} = 0$ (meaning that females on average show no preference, so there is no sexual selection). At all other points of equilibrium, however, the mean male trait is displaced from the viability optimum by the force of sexual selection. Thus, sexual selection in monogamous species can lead to maladaptive evolution of male secondary sexual traits. These results are qualitatively similar to those from models of sexual selection in polygynous mating systems (Lande, 1981; Kirkpatrick, 1982).

The major contrast in the evolutionary consequences of monogamy and polygyny is the degree to which the male trait can be displaced from its survival optimum by the force of sexual selection. Under polygyny, Lande (1981) found that the equilibria fall on a line that relates the mean female preference to the mean male trait:

$$\hat{z} \approx \theta_z + \omega_z^2 \hat{y}. \qquad (9)$$

Equation (9) shows that the mean male trait can be displaced any distance from the survival optimum θ_z, given sufficiently strong female preferences. Under monogamy, however, our numerical results and Equation (8) for infinitely strong preferences indicate that there is a limit to how far the mean male trait can equilibrate from its sur-
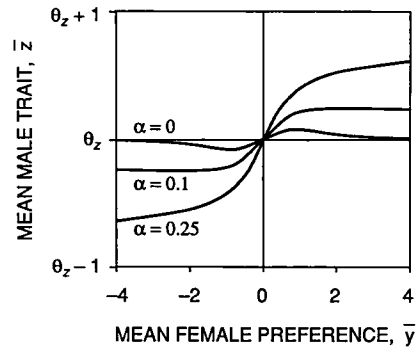
vival optimum. In the example of Figure 1, the mean male trait always lies within one phenotypic standard deviation of the survival optimum. Figure 1 also shows that the mean male trait lies much closer to the survival optimum in a monogamous mating system than in a polygynous one, given the same mean female mating preference.

The evolutionary consequences of varying α, the effect of nutrition on female fecundity, are shown in Figure 2. As expected, increasing the strength of the nutritional effect leads to increased variation in female reproductive success and, hence, to increased levels of sexual selection on males. Similar outcomes result from increases in σ_n^2, the variance in nutrition, and ω_z^2, which is inversely proportional to the intensity of stabilizing natural selection acting on the male trait.

Even in the absence of the nutritional variation emphasized by Darwin and Fisher, however, there can be sexual selection on males. Setting α or σ_n^2 to zero does not generally cause the equilibrium for the mean male trait to lie at its ecological optimum (Fig. 2). In this case, the mean female breeding date is at the optimal date. Female preference produces sexual selection by causing some males to mate nearer, on average, to this optimal date (O'Donald, 1972). With symmetric distributions for female breeding date and the male trait, our numerical results showed that the preferred males, on

average, mated closer to the optimal breed-
ing date and thus received an advantage.
The force of sexual selection is strongest for
intermediate levels of female preference and
vanishes when preferences are either absent
or infinitely strong (Fig. 2). With low levels
of nutritional variation, the equilibrium
curve for the mean of the male trait is no
longer a monotonic function of the mean
female preference. Very strong preferences
cause the most-preferred males to mate too
early in the season, with the result that those
males receive less of a sexual-selection ad-
vantage than if preferences are weaker.

We have assumed up to this point that
the phenotypic distributions and fitness
functions are Gaussian. In many cases,
however, these symmetric functions may be
inappropriate. For example, the distribu-
tion of breeding dates may be highly skewed,
with the majority of females arriving nearly
synchronously and later arrivals straggling
in over a period of several days. To deter-
mine the sensitivity of our model to the
symmetry of the distributions and fitness
functions used earlier, we numerically ana-
lyzed asymmetric forms for female breeding
dates, the breeding-date fitness function, and
the male trait, using the numerical methods
described in the Appendix. This is an ap-
proximate method, since Equations (4a)–
(4c) and several intermediate calculations
assume normality of the additive genetic
and phenotypic distributions. In general, the
results are qualitatively similar to those we
have already described. A striking result,
however, is that under certain conditions
the sexual-selection differential for the male
trait can actually be opposite in sign to the
mean female preference. We found that
highly left-skewed breeding-date distribu-
tions and highly right-skewed male trait dis-
tributions can cause the most-preferred
males to be selected against. The result is
interesting because were such distributions
to occur they could cause the male trait to
evolve in the direction opposite to that which
is favored by the female mating preferences.
This outcome occurred only under extreme
sets of parameters, however, and we suspect
that it is unlikely to occur in nature.

