SEXUAL SELECTION, SPACE, AND SPECIATION

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Abstract.—A Fisherian model of sexual selection is combined with a diffusion model of mate dispersal to investigate the evolution of assortative mating in a sympatric population. Females mate with one of two types of polygynous males according to a male’s display of one of two sex-limited, autosomal traits; these male traits may be associated with differential phenotypic mortalities. Through a Fisherian runaway process, female preferences and male traits can become associated in linkage disequilibrium, leading to patterns of assortative mating. Dispersing males, whose rate of movement is dependent on mating success, carry female preference genes with them, and displaced males thereby produce daughters with preference genes for their respective traits in locally higher than average frequencies. The reduced diffusion of the more preferred males permits the success of other male types in adjacent areas. Thus, mating-success dependent diffusion, when coupled with the rapid divergence in phenotypes possible under the Fisher process, can lead to the coexistence of two female preferences and two male traits in sympatry. We argue that many existing approaches to sympatric speciation fail to explain observed male polymorphisms because they exclude explicit spatial structure from their speciation models.

Key words.—Fisher process, sexual selection, spatial model, sympatric speciation.

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The genetic obstacles to sympatric modes of speciation have been forcefully argued by a number of authors, most of whom maintain that geographical isolation during allopatriy must predate the evolution of intrinsic reproductive isolation in sympatry (Mayr 1963, 1970; Futuyma and Mayer 1980). The term geographical isolation is most commonly taken to denote a complete absence of gene flow between isolated populations (Mayr 1970). The terms “spatial isolation” or “microgeographical” isolation have been used in those cases in which a less severe inhibition of gene flow has been observed or postulated to occur between neighboring populations (Mayr 1976). The reproductive mechanisms that might act as intrinsic isolating mechanisms in sympatric populations have also received much attention, these being traditionally classified as either prezygotic or postzygotic (Dobzhansky 1970). The evolution of prezygotic isolating mechanisms may be the result of natural selection acting through a process of reinforcement (Dobzhansky 1940), or sexual selection acting via female preference in a Fisher-type process (Lande 1981; West-Eberhard 1983). Reinforcement, through selection acting against maladaptive hybrids, might conceivably operate in parapatry (Endler 1977; Bull and Possingham 1995), along an environmental cline (Lande 1982), or in a heterogeneous environment (Butlin 1989; Liou and Price 1994). The Fisher process is a conjectured mechanism in which female preference alleles for a novel male trait may become coupled genetically with alleles coding for that trait (Fisher 1930). Fisher processes, in the absence of reinforcement, are assumed to require complete isolation during a phase of allopatriy during which species undergo reproductive character displacement (but see Turner and Burrows 1995). In contrast, we present a model in which assortative mating evolves in sympatry, and in which the resultant incipient species coexist.

Proponents of sympatric speciation contend that disruptive natural selection, acting on resource use in a single panmictic population, may promote behavioral heterogeneity, and thereby favor character displacement (Tauber and Tauber 1989). Hence, through ecological specialization and restricted gene flow, a population may produce sympatric daughter species (Maynard Smith 1966; Rosenzweig 1978; Kondrashov 1986). In many polygynous species, and particularly in lekking species, male spatial position is correlated with mating success (Schwagmeyer 1988; Andersson 1994), and so one might expect less successful males to move away from areas in which they are not deemed attractive, a strategy similar to “scramble-competition polygyny.” Males with particular sexually selected traits can therefore find themselves distributed according to the spatial pattern of female mating preferences (Thornhill and Alcock 1983). In other words,
assuming that dispersal is local, males manifesting a given trait will congregate alongside females that prefer that trait at a given position in space. We seek to investigate whether mating-success dependent diffusion, in which unselected males have an increased probability of dispersing away from their current positions, can lead to the evolution of variable patterns of assortative mating in a single sympatric population occupying a homogeneous environment. Our model is based on the process first postulated by Fisher (1930), and is conceptually related to the models of Kirkpatrick (1982), Lande (1982), and Seger (1985). These models demonstrate how female mating preferences can become coupled with male traits through a self-reinforcing genetic process. We adopt a different mathematical framework, in which populations are continuous and overlapping, and in which the spatial distribution of males and females is tracked.

