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SEXUAL SELECTION AND THE EVOLUTION OF COSTLY FEMALE PREFERENCES: SPATIAL EFFECTS

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Abstract.—Models of Fisher's runaway process show that if there is a cost to female preference, no preference or male trait exaggeration will evolve. Surprisingly, this is true no matter how small the cost, which reveals that these models of Fisher's process are structurally unstable (Bulmer 1989). Here a model of Fisher's runaway process is presented to demonstrate that costly female preference evolves very easily when space is explicitly included in the model. The only requirement is that the optimal male phenotype changes across the species' range. The model shows that the spatial average of the female preference and male trait reach an evolutionary equilibrium that is identical to those of nonspatial models, but that the preference and male trait can deviate greatly from these averages at any point in space. For example, if random mating results in the lowest cost to females, then at equilibrium the spatial average preference will be zero. Nevertheless, there will be some locations at which females prefer males with larger ornaments and others where they prefer males with smaller ornaments. Results also show that the structural instability of nonspatial models of Fisher's process is less of a problem in spatial models. In particular, many of the main qualitative features of cost-free spatial models of Fisher's process remain valid even when there are small costs of female preference. Finally, the model shows that abrupt changes in the optimal male phenotype across space can result in an amplification of this pattern when preference has a small cost, but it can also result in a pattern similar to reproductive character displacement. Which of these occurs depends on the magnitude of the cost of female preference. This suggests that some patterns of reproductive character displacement in nature might be explained simply by sexual selection rather than by hybrid dysgenesis and reinforcement.

Key words.—Cline, costly female preference, Fisher's runaway process, reinforcement, reproductive character displacement, sexual selection, spatial variation.

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In many sexual species males exhibit conspicuous traits such as bright coloration, greatly exaggerated morphological characters, or complex display behaviors and song (Andersson 1994). Although some such features might confer a survival advantage and therefore might have evolved through natural selection, it seems unlikely that this is universally true. In fact, as Darwin (1871) recognized, many of these conspicuous traits probably confer a survival *disadvantage* to those that bear them. Therefore, explaining the existence of these traits poses a difficult problem. Darwin proposed a solution with the theory of sexual selection. If males that exhibit these conspicuous traits are more successful in obtaining a mate, then these traits might evolve through what he termed sexual selection in spite of the fact that they result in a survival disadvantage. Darwin's idea rests upon the premise that females will prefer to mate with conspicuous males and that such males will thereby have a higher mating success. Both of these premises have now been abundantly cor-

roborated in natural systems lending support to Darwin's theory (Andersson 1994).

Although Darwin's theory of sexual selection provided a powerful explanation for the existence of many conspicuous traits, one difficulty still remained. Why is it that females exhibit a preference for such exaggerated traits when they must often come at a cost to males? An answer to this question was provided by Fisher (1958) in his verbal model of the self-reinforcing evolution of male trait and female preference (this idea was actually first suggested as a joke by Morgan 1903; for an interesting discussion, see Andersson 1994, p. 24). This has come to be known as Fisher's runaway process, and it postulates that a positive genetic correlation between female preference and male trait builds up as a result of any initial female preference. Therefore, females choosing conspicuous males are incidentally also choosing males that carry (unexpressed) genes for the female preference. Each generation this process reinforces itself and thereby causes the runaway evolution of both the male trait and the female preference. The end result is that the male trait evolves to a maladapted state from the perspective of survival, but this fitness penalty is paid for by enhanced mating success. Al-

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though Fisher's runaway evolution requires some initial female preference to set the process in motion, zero preference is an unstable state. A number of authors have now demonstrated the validity of Fisher's hypothesis using explicit mathematical models (O'Donald 1980; Lande 1981; Kirkpatrick 1982; Seger 1985), and there is now evidence that a positive genetic correlation exists between male trait and female preference in many species as well (Bakker 1993; Wilkinson and Reillo 1994; also see Andersson 1994, ch. 2).

In addition to Fisher's idea, several alternative hypotheses have been put forward to explain the evolution of female preference for conspicuous traits. One idea is that conspicuous traits function as indicators of some form of male quality that enhances a female's fitness or the fitness of her offspring (Zahavi 1975, 1977; Grafen 1990a,b; Kirkpatrick and Ryan 1991; Price et al. 1993). Another is that the sensory system of females is predisposed to prefer certain traits, because it has evolved to serve other functions (Ryan 1990; Kirkpatrick and Ryan 1991; Ryan and Keddy-Hector 1992). For example, preference for extreme traits might occur as a by-product of the female's sensory system being adapted to foraging in certain habitats. One advantage that both of these alternatives appear to have over Fisher's hypothesis is their ability to operate in the face of costs to female preference. Choosy females might pay a cost through increased predation risk and/or loss of time and energy (Pomiankowski 1987; Reynolds and Gross 1990; Andersson 1994). Models of Fisher's runaway process have shown that when such costs exist, the reinforcing evolution of trait and preference usually cannot occur (Lande 1980; Kirkpatrick 1985; Pomiankowski 1987; Bulmer 1989; Maynard Smith 1991; Pomiankowski et al. 1991). Selection against female preference counteracts the tendency for runaway evolution, and this results in the cost of preference being minimized at equilibrium and males exhibit no trait exaggeration. This suggests that Fisher's hypothesis cannot provide an explanation for the existence of costly female preference.

A dismissal of Fisher's hypothesis for the maintenance of costly female preference is premature, however, because Pomiankowski et al. (1991) have demonstrated how mutational bias in the male trait can result in nonzero preference evolving (also see Bulmer 1989). If mutational bias results in a decrease in the average male phenotype, then directional selection on the male trait toward the optimum can cause a correlated response in the female preference. As a result, female preference is positive at equilibrium.

Although mutational bias is one way in which costly female preference can be maintained, most models that demonstrate how costs prevent the evolution of female preference have neglected one very important factor—space. Lande (1982) presented the first spatial model of Fisher's hypothesis, but he assumed that female preference was cost-free. He found that sexual selection can greatly amplify geographic clines in the optimal male phenotype, and thus female preference and male trait can evolve to become extremely different on each side of the cline. Payne and Krakauer (1997) have also analyzed a spatial model of Fisher's process in which female preference is cost-free. They demonstrated that spontaneous spatial patterns in male trait exaggeration and female preference can evolve in the absence of clinal vari-

ation in the optimal male phenotype when male dispersal rate depends in mating success. In this paper a model is presented to show that *costly* female preference can also evolve very easily when space is explicitly considered. The only requirement is that the optimal male phenotype changes across space. The model also shows that costly female preference can cause the evolution of spatial patterns in mating that are very similar to reproductive character displacement.

THE MODEL

I use a continuous-time spatial version of the quantitative-genetic model presented by Pomiankowski et al. (1991). The model considers the evolution of a single quantitative male trait (denoted by z) under sexual and natural selection and a single quantitative female preference level for this trait (denoted by p) under natural selection. I also make the assumption that the phenotypic distributions of these two traits are adequately characterized by their means, \bar{z} and \bar{p} . Therefore, following standard quantitative genetic models (Lande 1979, 1980), the evolutionary dynamics of \bar{z} and \bar{p} are given by

$$\frac{d\bar{z}}{dt} = G_z\beta_z + B\beta_p \quad \text{and} \quad (1)$$

$$\frac{d\bar{p}}{dt} = B\beta_z + G_p\beta_p, \quad (2)$$

where G_z and G_p are the additive genetic variances of trait z and preference p , and B is the additive genetic covariance between the two. I assume that the genetic covariance between the male trait and female preference is smaller than the genetic variance in both the male trait and the female preference (i.e., $B < G_z$ and $B < G_p$). β_z and β_p are the selection gradients acting on the male trait and female preference, respectively. The first term of equation (1) represents the change in the male trait due to direct natural and sexual selection on the trait. It is large when the strength of selection on the trait β_z and/or the genetic variance of the trait G_z is large. The male trait also changes due to selection on the female preference because the two are genetically correlated. This effect is given by the second term of equation (1) and it is large when the strength of selection on the preference β_p and/or the genetic covariance B is large. Similar considerations hold for equation (2).

As in Pomiankowski et al. (1991), the genetic parameters are assumed to change on a time scale much longer than that of the traits and therefore they are treated as positive constants. The covariance B is assumed to be positive because assortative mating between females and males will tend to generate a positive genetic covariance (Lande 1981; Kirkpatrick 1982; Seger 1985). The validity of treating these genetic parameters as constants is considered more fully in the discussion (also see Rowe and Houle 1996).