We conclude that the male trait reaches
an equilibrium that is a compromise be-
tween natural selection (caused by variation

in survival) and sexual selection (caused by
variation in reproductive success). Sexual
selection on males arises from two sources:
males derive a reproductive advantage if
they are mated by females in higher nutri-
tional condition or if they are mated near
the optimal breeding date.

Our model assumes that the underlying
genetic variances and covariances are given
parameters, and it is general to any values
that they might assume under the action of
mutation, selection, and recombination.
These parameters affect the evolutionary
dynamics of populations that are not at
equilibrium but do not affect the location
or shape of the equilibrium curve, with the
exception of the additive genetic covariance
between the preference and breeding date,
g_{yb}. This covariance generates a phenotypic
correlation between the preference and
breeding date, which in turn affects the
strength of sexual selection that the males
experience. Numerical results show that in-
creasing values of g_{yb} tend to displace the
equilibrium curve upwards slightly towards
larger values of $\hat{z}$ for a given value of $\hat{y}$.

Stability of the Equilibria. — We are un-
able to determine analytically the stability
of the equilibria with respect to displace-
ments away from the curve, because the term
s_z in Equations (4a)–(4c) is not in an explicit
form. The following graphical analysis,
however, gives some idea about the range
of outcomes that may be possible. We will
assume that the equilibrium curve takes the
qualitative form shown in the figures and
that the sexual-selection differential is not
reversed with respect to the direction of fe-
male preference, which occurs only in cer-
tain exceptional cases as discussed above.

Consider first a situation in which there
is no genetic or phenotypic covariance be-
tween any pair of the characters. Under the
assumptions of our model, there is no se-
lection acting directly on female mating
preferences. In the absence of genetic cor-
relations (which would cause the mean pref-
erence to evolve as a correlated response to
selection on the other characters) or direct
selection on the preferences, the mean pref-
erence will not evolve from its initial state.
The mean breeding date and mean male
trait, however, will evolve in response to
selection. The mean breeding date will

equilibrate at the point indicated by Equation (7), while the mean male trait will evolve to the point on the equilibrium curve that corresponds to the initial value of female preference. Under weak selection, the equilibria will be stable with respect to perturbations taking the population away from the curve but neutrally stable with respect to perturbations that move the population along the curve. The situation is illustrated in Figure 3 (top). Evolutionary forces not considered here, such as selection on pleiotropic effects of the preference and random genetic drift, may cause a population to evolve rapidly along the curve of equilibria (see Lande, 1981; Kirkpatrick, 1982, 1987).

The nonrandom mating caused by variation in female choice is expected to create linkage disequilibrium between the male-trait and the female-mating-preference loci and to contribute a positive component to their genetic covariance, g_{zy} (O'Donald, 1980c; Lande, 1981; Kirkpatrick, 1982). This can cause the curve of equilibria to become unstable in polygynous mating systems (Lande, 1981). For monogamous systems, if the genetic covariance between the preference and trait becomes sufficiently large, we expect that the central portion of the curve will become unstable. Instability is most easily visualized for the case in which there is no covariance between the genetic component of female breeding date (x) and the other characters, which allows us to consider the evolution of the male trait and female preference in isolation from the evolution of breeding date. The slope of the evolutionary trajectories in the y-z plane will then be