A DISCRETE CHARACTER, CONTINUOUS TIME, SPATIAL MODEL

We consider a single population comprising haploid sexual animals in which male and female phenotypes are determined by two fully penetrant alleles at two loci, and in which generation overlap makes a continuous-time model applicable. The two loci are a q locus, expressed only in males, that determines a sexually selected trait, and a p locus, expressed only in females, that determines a mating preference for a given male trait. For generality, and brevity of nomenclature, we formulate the model such that an infinite number of alleles at each locus is possible, letting \( T \) represent the set of permissible p, and \( T \) be the set of permissible q. The number of individuals with a genotype \( pq \) at a time \( t \) and at a position \( x \) is given by \( Z_{pq}(x,t) \). For algebraic convenience we assume a 1:1 sex ratio at reproductive age, and hence half of these individuals will be males with a phenotype q and half females with a phenotype p, so that

\[
M_q(x, t) = \frac{1}{2} \sum_{p' \in T} Z_{p'q}(x, t) \quad (1a)
\]

and

\[
N_p(x, t) = \frac{1}{2} \sum_{q' \in T} Z_{pq'}(x, t) \quad (1b)
\]

represent the total number of males with a trait q and the total number of females with a preference p, respectively. The likelihood of a female p mating with a male q is described by a preference function \( f_{pq} \). Therefore the proportion of type p females that mate is

\[
\sum_q M_q f_{pq} = S(p) \quad (2a)
\]

and the proportion of males of type q that are chosen is

\[
\sum_p N_p f_{pq} = R(q) \quad (2b)
\]

We choose to restrict the set of possible preference functions such that female viability and fecundity are unaffected by her preferences, that is, there is no cost to a female in having a preference. This requires \( S(p) = 1 \) for all p, and means that the preference functions must be density dependent. The birth rate is 4r and is the same for each male-female pairing. Females have constant death rate \( \mu_q \), but for males the death rate may depend on the trait \( q \), so that \( \mu_q = \mu_q(M) \), where \( M \) is the vector of male abundances. Thus the overall death rate for genotype \( pq \) is \( \eta_q = (\mu_q + \mu_0)/2 \). Female preference is therefore a neutral character that evolves as a correlated response to natural and sexual selection on males. This is the essence of the “good-taste” model of sexual selection first proposed by Fisher (1930). The male trait can be favored for some arbitrary reason, and is selected in the males because the preference of females for this trait leads to an increase in the number of the male’s offspring. This selection reinforces the female preference through inheritance, in which females tend to produce attractive sons bearing the trait and daughters with a preference for the trait. In this way, an otherwise deleterious character such as conspicuous coloration, can be favored in a population through reproductive gains alone.

In our model the dispersal is considered to approximate a simple diffusion process in which the diffusion coefficient is held constant for females, but may vary according to mating success in males. If we let males have diffusion coefficients \( d_q = d_q(R_q) \) dependent on mating success) and females \( d_0 \) (constant), then, since half the individuals with \( pq \) genotype are male and half female, the overall diffusion coefficient for the \( pq \) genotype will be \( (d_q + d_0)/2 = D_q = D_q(R_q) \). Hence the change in abundance of genotype at a given point in space (one dimensional) and time is described by

\[
\frac{\partial Z_{pq}}{\partial t} = \frac{r}{4} \sum_q \sum_{p'} \left( Z_{pq} Z_{p'q} (f_{pq} + f_{p'q}) + Z_{pq} Z_{p'q} (f_{pq} + f_{p'q}) \right)
\]

Before investigating the mating-success dependent scenario, we consider some simple cases that illustrate how our model relates to previous models and results on the Fisher process.