The first step in providing explicit expressions for the dynamics, equations (1) and (2), is to specify male and female fitness functions, W_m and W_f . I use the same formulations as Pomiankowski et al. (1991), modified for continuous time:

$$W_m(z; \bar{z}, \bar{p}) = a\bar{p}(z - \bar{z}) - c(z - \theta)^2 \quad \text{and} \quad (3)$$

$$W_f(p) = -bp^2. \quad (4)$$

Expression (3) gives the fitness of a male with phenotype z in a population with mean trait and preference, \bar{z} and \bar{p} . The first term is the effect of sexual selection. If \bar{p} is positive, then males with trait values larger than average are favored by sexual selection and vice versa. The positive parameter a determines the strength of this effect. The second term in equation (3) is the effect of natural selection favoring a male trait value of θ . The strength of this effect is determined by the positive parameter c . Expression (4) is the effect of natural selection against female preference, and the positive parameter b determines the strength of this effect. This form of W_f assumes that natural selection favors females that mate randomly.

To gain an intuition for these fitness functions, one interpretation of the variables z and p is that z represents the size or intensity of a male character and p represents the amount of time a female spends searching for a mate. Positive values of p might imply time spent searching for a male with a larger than average trait, whereas negative values represent time spent searching for a male with a smaller than average trait. Alternative forms of W_m and W_f are considered in Appendix 4.

Taking into account the fact that the fitnesses, equations (3) and (4), are both sex limited (which will halve the overall selection gradients), the selection gradients can be approximated as (Iwasa et al. 1991; Abrams et al. 1993; Taylor 1996)

$$\beta_z = \left. \frac{\partial W_m}{\partial z} \right|_{z=\bar{z}} \tag{5}$$

$$= \frac{1}{2}[a\bar{p} - 2c(\bar{z} - \theta)] \tag{6}$$

and

$$\beta_p = \left. \frac{\partial W_f}{\partial p} \right|_{p=\bar{p}} \tag{7}$$

$$= -b\bar{p}. \tag{8}$$

Expressions (5) and (7) give the rate at which fitness changes with an increase in trait value for males and females respectively when the population has mean values \bar{z} and \bar{p} . The selection gradient for males is the same as Lande's (1982) psychophysical model of mate choice. A version of his absolute preference model is presented in Appendix 4.

Models of sexual selection such as system (1, 2) do not usually treat population dynamics explicitly. Rather, there is an implicit assumption that either the population is growing in a density-independent manner or that density regulation occurs by a mechanism that is independent of the traits being modeled. Although it is not really necessary to choose between these two alternatives in nonspatial models, the spatial model developed below allows for the effects of differences in population density across space, and therefore it is the second interpretation that I choose.

Using a discrete-time version of system (1, 2), Pomiankowski et al. (1991) showed that the only equilibrium is $\hat{z} = 0$ and $\hat{p} = 0$. This demonstrates that when there is a cost to female preference, no preference will evolve. They then showed that by introducing a mutational bias that tends to decrease the mean male phenotype, nonzero female prefer-

ence can evolve. It turns out that explicitly incorporating space into the model has the same qualitative effect. It arises because of what might be termed migration bias; the movement of individuals causes a net change in the average local phenotype as a result of gene flow.

To build space into the model, I consider movement along a single continuous spatial dimension. Although most spatial distributions of organisms are at least two dimensional, my results remain qualitatively valid in such cases if the relevant geographic variation occurs primarily in one dimension. There are a number of ways to model movement, and in Appendix 1 a model is presented that assumes each individual has the same probability of movement in any small interval of time, and if an individual does move, then the distance moved is drawn from some probability distribution (termed the dispersal kernel). If the variance of the dispersal kernel is small, then movement is reasonably modeled using diffusion (Murray 1993; Appendix 1). I make this assumption below, but the results of Appendix 1 provide a starting point for exploring more general dispersal patterns.

With movement modeled by diffusion we get a system that is identical to (1, 2), but with additional terms added to each equation that reflect the influence of individual movement on the mean trait values at each location in space (Nagylaki 1975; Pease et al. 1989):

$$\begin{aligned} \frac{\partial \bar{z}}{\partial t} = & D \frac{\partial^2 \bar{z}}{\partial x^2} + 2D \frac{d \ln n}{dx} \frac{\partial \bar{z}}{\partial x} - G_z c [\bar{z} - \theta(x)] \\ & + \left(\frac{G_z a}{2} - Bb \right) \bar{p} \end{aligned} \tag{9}$$

and

$$\begin{aligned} \frac{\partial \bar{p}}{\partial t} = & D \frac{\partial^2 \bar{p}}{\partial x^2} + 2D \frac{d \ln n}{dx} \frac{\partial \bar{p}}{\partial x} - Bc [\bar{z} - \theta(x)] \\ & + \left(\frac{Ba}{2} - G_p b \right) \bar{p}. \end{aligned} \tag{10}$$

In these equations, $\bar{z}(x, t)$ and $\bar{p}(x, t)$ are now both functions of space, x , and time, t , and the optimal male phenotype $\theta(x)$ is allowed to vary across space. The last two terms of equations (9) and (10) are simply the two terms of equations (1) and (2) evaluated explicitly using the selection gradients (5) and (7). In both equations, D is 1/2 times the average squared dispersal distance per unit time, and therefore measures the dispersal rate; $n(x)$ is the population density at location x , and it is assumed to be positive for all x within the species' range.

The first two terms of equation (9) represent two different ways in which individual movement can affect the mean male phenotype at location x . First, ignoring spatial variation in population density $n(x)$, random movement of individuals causes the mean phenotype at a given location to become more similar to those nearby. As an example, if the mean male phenotype changes linearly through space, then mathematically we have $\partial^2 \bar{z} / \partial x^2 = 0$. In this case the dispersal of individuals will not change the mean male phenotype because the mean phenotype of individuals immigrating from one side is exactly compensated for by the mean phenotype of individuals immigrating from the other. Therefore, the dispersal of individuals changes the mean phenotype at a given location only

if the mean male phenotype varies nonlinearly throughout space, and this effect is given by the first term in equation (9). Spatial variation in population density can also cause the mean male phenotype at a given location to change, however, no matter how the male phenotype varies in space. For example, if both the mean male phenotype and the population density increase linearly through space, then random movement of individuals will cause the mean male phenotype at a given location to increase because most immigrants will come from the right where the mean phenotype is higher. This effect is given by the second term of equation (9). Of course, the same holds true for the first two terms of equation (10) as well.

In general there is a third partial differential equation (PDE) that describes the population dynamics throughout space as well. As mentioned earlier, I assume that the population density has reached a stable equilibrium that is determined by factors other than the traits modeled here. An interesting extension of the present model would be to allow the male trait and female preference to affect the population dynamics.

To completely specify the model it is also necessary to make some assumption about the way individuals move at the boundaries of the geographic region and to specify initial conditions. I assume that the boundaries are reflecting, which means that individuals do not move across them. This assumption is reasonable whenever a species' range has boundaries that are dictated by the environment. Under these conditions, \bar{z} and \bar{p} must satisfy reflecting boundary conditions (Appendix 1):

$$\frac{\partial \bar{z}}{\partial x} = 0 \quad \text{and} \quad (11)$$

$$\frac{\partial \bar{p}}{\partial x} = 0 \quad (12)$$

at the boundaries. In fact, \bar{z} and \bar{p} must satisfy these boundary conditions for a much broader class of boundary conditions on individual movement (Appendix 1). I leave the initial conditions, $\bar{z}(x, 0)$ and $\bar{p}(x, 0)$ arbitrary.