$$\frac{\Delta \bar{z}}{\Delta \bar{y}} = \frac{g_z{}^2}{g_{zy}} . \qquad (10)$$

If the genetic covariance becomes sufficiently large so that $\Delta \bar{z}/\Delta \bar{y}$ is smaller than the slope of the steepest segment of the equilibrium curve, a central region of the equilibrium curve will become unstable. (This could occur as the result of changes in either the genetic parameters $g_z{}^2$ and g_{zy} or in the shape of the equilibrium curve.) However, because the equilibrium curve is bounded in z, the outer segments of the curve are expected to remain stable always. Under these
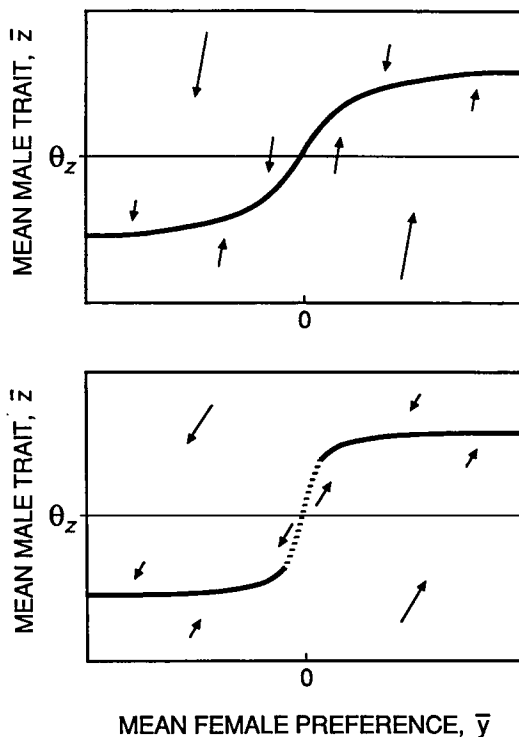

FIG. 3. Top) Case in which entire curve of equilibria is stable. Bottom) Case in which instability of the central segment of the equilibrium curve results when the genetic covariance g_{zy} is sufficiently large relative to the slope of the central segment of the equilibrium curve. The solid regions of the curve are stable; the dashed region is unstable. Arrows indicate evolutionary trajectories.

conditions, there will be two alternative stable states for the male trait: one in which it is enlarged and one in which it is reduced relative to the natural selection optimum, as illustrated in Figure 3 (bottom). This pattern is qualitatively similar to that seen in models of polygynous mating systems when there are two alternative niches (i.e., survival optima) for the male trait (Lande and Kirkpatrick, 1988).

Evolution of the preference caused by other evolutionary factors may take the population along the curve of equilibria into an unstable region, triggering a rapid evolutionary transition to the alternate state. Although we lack analytical evidence, we suspect that the curvature of the equilibrium curve may bias the direction in which populations move along stable regions of the curve under random genetic drift and

other perturbations. In some cases, this may even tend to push populations from a stable segment of the curve into the unstable segment, initiating repeated transitions between the alternative stable states.

In summary, we envision that there are two qualitative outcomes. Under the first, the equilibrium curve is stable everywhere. Under the second, large values of g_{zy} destabilize the central segment of the equilibrium curve and establish two alternative stable states for the male trait.

DISCUSSION

Our model of the Darwin-Fisher hypothesis for sexual selection in monogamous birds indicates that, in the absence of other evolutionary forces, the evolutionary equilibria for the male trait and female mating preference form a curve, rather than a single point. In general, the male trait equilibrates at a point away from its viability optimum. This maladaptive outcome is caused by the female mating preferences, from which the more extreme males obtain a sexual-selection advantage that compensates for their reduced survival.

Male characters in monogamous species are typically less exaggerated than in polygynous species. We suggest two reasons why this may be so. First, the evolutionary departure of the male trait from its viability optimum is limited by variation in female fecundity. This constraint makes intuitive sense, because the only advantage gained by preferred males is the higher fecundity of their early-breeding mates. In contrast, preferred males in a polygamous species gain more mates, and the potential fitness gain through reproductive success is virtually unlimited. The effect of the constraint in monogamous species is to bend the curve of equilibria and, consequently, to limit the range of evolutionary outcomes (see Fig. 1).