Relationship to Previous Studies

Nonspatial Model with Trait Cost

Our model is closest conceptually to the models of Kirkpatrick (1982) and Seger (1985). When stripped of the spatial dimension and with suitable choice of p and q, our model can be made comparable to these earlier models, except whereas their models are discrete in time, ours is continuous. It is straightforward to show, but rather tedious, that in the absence of diffusion the changes in numbers of males and females are

\[
\frac{dM_q}{dt} = M_q A(M, q) \quad q = 1, 2 \quad (4a)
\]

and

\[
\frac{dN_p}{dt} = r N_p + \frac{1}{2} (Z_{p1} R_1 + Z_{p2} R_2) - \frac{1}{2} (Z_{p1} \eta_1 + Z_{p2} \eta_2)
\]

\[
p = 1, 2 \quad (4b)
\]
where \( A(M, q) = r(1 + R_q) - \eta_q \). The first equation, describing the males, can be understood in terms of the summed contribution to the next generation of males inheriting a trait \( q \) from their mothers, males inheriting a trait \( q \) from their fathers, and a trait-dependent mortality term; the second equation, describing the females, can be understood as the sum of the daughters produced by mothers with the preference \( p \), fathers expressing a trait \( q \), and a trait-dependent mortality in fathers with trait \( q \). The total change in population size is given by

\[
\frac{dZ_{TOT}}{dt} = 2rZ_{TOT} - 2(\eta_1 M_1 + \eta_2 M_2). \tag{5}
\]

To make our model comparable to a Kirkpatrick- or Seger-style model, we impose a constant population size and two alleles at each locus. Females of type \( p = 1 \) are unfussy and will mate with either of two types of male \( q = 1, 2 \); whereas females of type \( p = 2 \) prefer males \( q = 2 \). Thus \( f_{11} = 1/M_{TOT} \) and \( f_{22} > f_{11} \). Males with trait \( q = 2 \) have a lower viability than males with trait \( q = 1 \), such that

\[
\eta_1 = (1 - \nu)\eta_2 \tag{6a}
\]

and

\[
\eta_2 = 2rM_{TOT}(M_{TOT} - vM_1). \tag{6b}
\]

This also keeps the total population size constant.

Finally we apply appropriate preference functions \( f_{21}, f_{22} \) to capture the specific results of the Seger and Kirkpatrick models. Kirkpatrick (1982) employs a fixed relative-preference rule, in which each female has an unlimited choice of males: \( f_{21} = 1/(M_1 + a_2 M_2) \), \( f_{22} = a_2 f_{21} \). The position and stability of equilibria can be analytically predicted, and are found to be equivalent to those of Kirkpatrick, as illustrated in Figure 1a.

Seger (1985) considers a “best-of-two” female preference rule: \( f_{21} = (1 - c_2 M_2/M_{TOT})M_{TOT} \), \( f_{22} = (1 + c_2 M_1/M_{TOT})/M_{TOT} \). Again, the position and stability of equilibria can be predicted and is equivalent to that demonstrated by Seger (Figure 1b).

**Spatial Model with a Cline: Heterogeneous Domain**

Lande (1982) has analysed character divergence in a polygenic model of clinal speciation, without geographic isolation, by investigating the joint evolution of geographic variation in female mating preferences and male secondary sexual traits. As in the Kirkpatrick and Seger models, female mating preference evolves as a correlated response to selection on males, but selection on males varies in space, and hence the selective forces behind the Fisher runaway process vary graphically. Lande found that equilibrium clines in male secondary sexual characters are greatly amplified in relation to the optimum phenotypes favored by natural selection. Although Lande analyzed polygenic characters, while our model treats discrete characters, the qualitative results are similar.

Assume that diffusion is constant \( (D_1 = D_2 = \text{constant}) \) and that mortality is spatially dependent according to \( \eta_1 = (1 - \nu)\eta_2 \), where the spatially varying coefficient of relative viability is \( \nu = \nu(x) \). In numerically simulating the behavior