Before analyzing the above pair of PDEs it is useful to nondimensionalize them. Doing so reduces the number of parameters and it also provides more insight into the model's behavior. Using a subscript s to denote nondimensional (i.e., scaled) variables, I write $\bar{z} = \tilde{z}\tilde{z}_s$, $\bar{p} = \tilde{p}\tilde{p}_s$, $t = \tilde{t}\tilde{t}_s$, and $x = \tilde{x}\tilde{x}_s$, where \tilde{z} , \tilde{p} , \tilde{t} , and \tilde{x} are constants that involve the dimensions. By choosing $\tilde{z} = 1$, $\tilde{p} = \tilde{z}B/G_z$, $\tilde{t} = \tilde{x}^2/D$, and $\tilde{x} = 1$, system (9, 10) becomes

$$\frac{\partial \tilde{z}_s}{\partial \tilde{t}} = \frac{\partial^2 \tilde{z}_s}{\partial \tilde{x}^2} + 2 \frac{d \ln n}{d \tilde{x}} \frac{\partial \tilde{z}_s}{\partial \tilde{x}} + \alpha_1[\tilde{z}_s - \theta(\tilde{x})] + \alpha_2 \tilde{p}_s \quad \text{and} \quad (13)$$

$$\frac{\partial \tilde{p}_s}{\partial \tilde{t}} = \frac{\partial^2 \tilde{p}_s}{\partial \tilde{x}^2} + 2 \frac{d \ln n}{d \tilde{x}} \frac{\partial \tilde{p}_s}{\partial \tilde{x}} + \alpha_1[\tilde{z}_s - \theta(\tilde{x})] + \alpha_3 \tilde{p}_s, \quad (14)$$

where

$$\alpha_1 = -\frac{G_z c}{D}, \quad (15)$$

$$\alpha_2 = \frac{G_z}{D} \left(\frac{aB}{2G_z} - \frac{B^2}{G_z^2} b \right), \quad \text{and} \quad (16)$$

$$\alpha_3 = \frac{G_z}{D} \left(\frac{aB}{2G_z} - \frac{G_p}{G_z} b \right). \quad (17)$$

The boundary conditions remain unchanged. This formulation allows the model to be directly compared to that of Lande (1982). In particular, with cost-free preference, $b = 0$, and therefore $\alpha_2 = \alpha_3$. As a result, equations (13) and (14) show that the dynamics of \tilde{z}_s and \tilde{p}_s are described by the same equation. This results because female preference evolves solely as a correlated response to selection on the male trait when preference is cost-free. When there is a cost to female preference, however, $\alpha_2 \neq \alpha_3$ and female preference evolves in part through a correlated response to selection on the male trait and in part through direct natural selection against the preference itself. In nonspatial models, the only equilibrium in cases with costly female preference is no preference. When space is explicitly included, however, the following results demonstrate that female preference will usually be nonzero at equilibrium. Appendix 4 presents analogous results for alternative forms of sexual selection.

RESULTS

Of primary interest are the equilibria and stability properties of system (13, 14). I first present two qualitative predictions of the model. Following that I present some quantitative results that demonstrate when the equilibria of the model are stable and that shed light on the mechanism driving the equilibrium patterns of male phenotype and female preference. This is followed by some numerical results. In what follows, equilibria will be denoted by a "hat" (e.g., \hat{z}_s and \hat{p}_s).

Qualitative Results

Result 1.—The incorporation of space generally leads to the evolution of costly female preference provided that the optimal male phenotype changes across space. This is most easily demonstrated by showing that $\hat{p}_s \equiv 0$ (uniform zero preference across space) is not an equilibrium. In particular, $\hat{p}_s \equiv 0$ is never an equilibrium when the boundary conditions hold; moreover, a very precise relationship must hold between $n(x)$ and $\theta(x)$ for $\hat{p}_s \equiv 0$ to be an equilibrium even if the boundary conditions are neglected.

With equation (14) set to zero, we can see that if $\hat{p}_s \equiv 0$ then we must also have $\hat{z}_s = \theta(x)$ (note that the boundary conditions on \tilde{p}_s will also be satisfied when $\hat{p}_s \equiv 0$). Using these in equation (13) shows that if $\hat{p}_s \equiv 0$ is an equilibrium, then we must also have that

$$0 = \frac{d^2 \theta}{d \tilde{x}^2} + 2 \frac{d \ln n}{d \tilde{x}} \frac{d \theta}{d \tilde{x}}. \quad (18)$$

Thus, if an equilibrium of identically zero female preference is to exist, the optimal male phenotype must satisfy equation (18). The general solution of (18) is

$$\theta(x) = C_1 + C_2 \int \exp \left\{ -2 \int^x \frac{d \ln n}{d \tilde{x}} \Big|_{\tilde{x}=s} ds \right\} dx, \quad (19)$$

where C_1 and C_2 are constants. Additionally, because $\hat{z}_s = \theta(x)$, we also require that θ satisfies boundary condition (11). From equation (19) it can be seen that the only choice of constants that also satisfy boundary condition (11) are $C_2 = 0$, which gives $\theta = C_1$. Therefore, female preference cannot

be zero everywhere unless the optimal male phenotype does not change across space. The reason is simple. For the female preference to be zero everywhere at equilibrium, it must also be the case that the male trait is optimally adapted everywhere. Otherwise selection on the male trait would cause a correlated response in the female preference. But gene flow prevents males from being optimally adapted as long as the optimum changes across space.

In some instances it is of interest to consider evolution on a spatial domain that is large enough to ignore any effects of the boundaries. In this case it is possible for there to be an equilibrium with zero female preference everywhere (with males being optimally adapted) and for which the optimal male phenotype changes across space. For this to occur, the optimal male phenotype must be of the precise form given in equation (19). For example, when the population density is uniform across space we have that $d \ln \hat{n}/dx = 0$, and therefore $\theta(x)$ must be linear in x . As another example, if population density is proportional to a Gaussian curve (e.g., $n \propto e^{-x^2}$), then we must have

$$\theta(x) = C_1 + C_2 \int e^{2x^2} dx.$$

Result II.—The equilibrium pattern of female preference across space always involves both positive preferences and negative preferences: in particular, the average female preference across space, weighted by the local population density squared, is zero. In other words, there are always locations where females prefer males with larger than average traits and other locations where females prefer males with smaller than average traits. To see this simply set equations (13) and (14) to zero, multiply by n^2 , and integrate over x . This gives

$$0 = \alpha_1 \int_Y [\hat{z}_s - \theta(x)]n^2 dx + \alpha_2 \int_Y \hat{p}_s n^2 dx \quad \text{and} \quad (20)$$

$$0 = \alpha_1 \int_Y [\hat{z}_s - \theta(x)]n^2 dx + \alpha_3 \int_Y \hat{p}_s n^2 dx. \quad (21)$$

where Y denotes the spatial domain. Assuming $b \neq 0$ (and therefore $\alpha_2 \neq \alpha_3$), these two equations imply

$$\int_Y \hat{p}_s n^2 dx = 0 \quad \text{and} \quad (22)$$

$$\int_Y [\hat{z}_s - \theta(x)]n^2 dx = 0. \quad (23)$$

Both equalities (22) and (23) also hold after multiplication by a constant. Therefore, multiplying each by $1/\int n^2 dx$ shows that the average female preference across space, weighted by the squared local population density, is zero. Similarly, the average deviation of the mean male trait from the optimum, weighted by the squared population density, is also zero. Appendix 4 presents the analogous results for a different form of sexual selection.

The above results reveal an interesting feature of the evolution of costly female preferences in space. The evolution of the spatial average female preference and the spatial av-

erage male maladaptation follows the dynamics of nonspatial models; for example system (1, 2). The difference between the spatial and nonspatial models is that, although the equilibrium spatial *average* female preference and male maladaptation are both zero, they are not identically zero throughout space.

Quantitative Results

The above analysis demonstrates some qualitative features of the equilibrium pattern of female preference and male phenotype. Of course these predictions are relevant only if such patterns represent a stable equilibrium. Therefore the first quantitative issue of interest is to determine the conditions for stability. Following this, some quantitative results are presented for the equilibrium female preference and male phenotype.

Stability of equilibria

Provided that selection against female preference is weak (i.e., b is small), the equilibrium described above is locally stable if $B/G_z < 2c/a$ (Appendix 2). This inequality states that the ratio of the genetic covariance to the genetic variance in the male trait must fall below a threshold that is itself a ratio of the strength of natural selection to the strength of sexual selection on males. The ratio B/G_z measures how tightly coupled the evolution of the two traits is, and stability requires that this coupling be very weak if the strength of sexual selection is very large and/or the strength of natural selection is very small. This inequality has appeared previously as the stability condition in other models of Fisher's runaway process where there was no cost to female preference (e.g., Lande 1981; Pomiankowski et al. 1991). In those models, this inequality is both necessary and sufficient for stability, but here the conditions for stability are slightly broader. The inequality is sufficient for stability, but it is possible that stability occurs when this inequality is not satisfied. Thus, if a cost-free model such as Lande's (1982) has a stable equilibrium, then including a small cost to preference will not alter this stability. A general condition for stability with any strength of selection against female preference is given in Appendix 2.