Considerable male-trait evolution is nevertheless possible in monogamous species within the limit of the Darwin-Fisher mechanism. Weaker viability selection on the male trait, for example, will permit mate choice to have a greater evolutionary effect [see Eqs. (6) and (8)]. Thus, the hole-nesting habits of parrots and the dangerous bills of egrets may have relaxed the force of natural selection on male plumes and col-

oration and encouraged the exaggeration of those traits via mate choice. The male trait may evolve rapidly, either along the curve of equilibria when it is stable or between two alternative stable states when it is not. These processes could cause the divergence of isolated subpopulations and lead to speciation. The observation that males in closely related monogamous species are frequently divergent in secondary sexual characters shows that these traits often evolve more rapidly than other kinds of characters.

The second factor that is likely to place important limits on the strength of sexual selection in monogamous birds is direct selection acting on female mating preferences. Males of monogamous species typically contribute parental care and other resources to their mates and offspring. Darwin (1871 p. 262) suggested that females choose males on the basis of their vigor as well as secondary sexual traits, and male vigor could influence the quality of parental care that the male provides. Field studies suggest that male parental contributions can have important effects on female fecundity (Searcy, 1982; Price, 1984; Searcy and Andersson, 1986). Males with extreme traits may attract predators to the nest (Baker and Parker, 1979) or to themselves, thereby leaving their mates without help in rearing the young. These effects will impose direct selection on the preferences, since females mated to males that provide the best parental care will leave more offspring. Selection of this form causes the curve of equilibria to be reduced to a single point (Lande, 1981; Kirkpatrick, 1985, 1987). At this equilibrium, the mean female preference maximizes immediate female fitness, while the male trait equilibrates at the corresponding point on the equilibrium curve (see Fig. 1). We anticipate that male parental care will tend to favor preferences for less conspicuous males and thus greatly limit the potential for maladaptive evolution of the male trait. Direct selection on preferences can also arise when females with extreme preferences fail to mate, when females are selected to avoid hybridization with other species, or when the sensory systems used by females in mate choice are also used in other contexts. These forms of selection will again favor particular preferences over oth-

ers, but not necessarily those for less conspicuous males.

Diagnostic empirical tests of the Darwin-Fisher mechanism involve the statistical relations between nutritional condition, breeding date, and female fecundity. According to the Darwin-Fisher model, a correlation between breeding date and fecundity persists at evolutionary equilibrium only because of a common correlation with nutritional condition. Thus, there should be no direct selection on breeding date in an equilibrium population, despite the persistence of a correlation between breeding date and fecundity (Price et al., 1988). Given a satisfactory measure of nutritional condition, one could test this prediction by checking for a zero partial regression of female fitness on breeding date when nutritional condition is held constant. A breeding design or extensive offspring–parent data would be needed to test directly the expectation that the correlation between breeding date and fecundity is nongenetic, but as Fisher (1958) pointed out, this would be no simple undertaking.

Our model also directs attention to a set of tractable genetic issues. In particular, assortative mating should promote genetic coupling between male traits and breeding date and between male traits and sexual preferences for those traits. Assortative mating has been detected in monogamous birds (e.g., Murton et al., 1973; Murton and Westwood, 1977; O'Donald, 1980a), but the genetic correlation between a male trait and a female preference has yet to be measured directly. Other genetic correlations, such as that between the male trait and female breeding date, also have not been explored.

The present model may help explain the evolution of exaggerated courtship characters that are expressed in both the males and females of many monogamous species. In a variety of bird families (e.g., parrots, pigeons and doves, estrildid finches, grebes, penguins, herons and egrets), both males and females have highly developed plumes or bright colors that are used in courtship displays (Goodwin, 1967, 1982; Stonehouse, 1975; Forshaw, 1978; Burley, 1986). Huxley (1914) coined the term "epigamic" for such traits because the term "secondary sexual" implies sexual dimorphism. The sexes are often virtually indistinguishable in behavior as well as in epigamic morphologies. In many ornate but monomorphic bird species, the male and female simultaneously or alternately perform the same complex behavior patterns during courtship (Huxley, 1914; Armstrong, 1965; Warham, 1975; Serpel, 1981). Behavioral monomorphism may even extend to copulatory postures. In grebes, for example, the male and female alternately mount one another (Huxley, 1914). Some monomorphic, monogamous bird families show signs of rapid diversification in epigamic characters. Conspecific species may differ greatly in coloration or plumage (e.g., the speciose parrot genera *Platycerus, Pyrrhura,* and *Trichoglossus,* or the fruitdove genus *Ptilinopus*), and there may be extensive geographic variation within species. For example, the 21 geographic races of the rainbow lory (*Trichoglossus haematodus*) show tremendous variety in coloration. The fig parrots *Opopsitta guilielmiterti* and *O. diophthalma* both have numerous geographic races that differ markedly in coloration (Goodwin, 1967; Forshaw, 1978).