![Fig. 1. Phase-plane diagram showing stability of nonspatial models with trait cost. By setting \( D = 0 \) and choosing appropriate preference and mortality functions, our continuous time model can be reduced to be equivalent to the discrete time models of Kirkpatrick (1982) and Seger (1985), which give simple illustrations of the Fisher runaway process. In both cases the preferred male trait incurs reduced viability such that \( \eta_1 = (1 - \nu)\eta_2 \). As described in the main text, the death rates are scaled to produce a constant overall population size. Without loss of generality we set \( \nu = 1 \). (A) Fixed relative preferences: \( f_{21} = 1/(M_1 + 3M_2), f_{22} = 3f_{21}, \nu = 0.2 \). In the diagram, the dotted line is the predicted position of stable equilibria, the solid lines are numerically computed trajectories. This reproduces Kirkpatrick’s result. (B) Best-of-two preferences: \( f_{21} = (1 - M_2/M_{TOT})M_{TOT}, f_{22} = (1 + M_1/M_{TOT})M_{TOT}, \nu = 0.3 \). In this case the line of equilibria with all genotypes coexisting is unstable (although it can become stable at large linkage disequilibrium). This reproduces Seger’s result.](image-url)
M. model can reproduce results akin to those of Lande (1982), whereby trait-associated viability. Here, $f_{12}$ = (1 + $M_2/N_{TOT}$)$/M_{TOT}$, $f_{12}$ = (1 - $M_1/N_{TOT}$)$/M_{TOT}$, $f_{21}$ = (1 - $M_2/N_{TOT}$)$/M_{TOT}$, $f_{21}$ = (1 + $M_1/N_{TOT}$)$/M_{TOT}$, $\eta_1$ = (1 - $\nu_2$)$/\eta_2$, where viability $\nu(x)$ = 0.4, $D$ = 0.005 (constant), $r$ = 1. The solid line marks the equilibrium distribution of the male traits, the dotted line the spatial dependence of the viability $\nu(x)$.

of this scenario we used a best-of-two preference rule, but similar results can be obtained using a fixed relative preference. Type $p$ = 2 females prefer $q$ = 2 males to an extent equal to that of $p$ = 1 females for $q$ = 1 males. Results equivalent to Lande’s are described in Figure 2.

MATING-SUCCESS DEPENDENT DISPERSAL

Spontaneous Trait Segregation in a Homogeneous Domain

If we take any of the above models and place it in a spatial context with constant diffusion and no geographic variation in selection, then it can be shown that the final equilibrium distribution of genotypes will always be homogeneous. The proportions of different genes will depend on the starting conditions, but spatial patterning is not attainable. For stable patterns to arise requires either that there be an imposed heterogeneity, or that the different phenotypes have different diffusion coefficients (see Turing 1952; or any of the subsequent extensive literature on “reaction-diffusion” equations and pattern formation). If, however, the diffusion is not constant, then we find that it is possible for male character traits to become separated in space even in the absence of geographically varying selection.

The basic model framework is given in equation (3), and uses the best-of-two preference rule and mating-dependent diffusion. We consider two male traits and two female preferences, such that $p$ = 2 females prefer $q$ = 2 males to an extent equal to the preference of $p$ = 1 females for $q$ = 1 males. There is no trait viability, so $\eta_1$ = $\eta_2$. The diffusion of females is constant, but that of the males depends on the proportion of successful matings, and is therefore some function of $R_1/N_{TOT}$ for $q$ = 1 males, and $R_2/N_{TOT}$ for $q$ = 2 males. In the simulations we use $D_q = d_1 e^{-d_2 R_q/N_{TOT}}$, where $d_1$ and $d_2$ are positive constants. As before, we assume no cost to females in having a preference, so that $S_p$ = 1; it is for this reason we choose to apply the best-of-two preference rule. The model was simulated numerically over a closed domain (no-flux boundary conditions) using NAG library routine D03PCF. Figure 3 shows an example of how initially randomly distributed genotypes can ultimately lead to an equilibrium in which males with different traits become localized in different regions of space, with only a narrow boundary zone in between, which we refer to as a “sympatric boundary zone.”

In biological terms, we interpret the segregation process to be operating as follows. Any local concentration of a female preference for a male trait, $q$ = 1 say, leads to a unique male-trait, female-preference evolution, driven by a Fisherian runaway process. In our model, however, the unfavored ($q$ = 2) males in that particular neighborhood will disperse at a higher rate than the locally favored males, and so the $q$ = 2 males will start to congregate in regions just outside the unfavorable locality. The crucial point is that these males carry with them, on average, more genes coding for a preference for their own trait than for the alternative trait, and so a new Fisher process may develop that runs away in favor of the trait that was not favored in the first locality. Since in this second locality the $q$ = 2 males have become favored they become more sedentary, whereas the $q$ = 1 males are unfavored and disperse more rapidly; the exact opposite of the behavior in the first locality. Thus the population becomes polarized in space.