The equilibrium pattern of female preference

Given a stable equilibrium, insight into how such costly female preference is maintained can be gained by deriving an expression for the equilibrium female preference across space in terms of the equilibrium male phenotype. I focus on the case where population density is uniform across space because it admits analytical solutions, and including population density variation tends only to alter predictions slightly (unpubl. numerical results). The equilibrium female preference across space is given by (Appendix 3)

$$\hat{p}_s(x) = \hat{z}_s(x) - \int_{\omega_1}^{\omega_2} \psi(\xi, x)\hat{z}_s(\xi) d\xi, \quad (24)$$

where $\hat{z}_s(x)$ is the equilibrium male phenotype, ω_1 and ω_2 are the lower and upper boundaries of the spatial axis, and $\psi(\xi,$

x) is a probability distribution in ξ (i.e., $\int_{-\infty}^{\infty} \psi(\xi, x) d\xi = 1$ for each x) that weights the influence of male phenotypes at other locations on location x . Here ξ is a dummy variable of integration. A general expression for ψ is given by equation (A36) in Appendix 3, but considering the case where the boundaries are far away provides the most insight. In this case we have (Appendix 3)

$$\psi(\xi, x) \approx \frac{\sqrt{k} \exp(-\sqrt{k}|x - \xi|)}{2}, \quad (25)$$

where k is a positive constant given by

$$k = \frac{G_z}{D} \left(\frac{G_p}{G_z} - \frac{B^2}{G_z^2} \right) b.$$

Expression (24) reveals that the equilibrium preference at a given location is simply the difference between the mean male phenotype at that location and the spatial average of the mean male phenotype at nearby locations. This spatial average in the second term of equation (24) weights locations less with increasing distance and represents the average male phenotype of immigrants to location x . This reflects the mechanism by which nonzero female preference is maintained. In particular, female preference at location x will be positive if the mean male phenotype at that location is, on average, larger than the mean male phenotype of immigrants. The reason is that, in such cases, the dispersal of individuals tends to reduce the mean male phenotype at that location. Consequently, the selection gradient on the male phenotype at that location must be positive to maintain the male trait value at $\hat{z}_s(x)$. Because female preference is genetically correlated, the preference gets dragged along and is therefore positive (Fig. 1). This reasoning suggests that, roughly speaking, where the equilibrium male phenotypic pattern is concave down, the female preference will be positive and vice versa. Notice that this effect of the dispersal is qualitatively similar to the effect of mutational bias in males as presented by Pomiankowski et al. (1991), and might be termed migration bias.

Expression (25) also shows that $1/\sqrt{k}$ is a measure of spatial neighborhood over which the male phenotype is averaged. This is sometimes referred to as the characteristic length, and it is the spatial scale on which migration tends to overwhelm selection (Slatkin 1978; Lande 1982). Therefore, for a fixed equilibrium pattern of male phenotype, if dispersal rate D is low, the genetic covariance B is low, the cost of preference b is high, or the genetic variance in female preference G_p is high, then the averaging in equation (24) is taken over a very small, local neighborhood. In other words, the spatial scale on which migration tends to overwhelm selection is very small. As a result the average difference in male trait value on this scale will be nearly zero and therefore, from (24), the local female preference will also be nearly zero. Biologically this occurs because reduced dispersal and reduced genetic covariance will both decrease the correlated response to selection that the female preference undergoes. Similarly, increased cost of preference and increased genetic variance for preference will both enhance the evolutionary change in preference toward zero through the direct effects of selection. However, I stress that the above considerations assume a

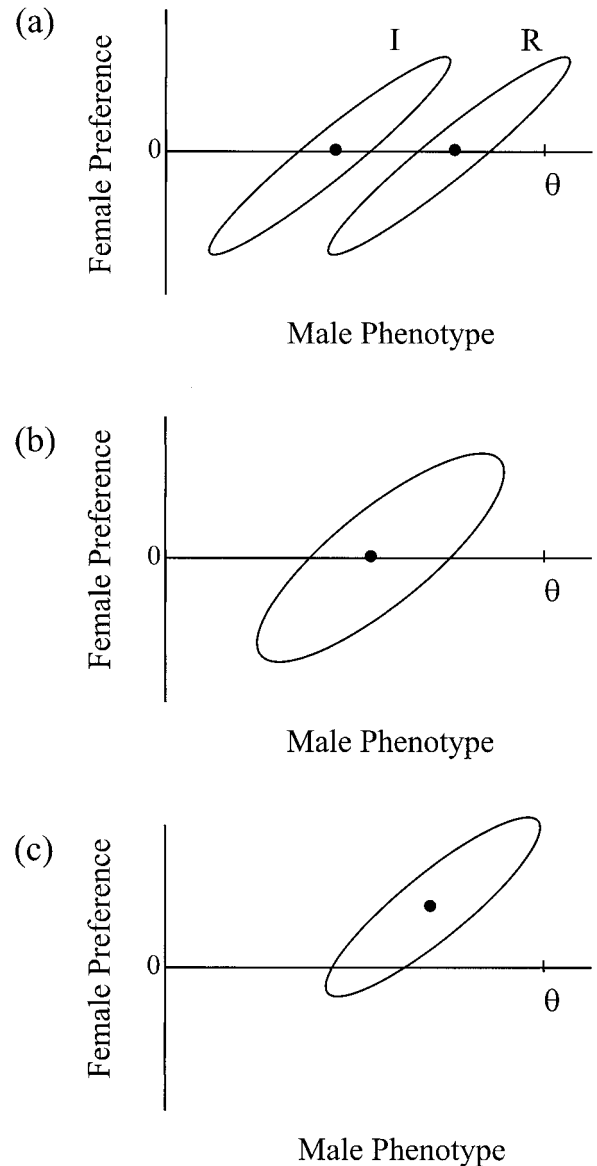


FIG. 1. An illustration of why female preference cannot be zero everywhere at equilibrium. Suppose that female preference starts at zero everywhere. The figure focuses on a particular spatial location, and θ represents the optimal male phenotype at this location. (a) The ellipse marked R represents the distribution of breeding values for male phenotype and female preference at a particular spatial location termed the "resident." Its major axis has positive slope reflecting a positive genetic covariance. The distribution of breeding values of the immigrants to this location is represented by the ellipse marked I. In this example, immigrants have a lower mean breeding value for the male trait but the mean breeding value for the female preference is zero everywhere. (b) The breeding value distribution at the resident location after dispersal. The mean breeding value for the male trait has decreased but that of the female preference remains unchanged. (c) The distribution of breeding values after selection. Directional selection for a larger male trait causes a correlated response in the female preference taking its mean value away from zero. Selection on the preference cannot keep it at zero because selection acts against both males and females in the lower left of the distribution in (b), but it acts against females and in favor of males in the upper right of the distribution.

fixed $\hat{z}_s(x)$. But changing the values of these parameters might also change $\hat{z}_s(x)$ and it is necessary to consider this as well when determining how female preference will change overall. This is illustrated in the numerical examples below.

One other feature of equation (24) worth noting is that the relationship between female preference and the spatial pattern of male phenotype at equilibrium is independent of both a and c . Therefore, although these parameters will influence the equilibrium pattern in the male phenotype, they do not influence the relationship between that and the equilibrium female preference.

The equilibrium pattern of male phenotype

The above results reveal how costly female preference is maintained at equilibrium, but to understand what this spatial pattern will actually look like in any given instance, it is necessary to determine the equilibrium pattern of male phenotype across space. Although it is possible to obtain a general expression for the equilibrium male phenotype (unpubl. data), it is quite complicated. It is relatively easy, however, to guess its qualitative features for some regions of parameter space. For instance, whenever the strength of natural selection on the male trait outweighs the strength of sexual selection, the male phenotype will evolve to an equilibrium that is largely determined by natural selection. This will be true whenever the cost to preference b is high and/or its genetic variance G_p is also high because little preference will then evolve. It will also be true if the cost to males of being maladapted is high, the strength of sexual selection is low and/or the genetic correlation between male trait and female preference is low. In all such cases the equilibrium male phenotype will tend to be a spatial averaging of the optimal male phenotype across space (Slatkin 1978). Given this male equilibrium, we can then use equation (24) to understand the equilibrium female preference.

It becomes more difficult to guess the pattern of male phenotype when the cost of preference is small. Nonspatial models exhibit a form of structural instability whereby substantial female preference and maladaptation of male phenotype can evolve when there is zero cost to preference, but female preference evolves to zero and the male trait reaches its optimum when any amount of cost is introduced, no matter how small. As a result, cost-free models and models with very small costs give qualitatively different predictions. The derivations below show that, although an analogous form of structural instability occurs here as well, it is less of a problem. In particular, when there is a small cost of female preference, the major features of Lande's (1982) cost-free model remain unchanged. All results presented here assume that the population density is uniform across space.