Huxley (1914) proposed a process of mutual sexual selection to account for such evolution of epigamic traits in monomorphic species. We can reconcile his proposal with our quantitative-genetic model in the following way. Evolution by mutual sexual selection may proceed in monogamous, sexually monomorphic species because nutritional condition affects the breeding date and fecundity of both sexes. As before, we assume that females in good condition breed earlier and are more fecund than females in poor condition. Likewise, we suppose that healthier males are ready to breed earlier and are more fecund (i.e., are better at protecting or provisioning their mates or offspring than are males in poor condition). Within the pool of fecund males and females that are ready to breed, both sexes choose mates on the basis of an epigamic trait that is expressed equally in males and females. Males and females with more extreme development of the epigamic trait tend to breed sooner. Birds ready to breed but with less extreme development of the epigamic trait tend to lag behind and so may pair with later-breeding, less fecund mates.

If we assume, for convenience, that there are no sexual differences in either the expression or the inheritance of the epigamic trait, sexual preference, or the breeding date, we can use Equations (4a)–(4c) to model the evolution of the three traits (after dropping the factors of ½ which accounted for sex-limited expression of the traits). The sexual-selection differential for the epigamic trait will no longer be given by the equations derived in the Appendix [in particular, Equations (A7)–(A9) will not be valid], because of the process of mutual mate choice. Nevertheless, the evolutionary equilibrium should be similar to the curve shown in Figure 1, because there is no direct selection on sexual preference. Thus, part of the diversity of epigamic traits in monomorphic, monogamous species may be due to indeterminacy of evolutionary outcome.

The Darwin-Fisher argument is only one mechanism that can give rise to sexual selection in ostensibly monogamous species. At least five others have been suggested by previous workers. First, as Fisher (1958) pointed out, male mortality during the breeding season favors the most attractive males, since males that are not paired early are at greater risk of dying either before they are mated or before they have successfully raised their young. Second, if there is an excess of males at the breeding grounds, as can happen if females experience higher mortality or delayed maturity, then only the more-attractive males will be mated. This occurs commonly and is the way in which sexual selection has been detected in many empirical studies (Catchpole, 1980; Proctor-Gray and Holmes, 1981; Payne, 1982; Jårvi, 1983; Flood, 1984; Price, 1984; Grant and Grant, 1987). Third, many putatively monogamous species of birds are actually weakly polygynous (Gowaty, 1985). This occurs when some males obtain second mates (Gowaty, 1985; Alatalo et al., 1986; Møller, 1986; Dhondt, 1987) or extra-pair copulations (Ford, 1983; Westneat, 1987a, 1987b; Møller, 1988). Fourth, studies of captive zebra finches show that mating with an attractive male can induce females to increase their reproductive effort (Burley, 1986). Fifth, even in the absence of the nutritional effects postulated by Darwin and Fisher, female mating preferences in mo-

nogamous species affect the date on which different male phenotypes are mated (O'Donald, 1972). As shown by our model, this leads to variation in reproductive success and to sexual selection on males if breeding date influences the probability that a pair successfully fledges chicks. (Unlike other mechanisms of sexual selection, this can lead to the evolution of male traits in the direction opposite to what is preferred by females, in some cases.) These five mechanisms can operate in isolation or in conjunction with the Darwin-Fisher mechanism.