Our numerical simulations indicate that the polarized distributions can reach an equilibrium in which neither “trait stronghold” can invade the other. The number and position of these trait strongholds depends on the imposed initial conditions, but the final distribution seems to have a typical “representative length scale” (average size of the trait region), which depends on a balance between the birth rate and the diffusion rates. The nature of the equilibrium distribution is interesting. The shape of each boundary zone is stable (as can be seen from Fig. 3) and, once formed, remains constant; but the position of the zones are only neutrally stable, and are in principle open to drift. (This can be deduced from the fact that the position of the different regions is dependent on the initial conditions.) Note, though, that it would only require a small degree of environmental heterogeneity for the position of the sympatric boundary zone to become stably fixed in space (see Fig. 5, below).

In each trait stronghold the opposite trait is annihilated and so the linkage disequilibrium, by definition, tends to zero. In the boundary zone between the trait regions, however, the linkage disequilibrium is always maintained, even at equilibrium. This can be seen in Figure 4. In these zones the competition between the two trait-preference types is always maintained, albeit in a perpetual stalemate, and so the sexually selective pressures are constantly acting. In our diffusion-modified Fisher process any males that stray into the ‘wrong end of town’ will not only be unsuccessful in their mating attempts, but will tend to quickly wander back to their own region.

Mating-Success Dependent Dispersal in Other Contexts

So far we have considered a model stripped bare of other selective influences, so as to highlight the point that a com-
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FIG. 3. Example dynamics of trait segregation under mating-success dependent diffusion. Here the rate of male dispersal is dependent on their success in attracting mates, so we take the diffusion to be a function $D_q = d_1 e^{-d_2 R_q}$, where the positive parameters $d_1 = 0.001$, $d_2 = 3.0$, and $R_q$ (as defined in the text) is the proportion of successful matings experienced by males with trait $q = 1, 2$. The best-of-two preference rule is used, with type $p = 1$ females preferring type $q = 1$ males to an extent equal to the preference of type $p = 2$ females for type $q = 2$ males: $f_{11} = (1 + M_1/M_{TOT})/M_{TOT}, f_{12} = (1 - M_1/M_{TOT})/M_{TOT}, f_{21} = (1 - M_2/M_{TOT})/M_{TOT}, f_{22} = (1 + M_2/M_{TOT})/M_{TOT}$. All animals have equal viability. In the plots, the initial (random) distribution of genotypes is indicated by the dotted line. The solid lines give the distributions after every 20 time units (arrows show direction of change with time). The position of the final distribution is dependent on the initial conditions, but, as in the examples shown here, an equilibrium is always reached in which there is a neutrally stable spatial segregation of the male traits (recall: $M_1 = Z_{11} + Z_{21}, M_2 = Z_{12} + Z_{22}$).

Combination of the Fisher process and mating-success-dependent diffusion is sufficient in itself to establish and to maintain a spatial segregation of male character traits. In reality our proposed diffusion-modified Fisher process would very probably act in concert with other selective forces.

In a selectively heterogeneous region similar to that of Figure 2, for instance, the resulting character cline would be emphasized still further (Fig. 5). Or, to put it another way, under the influence of a diffusion-modified Fisher process a much smaller degree of selective heterogeneity is required before a spatial cline in phenotypic traits is observed than would otherwise be the case. In Figure 5 the selective heterogeneity ensures that both the position and the shape of the sympatric boundary zone are fully stable. Asymmetries could also occur in trait viability, mating preferences, dispersal behavior, or any combination thereof. Although we have not studied these explicitly, it is likely that in some cases the effect of two asymmetries could act to balance each other, as in the Kirkpatrick and the Seger models, but in others may mitigate the spatial segregation. In contrast, a process that would enhance the degree of trait segregation is mating-dependent advection. In our model the female mating preference only controls the rate of male diffusion, but it does not modify the direction of that movement. If we were to add behavioral advection, that is, assume that animals are able to move towards regions where they expect that their mating chances will be improved, then the basic phenomena we describe would become more exaggerated.