First, define

$$z_s^* = \frac{1}{\omega_2 - \omega_1} \int_{\omega_1}^{\omega_2} \hat{z}_s(\xi) d\xi, \tag{26}$$

$$p_s^* = \frac{1}{\omega_2 - \omega_1} \int_{\omega_1}^{\omega_2} \hat{p}_s(\xi) d\xi, \text{ and} \tag{27}$$

$$\theta^* = \frac{1}{\omega_2 - \omega_1} \int_{\omega_1}^{\omega_2} \theta(\xi) d\xi, \tag{28}$$

as the (unweighted) spatial averages of the male trait, female preference, and the optimal male trait, respectively. When the cost of female preference becomes small (i.e., b becomes small), $\psi(\xi, x)$ converges to $1/(\omega_2 - \omega_1)$. As a result, from equation (24) we have that $\hat{p}_s(x) \approx \hat{z}_s(x) - z_s^*$. Moreover, equation (23) shows that $z_s^* = \theta^*$, and therefore this can be rewritten as $\hat{p}_s(x) \approx \hat{z}_s(x) - \theta^*$. From this, a differential equation for the equilibrium spatial pattern of male phenotype (when b becomes small) can be obtained by substituting this expression into equation (13) and setting $\partial \bar{z}_s / \partial t$ to zero. This equation is approximate, but it becomes increasingly accurate as b gets smaller. Now, by defining $\tilde{\theta}(x)$ as the deviation of the optimal male phenotype from its spatial average (i.e., $\theta(x) = \theta^* + \tilde{\theta}(x)$), calculations analogous to those of Appendix 3 to show that

$$\hat{z}_s(x) \approx \frac{G_z c}{G_z c - \frac{aB}{2}} \int_{\omega_1}^{\omega_2} \tilde{\psi}(\xi, x) \tilde{\theta}(\xi) d\xi + \theta^*, \tag{29}$$

where $\tilde{\psi}(\xi, x)$ is given by equation (A36), but with $k = 1/D(G_z c - (aB/2))$. Again, this is an approximation that becomes increasingly accurate as the cost of preference, b , gets smaller. Therefore, when the cost of preference is small, the equilibrium male phenotype at any location is approximately equal to the average optimal male phenotype, θ^* , plus a quantity proportional to the spatial average of the deviations in the optimum male phenotype from θ^* , where each spatial location is weighted less with increasing distance. The constant of proportionality, $G_z c / [G_z c - aB/2]$, has been referred to as an "amplification factor" by Lande (1982) because it is greater than one and therefore tends to amplify the pattern in the optimal male phenotype, $\tilde{\theta}(x)$. In this case, the equilibrium female preference is simply the first term of expression (29):

$$\hat{p}_s(x) \approx \frac{G_z c}{G_z c - \frac{aB}{2}} \int_{\omega_1}^{\omega_2} \tilde{\psi}(\xi, x) \tilde{\theta}(\xi) d\xi. \tag{30}$$

Assuming the boundaries of the spatial domain are far enough away that they have no effect (as in Lande 1982), ψ can be approximated by expression (25). In this case, expression (29) is identical to Lande's result, but with one qualitative difference. In his result θ^* is replaced by an essentially arbitrary constant. Here θ^* is determined by the clinal pattern in optimal male phenotype and is therefore fixed. This is an analogue, for spatial models of Fisher's process, of the structural instability found in nonspatial models (Pomiankowski 1987; Bulmer 1989; Barton and Turelli 1991). Nonspatial models have a neutral line of equilibria along which a population can drift when there are no costs to preference. When there are costs, however, this line collapses to a single point equilibrium no matter how small the cost. In Lande's (1982) spatial model, he found a single equilibrium spatial pattern of male phenotype that was neutrally stable to changes in the spatial average male phenotype. In other words, the spatial pattern of male phenotype was neutrally stable with respect to vertical shifts in the entire curve. The present results demonstrate that, with any nonzero cost to female preference, this neutral stability disappears and the equilibrium spatial pattern

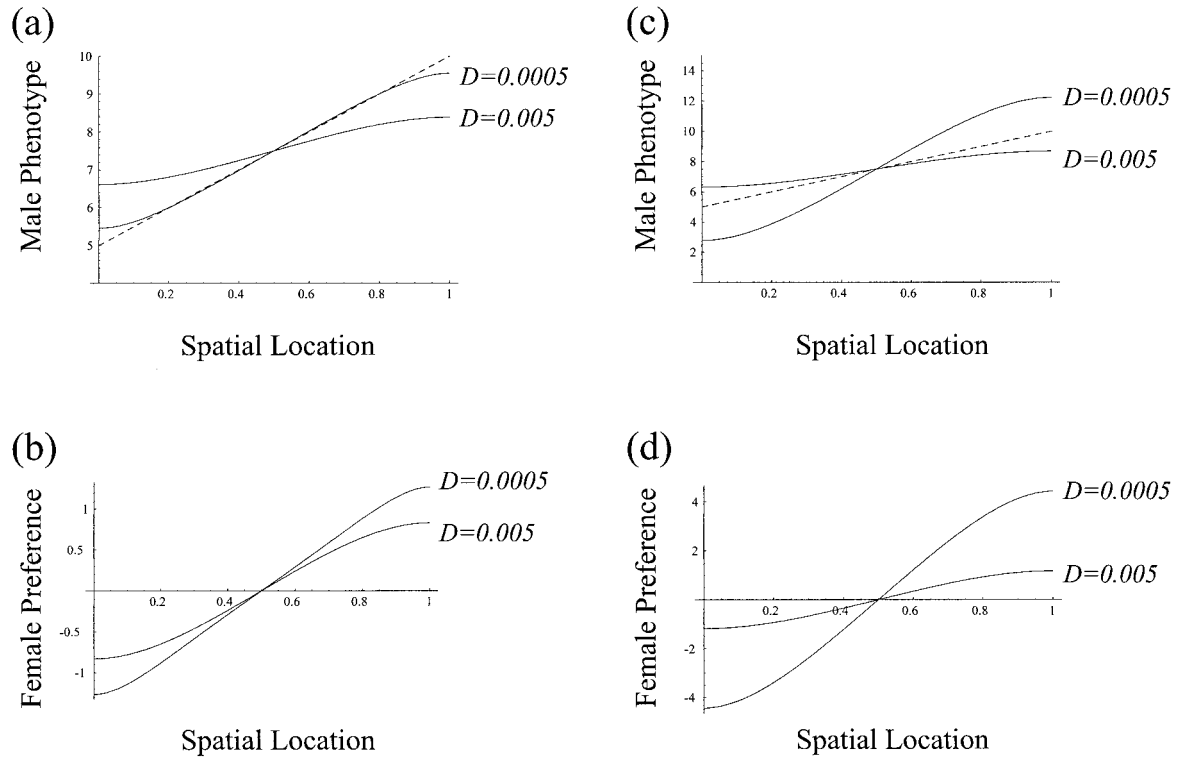


FIG. 2. Numerical results when the optimal male phenotype changes linearly across space. Parameter values $G_x = G_p = 1$, $B = 0.1$, $c = 1/30$, and $\theta(x) = 5 + 5x$. Graphs depict two values of the dispersal rate, D . Dotted line is the optimal male phenotype. In panels (a) and (b), $a = 0.1$ and $b = 1/300$, whereas in panels (c) and (d), the effect of sexual selection on male fitness is greater ($a = 0.5$) and selection against female preference is weaker ($b = 1/3000$).

of male phenotype is instead anchored at a point where the spatial average male phenotype is equal to θ^* . The important point, however, is that this structural instability does not affect one of the primary findings of Lande's model—sexual selection can greatly amplify geographic patterns in the optimal male phenotype across space. More specifically, as the cost of female preference decreases, the spatial pattern of male phenotype (and female preference) converges to the pattern found by Lande (1982) when preference is cost-free.

Numerical Examples

I now turn to some numerical examples to illustrate the behavior of the model. All results below assume that population density is uniform throughout space, and combinations of parameter values are chosen to result in a stable equilibrium. Not too much attention should be paid to absolute values on the axes because the spatial axis is scaled to unity, and the scale of measurement of the male and female traits are left unspecified.