The model we have developed is based on the assumption that sexual selection is occurring through female choice of male traits. Many secondary sexual characters may have evolved without female choice through the agency of male-male competition, or through female choice of resources that males control (as opposed to choice of the males themselves). Empirical studies are beginning to assess this possibility. Alatalo et al. (1986) and Slagsvold (1986) examined order of male pairing in the Pied Flycatcher, a species with low levels of polygyny. They were able to show experimentally that territory variables, rather than plumage or song, were the most important criteria by which settling females choose locations to breed. While those studies provide no evidence that females are currently using aspects of male song or plumage as cues, Lifjeld and Slagsvold (1988) showed that male characteristics were also a basis for female choice in homogeneous habitats. Experimental playback of male songs has implicated both male interactions and female choice in several species (e.g., Baker et al., 1987; Grant and Grant, 1987). Møller (1988) showed by experimental manipulation that female swallows choose males on the basis of male tail length. Thus, there is some experimental evidence for female choice, although more investigations on the relative roles of female choice, male competition, and their interaction are badly needed.

Other patterns associated with monogamy are clearly related to sexual selection, and part of their explanation may lie in the Darwin-Fisher hypothesis. Such patterns include the distribution of sexual dimorphism and monomorphism among closely

related species (Baker and Parker, 1979; Møller, 1986), delayed plumage-maturation of males (Rohwer et al., 1980; Price, 1984; Lyon and Montgomery, 1986), the evolution of song repertoires (McGregor and Krebs, 1982; Searcy and Andersson, 1986), and seasonal plumage variation (Baker and Parker, 1979; Rohwer et al., 1980). These observations also suggest that considerations not included in our model, such as age structure, male preferences, and male-male competition, are important. The challenge will be to incorporate these factors into the theory in a way that will produce empirically useful predictions.

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APPENDIX

Here, we present the derivations of s_x, the genetic selection differential on female breeding date, and s_z, the selection differential for the male trait. The genetic selection differential for breeding date, s_x, can be calculated directly from Equations (2) and (3), which gives Equation (A1) (at the bottom of the page). The fraction on the right-hand side is the mean of the genetic component of female breeding date after selection (determined by averaging over the weighted reproductive success of females), while $\bar{x}$ is the corresponding mean before selection. $\overline{W}^{**}$ is the mean reproductive fitness in the population:

$$\overline{W}^{**} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p_f(y, n, b) W_f(n, b) \, dy \, dn \, db.$$

$$(A2)$$

Evaluating the integrals and noting that $\bar{x} = \bar{b}$ yields the expression for s_x shown in Equation (5).

The selection differential for the male trait, s_z, is a sum of two components, the first due to natural selection and the second to sexual selection:

$$s_z = s_z^* + s_z^{**}.$$

$$(A3)$$

The natural selection differential is

$$s_z^* \approx \frac{(\theta_z - \bar{z})\sigma_z^2}{\omega_z^2}.$$

$$(A4)$$

The sexual selection differential is by definition

$$s_z^{**} = \bar{z}^{**} - \bar{z}^* = \bar{z}^{**} - (\bar{z} + s_z^*)$$

$$(A5)$$

where $\bar{z}^*$ is the phenotypic mean of the male trait after viability selection and $\bar{z}^{**}$ is its mean following sexual selection. The value of $\bar{z}^{**}$ is calculated by weighting each male by the reproductive success of the female with which he mates and then averaging over all males,

$$s_x = \frac{\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x p_f(y, n, x - n + e) W_f(n, x - n + e) \, dy \, dn \, dx \, de}{\overline{W}^{**}} - \bar{x}.$$

$$(A1)$$

as shown in Equation (A6) (at the bottom of the page), where $M(z, y, n, b)$ represents the frequency of mated pairs consisting of a male with trait z and a female with preference y, nutritional state n, breeding on date b. This distribution is determined by the relative frequency of males with phenotype z and females with mating preference y that are in nutritional condition n and breeding on date b, biased by the preference of y females for z males. Thus,