In its current form, our model is able to produce complete spatial segregation of the genes coding for the males traits (i.e., there are regions where one or other trait is excluded), but does not lead to full segregation of the corresponding female preference genes. We conjecture that complete female segregation might be possible should females also exhibit some form of mating-success-dependent dispersal, for example, if female dispersal varied according to the proportion of acceptable males encountered at different leks. Since our model species is polygynous, modeling behavioral female dispersal would bring in other complicating factors, such as variation in female reproductive rates, but nonetheless such
Linkage disequilibrium is maintained in sympatric boundary zones between trait regions. The model and parameters are the same as for Figure 3, but random nature of initial conditions necessarily entails different final equilibrium. (Top) Equilibrium distribution of $M_1$ gene frequency ($= 1 - M_2$). (Bottom) Corresponding equilibrium values of linkage disequilibrium. Note that, even though at equilibrium, a state of linkage disequilibrium is maintained in the zones between contiguous regions of opposing traits.

As a further refinement, we consider how the model should be modified when assuming departure from an even sex ratio. Suppose the male:female ratio is $m:n$, with the birth rates of males and females being $mr$ and $nr$, respectively, subject to $m + n = 4$. Thus the total birth rate is $4r$, as before. Let $M_q$ and $N_p$ be the numbers of males and females. Thus $M_q = M_q m/2$ and $N_p = N_p n/2$, where $M_q$ and $N_p$ retain their previous definitions. The no-cost condition on female preferences is $1 = \hat{S}_q = \Sigma q', M_q \tilde{f}_{pq}$, and hence $\tilde{f}_{pq} = f_{pq} 2/m$. If we now write down the basic equation for the genotype dynamics (equivalent to eq. [3] in the 1:1 case) it is possible to rearrange it into the form

$$\frac{\partial Z_{pq}}{\partial t} = \frac{mn}{8} \sum q' \left[ (Z_{pq} Z_{p'q'} f_{pq} + f_{p'q}) + Z_{pq} Z_{p'q} (f_{pq} + f_{p'q'}) \right] - \frac{(m \mu_q + n \mu_c)}{8} Z_{pq} + \frac{(m d_q + n d_c)}{8} \frac{\partial^2 Z_{pq}}{\partial x^2}. \quad (7)$$

But, this is the same as taking equation (3) and applying the following substitutions:

$$\eta_q \rightarrow \tilde{\eta}_q = \frac{(m \mu_q + n \mu_c)}{8}, \quad D_q \rightarrow \tilde{D}_q = \frac{(m d_q + n d_c)}{8},$$

$$r \rightarrow \tilde{r} = \frac{mn}{2}$$

with all other definitions kept as above. Hence to study the behavior for different sex ratios we retain the form of equation (3) and need only alter parameter values. This demonstrates that the actual value of the sex ratio will not have any qualitative bearing on our results.

**FIG. 5.** Cline sharpening under mating-success dependent diffusion. The preference functions, and an imposed cline in trait-associated viabilities (dotted line), are as in Figure 2, but with mating-success dependent diffusion as in Figure 4: $D_q = d_q e^{-d_q R_e}$. The shallowest solid line is the equilibrium distribution for $d_2 = 0$ (identical to Fig. 2), the intermediate for $d_2 = 3$ and the steepest for $d_2 = 6$. This illustrates how any preference dependent diffusion will serve to emphasize the polarized separation of male traits in a heterogeneous environment.