The simplest case is when the optimal male phenotype changes linearly through space. From expression (19) we can see that if the spatial boundaries are very far away, then the males evolve to be optimally adapted everywhere and female preference is zero everywhere at equilibrium. When the boundaries are explicitly accounted for this is no longer true (Fig. 2a). The reason is that subpopulations near the left boundary receive more immigrants from the right than from the left, and therefore, the mean male phenotype tends to be

dragged upward. The reverse holds on the right boundary. As a result, expression (24) shows that female preference will be negative near the left-hand boundary and positive near the right boundary (Fig. 2b). Interestingly, this pattern of female preference actually causes the male phenotype in these locations to be better adapted than would be the case in the absence of sexual selection. Thus, when female preference is costly, runaway sexual selection can actually result in the male phenotype being closer to its natural selection optimum. Expressions (29) and (30) also show that, if the cost of female preference is small enough, then sexual selection will amplify the geographic pattern in the optimum. This can be seen in Figures 2c, d (note the change in scale on the vertical axes). Notice that, when the cost of preference is small, the runaway evolution of negative female preference near the left boundary drives the male phenotype past its optimum, and the same is true near the right boundary. It is also apparent that a large enough dispersal rate can reverse this tendency of runaway sexual selection (Fig. 2c, $D = 0.005$), because gene flow then homogenizes the population. Of course, in this case, a large dispersal rate also results in a smaller amount of female preference evolving at equilibrium (Fig. 2d). In fact, in the limit as the dispersal rate becomes very large, the model reduces to a nonspatial model with costly female preference, and therefore we expect no preference to evolve under such conditions.

It is also interesting to ask what happens to the male phenotype and female preference if a barrier to gene flow arises

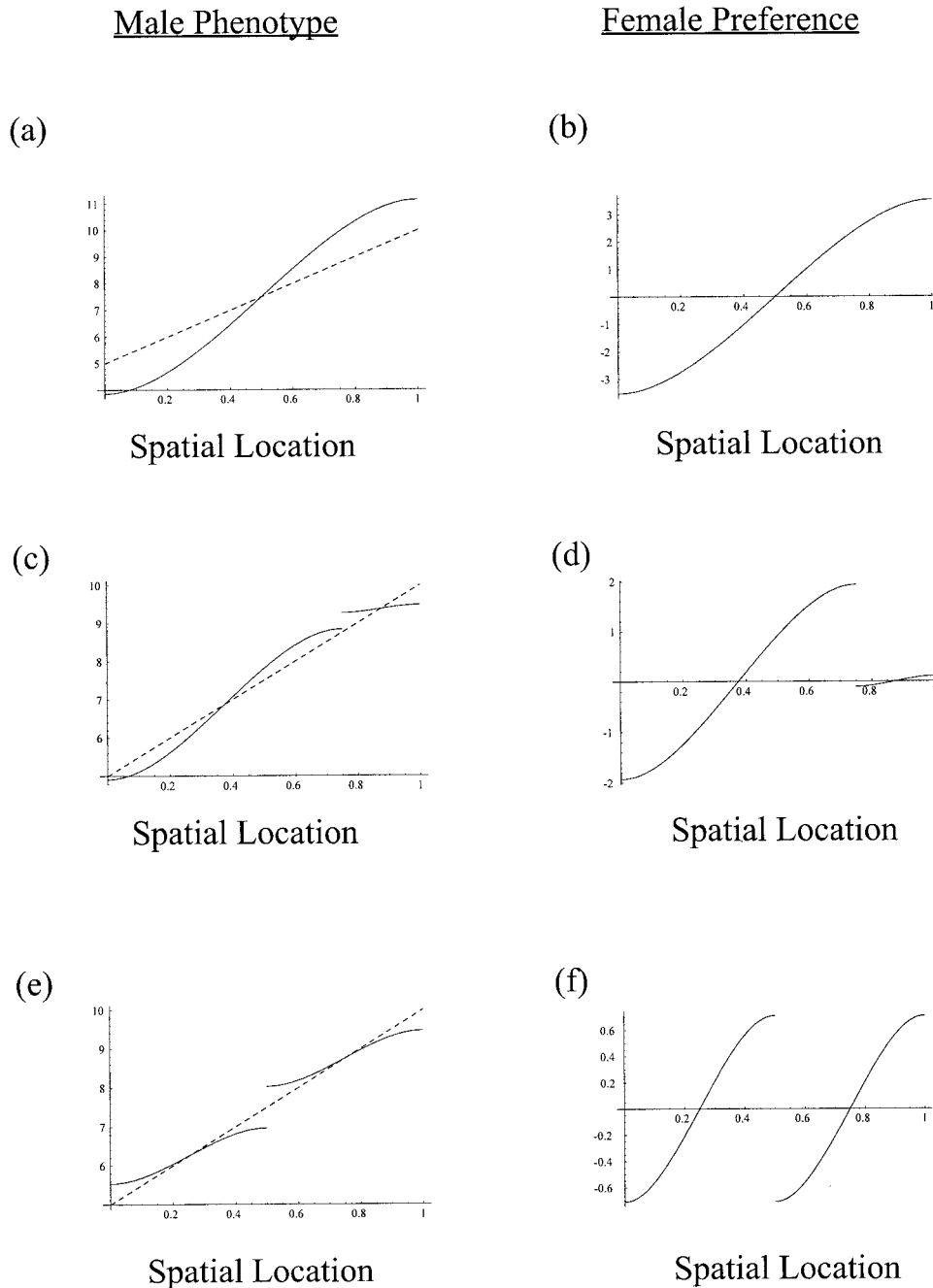


FIG. 3. The effect of introducing a barrier to gene flow at some location in the species' range, when the strength of selection against female preference is very weak. Parameter values $G_z = G_p = 1$, $B = 0.1$, $c = 1/30$, $a = 0.5$, $b = 1/3000$, $D = 0.001$, and $\theta(x) = 5 + 5x$. Dotted line is the optimal male phenotype. (a) The equilibrium male phenotype with no barrier to gene flow. (b) The equilibrium female preference with no barrier to gene flow. (c) The equilibrium male phenotype when a barrier to gene flow is introduced near the edge of the species' range. (d) The equilibrium female preference when a barrier to gene flow is introduced near the edge of the species' range. (e) The equilibrium male phenotype when a barrier to gene flow is introduced in the middle of the species' range. (f) The equilibrium female preference when a barrier to gene flow is introduced in the middle of the species' range.

at some location in the species' range (Endler 1977; García-Ramos and Kirkpatrick 1997). From the above considerations we might expect rapid divergence in female preference because, with a linear cline, preference is always negative at one end of the range and positive at the other. A barrier to gene flow would effectively create two ranges side-by-side and each would exhibit this pattern. Figure 3 shows that this

is exactly what happens. Furthermore, when the range is fragmented into a large and a small patch, gene flow across the small patch can cause the males to exhibit essentially no spatial variation in phenotype, and therefore very little preference evolves as well (Fig. 3c, d). In contrast, if the two patches are of comparable size, then opposite female preferences evolve on either side of the barrier (Fig. 3f). A coun-

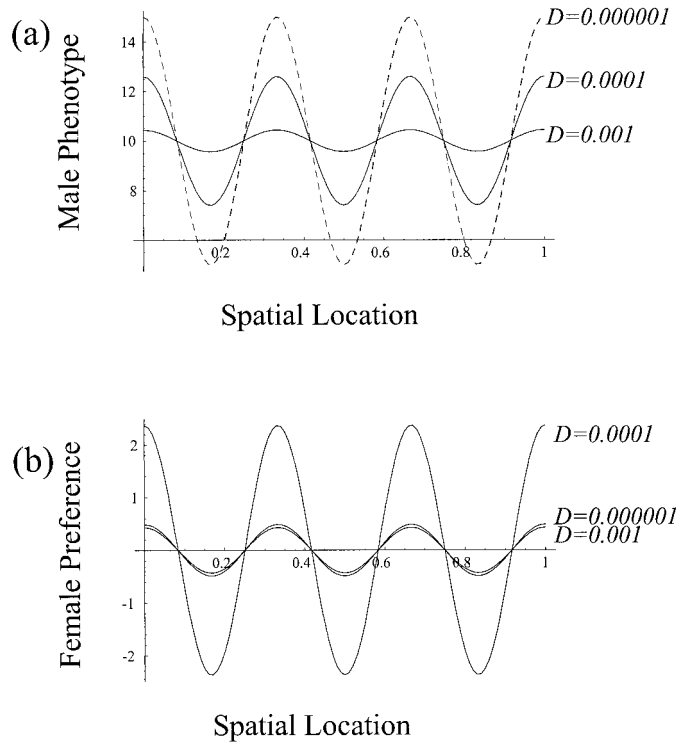


FIG. 4. The effect of changes in dispersal rate, D , when the optimal male phenotype varies periodically in space. Parameter values $G_z = G_p = 1$, $B = 0.1$, $a = 0.1$, $b = 1/300$, $c = 1/30$, and $\theta(x) = 5 \cos(6\pi x) + 10$. Dotted line is the optimal male phenotype. (a) The equilibrium male phenotype across space. The plot for $D = 0.000001$ is not shown because it is indistinguishable from the optimum on this scale. (b) The equilibrium female phenotype across space.

ter-intuitive finding is that, in this example, females to the left of the barrier prefer large traits, whereas those to the right prefer small traits even though the mean male trait is larger to the right than to the left. Also notice that, initially runaway sexual selection can amplify the geographic pattern in the optimum (Fig. 3a), but after the range is fragmented, the effect of sexual selection can be overwhelmed by gene flow in one (Fig. 3c) or both (Fig. 3e) of the habitat patches.