$$M(z, y, n, b) = U(z, b) \, p_t(y, n, b) \, \psi^*(z \,|\, y, b) \quad \text{(A7)}$$

where

$$\psi^*(z \,|\, y, b) = \frac{\psi(z \,|\, y)}{\displaystyle\int_{-\infty}^{\infty} \psi(z \,|\, y) U(z, b) \, dz} \quad \text{(A8)}$$

accounts for the bias in male mating success caused by female preferences (Lande, 1981), and $U(z, b)$ is the probability that a male has trait phenotype z and is unmated at breeding date b. Before any females arrive at the breeding grounds, $U(z, b)$ is equal to the distribution of males surviving viability selection and so is normal with mean $\bar{z}^*$ and variance approximately σ_z^2. Values for $U(z, b)$ after females begin to arrive are given implicitly by the differential equation

$$\frac{d}{db} U(z, b) = - \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} M(z, y, n, b) \, dy \, dn. \quad \text{(A9)}$$

The right-hand side of (A9) is the rate at which pairs involving males with phenotype z are formed on breeding date b and, hence, removed from the pool of unmated males.

Equations (A5)–(A9) give an implicit expression for s_z^{**}, the sexual-selection differential. Calculating s_z^{**} analytically is difficult because, although $U(z, b)$ is a normal distribution in z at the outset of the breeding season, it becomes highly skewed as males with more-preferred trait phenotypes are mated by arriving females. We therefore calculated s_z^{**} by integrating the equations on a computer.

The numerical results can be supplemented by considering the force of sexual selection on the male trait that results if female preferences become very strong. If every female had an infinitely strong preference and perfect discrimination abilities, males would be mated in perfect rank order of their trait phenotypes by the

arriving females. Infinitely strong preferences would produce a perfect correlation of -1 between the male phenotype and breeding date if females prefer males with extreme positive values of the trait or a correlation of $+1$ if they prefer males with extreme negative values. We can use this fact to determine the reproductive fitness of male phenotypes by calculating the date on which they will be mated and the average reproductive fitness of females breeding on that date. In general, the expected reproductive success of pairs breeding on date b is approximately

$$\overline{W}_b^{**}(b) \propto \exp\left[-\frac{b^2}{2\omega_b^2} + b\left(\frac{\theta_b}{\omega_b^2} - \frac{\alpha \sigma_n^2}{\sigma_b^2} \right) \right]. \quad \text{(A10)}$$

From this, we can calculate that, in the case of an infinitely strong female preference favoring positive values of z, the sexual-selection differential on the male trait is

$$s_z^{**} \approx \frac{\sigma_b \sigma_z (\bar{b} - \theta_b)}{\omega_b^2} + \frac{\alpha \sigma_n^2 \sigma_z}{\sigma_b}. \quad \text{(A11)}$$

The overall selection differential on the male trait, s_z, is determined by substituting Equation (A4) for s_z^* and either a numerical result or Equation (A11) for s_z^{**} into Equation (A3). In the case of infinitely strong female preferences, the result is analytic and is given by Equation (6).

At an evolutionary equilibrium, the selection differentials s_x for female breeding date and s_z for the male trait in general must equal zero, as described in the text. The condition under which s_x vanishes is given by Equation (5). For s_z to vanish, the natural- and sexual-selection differentials for the male trait must cancel each other. Using (A4) and (A5), this implies that the equilibrium value for the male trait is given by

$$\hat{z} \approx \theta_z + \frac{s_z^{**} \omega_z^2}{\sigma_z^2}. \quad \text{(A12)}$$

This equilibrium is affected by the equilibrium female preference, $\hat{y}$, which enters into (A12) through s_z^{**}. We evaluated Equation (A12) by calculating s_z^{**} numerically using Equations (A5)–(A9), assuming that the mean breeding date is at its equilibrium [Equation (7)].

$$\bar{z}^{**} = \frac{\displaystyle\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} z W_t(n, b) M(z, y, n, b) \, dz \, dy \, dn \, db}{\overline{W}^{**}} \quad \text{(A6)}$$