**DISCUSSION**

In polygynous species in which males contribute only gametes to succeeding generations and aggressive male interactions play a negligible role as a determinant of mating success, active searching by males for spatially scattered females, such as in "scramble-competition polygyny," can lead to heterogeneous distributions of male phenotypes. In our model, dispersing males will tend to take with them genes expressing preferences for their own traits, and the sexual preferences of scattered females will subsequently evolve in response to selection on the genetically correlated characters in the dispersed males. Consequently, spatial clusters of male traits and female preferences undergo feedback in a "diffusion-modified Fisher process," leading to linkage disequilibrium in regions of active dispersal (Fig. 4). Different regions in space will therefore allow different traits and preferences to become abundant (Fig. 3) forming "trait strongholds." Locally preferred males are prevented from spreading through the entire population because the more preferred males diffuse at a lower rate, and thus the combination of mating-success dependent diffusion and the Fisherian process...
permits the spatial distribution to become polarized, and leads to patterns of female preference for diverse male traits at equilibrium in a sympatric population. This situation is realized when the spatially distinct "trait strongholds" are stabilized by intervening "sympatric boundary zones."

In nonspatial models with discrete male traits, selectively neutral female preferences, and continuous generations, there is either a line of equilibrium frequencies toward which the male traits will move (Fig. 1a) or, more likely, complete polarization of the genotypes in which the frequency of male traits moves to extremum points, *sensu* Fisher (Fig. 1b). The form of the equilibrium will depend largely on the female preference rule (for discrete generations see Kirkpatrick 1982; Seger 1985). Several authors have demonstrated that direct selection acting on female choice will tend to collapse the line of equilibria to a single point (Bulmer 1989; Pomiankowski et al. 1991) regardless of the preference rule. Nonetheless, the Fisher process does provide a mechanism for establishing maladaptive traits in a population. Existing models have, however, failed to demonstrate how more than one incipient species could persist in a sympatric population when the environment is homogeneous. Lande (1982) was able to show that a sympatric population in which a single species was initially distributed with uniform density could spontaneously split and form two sexually isolated populations along a cline. Thiscline can be thought of as a monotonic boundary between ecologically distinct habitats. Female mating preferences were shown to amplify the geographical variation in male phenotypes, reinforced by natural selection acting against hybrids of reduced fitness.

We have presented a model with a single homogeneous environment in which selection is geographically constant. Coexistence of male trait types in a continuous area is achieved not by ecological differentiation, but through a limited diffusion of sexually successful male phenotypes, and an augmented diffusion of less successful phenotypes. Alternative male mating tactics of this sort are likely to be more common in Polygonius species, where male-male competition is high (Thornhill 1981; Thornhill and Alcock 1983). If a few competitively superior males are able to monopolize the majority of females, either directly through resource defense, or indirectly through mate choice, the less successful males could potentially increase their chances of mating by searching for more receptive females elsewhere (Parker 1978). Assuming that males encounter receptive females, male mobility should be a function of local female preferences in which reduced movement occurs when the density of receptive females is high (Parker and Stuart 1976).

How do our results relate to the debate on sympatric speciation? Many authors have contended that sympatric speciation requires the partitioning of a limiting resource (Mayr 1970; Tauber and Tauber 1977; Kondrashov and Mina 1986), where this resource is thought of as an ecological factor such as a new host or habitat. Strong natural selection could then lead to genetically based specialisations in a given niche. Maynard Smith (1966) demonstrated that ecological segregation could promote a single gene polymorphism in a panmictic population, and this result has been confirmed in a number of related studies (Pimm 1979; Kondrashov 1986; Bush 1994). In our model, one can think of the limiting resource as being, in effect, the distribution of the discriminating sex. It was Darwin (1871) who first stressed the importance of sexual selection in the divergence of incipient species, or the formation of races, and Fisher (1930) who stressed the potential of reproduction to promote genetic instabilities as a first step in the fission of species. Subsequently, Lande (1982) coupled sexual selection with ecological divergence to show how the Fisher process can lead to rapid changes in male traits along a cline, and more recently West-Eberhard (1983) has stressed the role of social competition in speciation: competition between conspecific rivals for some limiting resource. Turner and Burrows (1995) have presented a genetic model that demonstrates sympatric speciation in a homogeneous domain, showing how a dominant allele producing a reversed female preference can invade a polymorphic population in which the Fisher process has caused a maladaptive trait to become established. The new female preference is initially aided by natural selection because this preference pulls the male trait away from its extreme form, and a second Fisher process then sets in, driving the male trait to its opposite extreme. This model provides a novel mechanism for the emergence of assortative mating in sympathy, but does not allow for the coexistence of the sibling species.