Another situation of interest is where the optimal male phenotype varies in a patchy way. This can be modeled using a periodic function for the optimal male phenotype. As expected, increasing the dispersal rate in this example always decreases the extent to which males are locally adapted (Fig. 4a). Interestingly though, it appears that the largest amount of female preference evolves at an intermediate dispersal rate (Fig. 4b). When the dispersal rate is very low, males are locally well adapted, and therefore male phenotype changes substantially across space. Nevertheless, because few individuals disperse from one location to another (and this drives the evolution of female preference), very little preference evolves. In contrast, when dispersal rates are large, there is little change in male phenotype across space, and, again, very little preference evolves because dispersers tend to have a phenotype similar to that of the residents (Fig. 4).

Finally, one of the most interesting cases to explore is when the optimal male phenotype changes abruptly from one value to another across a relatively narrow zone (Fig. 5). In this

case, Lande (1982) found that, when preference is cost-free sexual selection can greatly amplify this geographic cline in the optimum. As a result, extremely different male phenotypes and female preferences can evolve on either side of the zone of transition, and this can result in reproductive isolation. An important result of the present analysis is that this conclusion remains valid, even when there is a small cost of preference. In particular, with a small cost of preference, expressions (29) and (30) hold, and they show that sexual selection can amplify the cline. This is illustrated in Figures 5a, b. With a moderate cost of preference, however, this is no longer true. Instead, at either end of the range the male trait is well adapted. Therefore dispersal does not alter the mean male phenotype much at these locations, and expression (24) shows that female preference will be zero. In the transition zone, dispersal into regions just to the left of center (Fig. 5c, d) cause the mean male phenotype in those regions to increase, and directional selection is negative at equilibrium. This results in female preference being negative at equilibrium as well. The reverse holds in regions just to the right of center in the zone of transition. Interestingly, the resulting overall pattern of preference is one very similar to reproductive character displacement. Mating is random outside of the zone of transition, but female preferences appear “displaced” from random mating in the zone of transition. Furthermore, female preference is displaced in such a way as to promote assortative mating in this zone. Such patterns are often thought to arise from selection for reduced hybridization between individuals from each end of the range if hybrids suffer reduced fitness, but these results demonstrate that such patterns of reproductive character displacement might arise simply from sexual selection without requiring any hybrid dysgenesis.

DISCUSSION

Although several previous models of sexual selection have shown that Fisher’s runaway process cannot result in the evolution of costly female preference (Lande 1981; Pomiankowski 1987; Bulmer 1989; Pomiankowski et al. 1991), all of these models have neglected the importance of the spatial distribution of individuals and the effect of dispersal. The model presented here demonstrates that, if the optimal male phenotype varies across space, then costly female preference evolves very easily. Furthermore, the magnitude of the female preference that evolves depends on the magnitude of the cost of preference. Costly female preference can evolve because gene flow prevents males from being optimally adapted everywhere, and therefore, directional selection on males at equilibrium prevents the female preference from remaining at zero due to its genetic correlation with the male trait (Fig. 1).

Many authors have emphasized the role that sexual selection can play in the origin of species (e.g., Lande 1981, 1982; West-Eberhard 1983; Deutsch 1997; Payne and Krakauer 1997). If sexual selection can result in large and somewhat arbitrary evolutionary changes in mate recognition systems, then isolated populations might often diverge with respect to one another, resulting in the formation of new species. Lande (1982) demonstrated that sexual selection across an abrupt environmental cline in the optimal male phenotype can lead

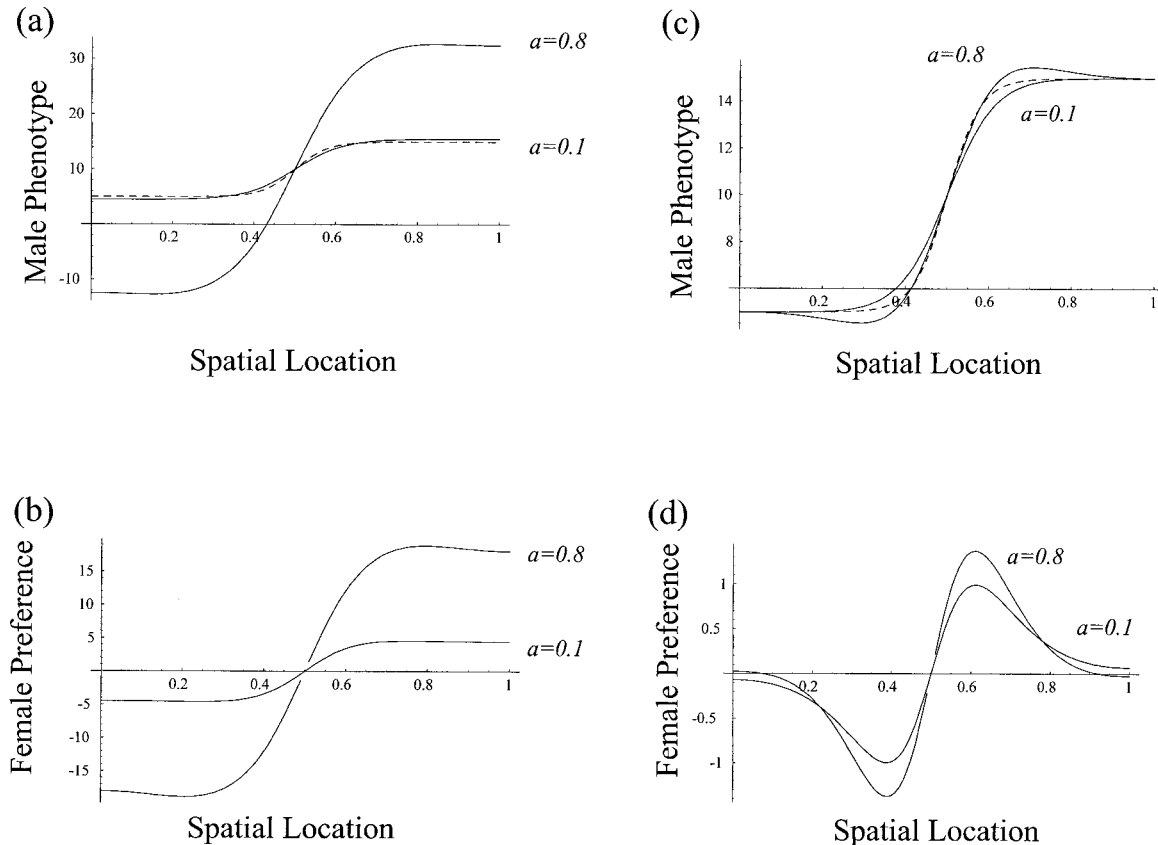


FIG. 5. The equilibrium pattern of male phenotype and female preference when the optimal male phenotype changes abruptly at a point in the species' range. Parameter values $D = 0.0001$, $G_z = G_p = 1$, $B = 0.08$, $c = 1/30$, and $\theta(x) = 5 \tanh[(x - 1/2)4\pi] + 10$. (a) and (b) have a small cost of female preference ($b = 1/5000$) and show the results for two strengths of sexual selection. In this case sexual selection can greatly amplify the pattern in the optimal male phenotype. (c) and (d) have a moderate cost of female preference ($b = 1/80$) and show the results for two strengths of sexual selection. In both cases a pattern of reproductive character displacement results in the female preference.

to dramatic evolutionary changes in mate recognition systems throughout a species' range. Payne and Krakauer (1997) have also shown that if male movement rate depends on mating success, then such evolution of mate recognition systems can occur, even in the absence of environmental clines. In some organisms, however, environmental clines are associated with divergent female mate preferences and/or male phenotypes within the transition zone and little or no divergence in the mate recognition system outside of this region (Howard 1993). Such reproductive character displacement is not predicted by models of sexual selection when mate preferences are cost-free. Instead, these patterns are often thought to arise from reinforcement (selection for reduced mating between the two types of individuals found on either side of the environmental cline; Butlin 1987, 1989; Howard 1993). An interesting finding here is that, when there is a moderate cost of preference, patterns very similar to reproductive character displacement are a common evolutionary outcome.