We deem our model to be sympatric because divergence occurs "within the dispersal area of the offspring of a single deme" (Mayr 1963). Unlike theories of ecological segregation, we assume no ecological heterogeneities in nonsexual resources. The rapid divergence permissible under the diffusion-modified Fisher process effectively acts as a temporal barrier to gene flow, with divergence at particular points in space occurring over a time scale well below that of parthenogenesis. This is because an increase in the preference for a given male corresponds to a reduction in the rate of diffusion of that male. We demonstrate a neutrally stable coexistence of sibling species possessing identical competitive abilities, with the action of the distribution of female preferences preventing competitive exclusion from driving some phenotypes to extinction (fully stable when acted on by even mild selective heterogeneity). Our interpretation of sympathy is unlike that of Kondrashov and Mina (1986) in which disruptive selection must act to somehow favor marginal phenotypes, and in which frequency dependent selection then acts to maintain ensuing polymorphisms. Needless to say, we have only modeled the evolution of character divergence and not full reproductive isolation.

The data on sympatric speciation are difficult to reconcile with any single mechanism of speciation. There is evidence that some speciose lineages such as the cichlid lineages found in the East African great lakes, arose in sympathy (Schliewen et al. 1994), and have remained sympatric. Females in some of these species have been shown to exercise choice when presented with males differing in their courtship colours (Hert 1989). In addition, many species do not appear to be separated by any obvious ecological barriers (Schliewen et al. 1994; Turner 1994), but may differ in their bathymetric distributions (Meyer 1990). We hypothesize that a diffusion-modified Fisher process is capable of leading to patterns such as these, whereby a population may evolve patterns of assortative mating when males and females segregate in a uniform envi-
environment according to the distribution of female preferences. For instance, the three-dimensional aquatic environment might provide compartments based on depth parameters into which dispersing males swim, some of these males may then secure preferential matings. This position is lent a degree of credibility by the observed importance of limited dispersal in influencing species diversity in the cichlids, which has been correlated with extreme localization of gene pools in the absence of any habitat barriers (Cohen and Johnston 1987). Darwin’s finches on the Galapagos island of Isla Genovesa are another lineage that appear at times to have undergone sympatric speciation (Grant and Grant 1989). Sympatric males of several species differ in their song types. Song type is heritable among males, and females display a preference for a given song type, although daughters do not appear to pair assortatively with regard to paternal song type. Unmated males show no regularity in territorial holding and disperse over a large area, while mated males occupy well-defined regions in space. Although there is some evidence of ecological segregation through feeding specializations in these species, there is no evidence of reproductive isolation. These observations are consistent with our diffusion-modified Fisher process: the process predicts an exaggerated divergence along a cline in which selection augments the process by acting against poorly adapted male beaks (cf. Fig. 5).

An intriguing case is the geographic variation in advertising call of the cricket frog, *Acris crepitans*. Ryan and Wilczynski (1991) have shown that their data on the clinal variation in call variables do not support hypotheses that assume differential stabilizing selection through species recognition, or clinal selection on pleiotropic characters such as body size. In addition, in *A. crepitans* populations there is no evidence for reproductive character displacement. Ryan and Wilczynski conclude that differences in habitat, and hence selective regimes, can explain some of the variation between populations, but can not explain all of it. Our model can provide a framework for thinking about this kind of result, since we examine the evolution of assortative mating prior to reproductive character displacement through reinforcement.

There are a number of candidate species for sympatric speciation, many of which involve host-associated shifts in feeding or mating behavior (Tauber and Tauber 1989). We have presented a model in which such shifts are not required, but this does not imply that the two mechanisms are mutually exclusive: the two mechanisms may often work together to accelerate the divergence between incipient species. Indeed, the success of our hypothesis is likely, in practice, to rest on its ability to account for those cases in which there is sympatric diversity in weakly heterogeneous environments.

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**Literature Cited**


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