The fact that patterns similar to reproductive character displacement can arise simply through sexual selection reveals that such patterns in nature need not be explained by reinforcement. The extent to which sexually selected patterns of reproductive character displacement occur in the wild however is unclear. Many studies of ecological clines have been conducted on hybrid zones between two genetically distinct pop-

ulations whose hybrids sometimes suffer a degree of reduced fitness (Harrison 1990; Howard 1993). The model presented here applies only to a single population distributed across an ecological cline. Whether any of the putative examples of reinforcement originated as a single population distributed along a cline and which subsequently acquired the genetic incompatibilities that now result in hybrid dysfunction is unknown (Endler 1977). More studies of intraspecific variation in mate preferences across a species' range would be valuable (e.g., Ryan and Wilczynski 1991; Ryan et al. 1992, 1996; Arnegard et al. 1999) both for understanding hybrid zones and for evaluating the extent to which patterns of reproductive character displacement arise from sexual selection.

Of crucial importance to the models predictions is the assumption that the genetic covariance between female preference and male phenotype is positive. At first glance, this assumption appears circular. Female preference causes a positive genetic covariance yet the model shows that no female preference can evolve without such a covariance being present in the first place. The error in this logic is that the model makes predictions about the *mean* preference and *mean* male phenotype only. There will always be some variation in female preference even if the mean preference is zero. Therefore a positive genetic covariance might still arise under these conditions. Presumably the covariance would be larger when

the mean preference is nonzero, but enough covariance might develop simply through variation in mate preference to set the Fisher process in motion. Once the mean female preference evolves away from zero, the covariance might then be expected to increase, thereby reinforcing further evolution of the preference. These considerations suggest that an exploration of the evolutionary dynamics of the genetic covariance across a species' range would be very useful.

Nonspatial models of Fisher's runaway process exhibit a form of structural instability (Bulmer 1989; Barton and Turelli 1991; Pomiankowski et al. 1991). Predictions of models with cost-free preference often display a line of equilibria along which the population can drift, but the incorporation of any cost of preference, no matter how small, collapses this line of equilibria to a single point at which no female preference or male trait exaggeration is present. This calls into question the validity of Fisher's process because it seems likely that there will often be some cost of preference, albeit sometimes small. A significant finding of the present model is that this form of structural instability is less significant in spatial models. In particular, many of the interesting qualitative features of spatial models of Fisher's process remain valid even with a small cost of preference. For example, Lande (1982) found that sexual selection can greatly exaggerate environmental variation when preference is cost-free. The present model shows that this is also the case when there is a small cost of preference. Spatial models do exhibit an analogous form of structural instability, but it is an instability with respect to the *spatial average* female preference and male phenotype. When preference is cost-free the spatial averages of these characters are arbitrary and lie on a line of equilibria, whereas any cost of preference causes the spatial average preference and male maladaptation to both be zero. This instability is less of a problem in spatial models because, although the spatial average preference and male maladaptation are zero, the male trait and female preference can nevertheless deviate substantially from these averages at locations throughout the species' range.

The above considerations allow a relatively simple understanding of how costly female preference, runaway sexual selection, and natural selection interact to produce spatial patterns of male phenotype and female preference. First, suppose that only natural selection is operating on males. Figure 6a depicts an example where the optimal male phenotype changes abruptly at one location. In the absence of sexual selection, we expect the mean male phenotype at each location to reach an equilibrium at which natural selection is balanced by gene flow (Slatkin 1978). Where the mean male phenotype is larger than the optimum, directional selection is continually pulling downward, but this is balanced by the immigration of individuals with phenotypes that are too large for that location. The reverse is true where the mean male phenotype is too small. Now consider how the picture changes when runaway sexual selection is allowed to occur between the male phenotype and a costly female preference. At locations where the equilibrium male phenotype is too large, female preference will be negative at equilibrium and vice versa. Thus, runaway sexual selection enhances the local adaptation of males by acting in concert with natural selection to counteract the homogenizing effects of gene flow (Fig. 6b). The extent to which this runaway process alters the mean

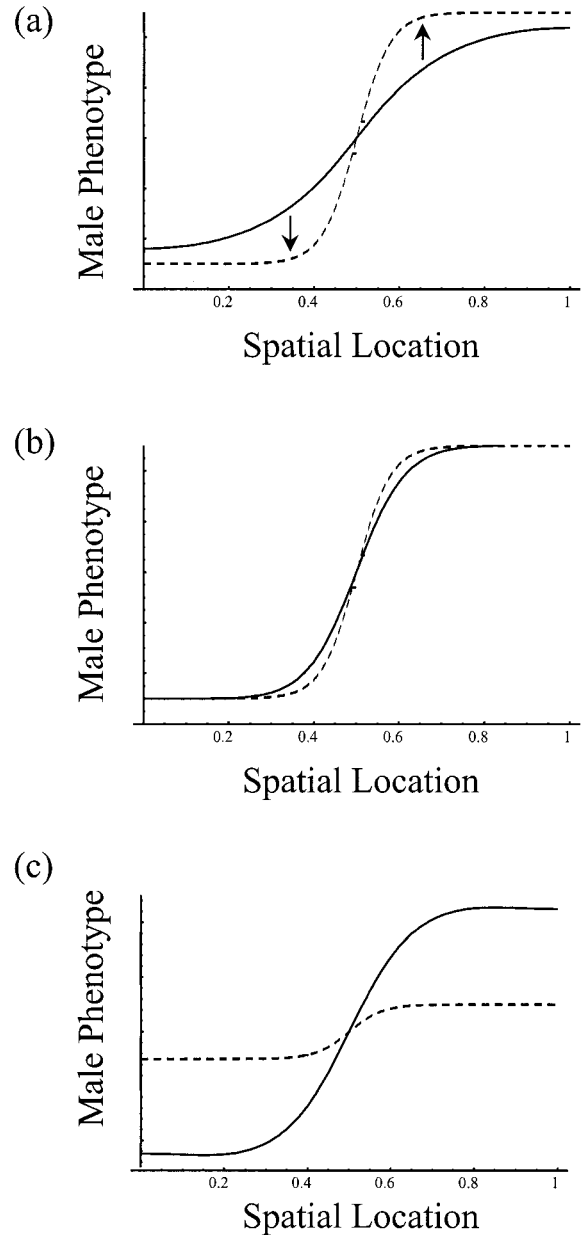


FIG. 6. An illustration of how natural selection and runaway sexual selection interact to produce spatial patterns in male phenotype. Dotted line is the optimal male phenotype. (a) Natural selection alone results in the mean male phenotype at each spatial location evolving until there is a balance between selection and gene flow. Directional selection is continually pulling the mean male phenotype toward the optimum (indicated by the arrows), but this is balanced by the immigration of individuals with maladapted phenotypes. (b) When sexual selection also operates but female preference has a moderate cost, preference evolves to be negative to the left of the center of the range and positive to the right. This preference acts, in conjunction with natural selection, to bring the mean male phenotype closer to the optimum. (c) If the cost of preference is small enough, sexual selection can actually drive the mean male phenotype past the optimum. Note the change in scale.

male phenotype depends on several factors, including the strength of the genetic correlation, B , the strength of sexual selection, a , and the cost of preference, b . In particular, as the cost of preference decreases, greater female preference will evolve and this results in a larger effect on the male phenotype. As the cost of preference becomes small enough, runaway sexual selection actually causes the mean male phenotype to surpass the optimum, and the geographic pattern in the optimum is then amplified by sexual selection (Fig. 6c). Of course, these arguments apply for different patterns of in the optimal male phenotype across space as well.

There are a number of extensions of the present model that warrant consideration. A simplifying assumption made here is that the population dynamics of the species are unaffected by the distribution of male phenotypes and female preferences. It would be interesting to relax this assumption and allow a feedback between the male and female characters and the population dynamics. Such feedback can affect the size of a species' range (García-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997) and thereby affect the degree of environmental variation experienced by the population. Because this variation is what drives sexual selection in the current model, this feedback process might have important effects on sexual selection.

I have also assumed that the movement of individuals can be adequately modeled using diffusion. This implicitly assumes that movement is very local. Many species exhibit occasional long-range dispersal (Endler 1977), and the effects of this on the conclusions of the model are uncertain. The results of Appendix 1 provide a starting point for exploring such movement patterns.

Finally, the model presented here also assumes the dispersal behavior of both sexes is the same. In some species, however, it is likely that males and females exhibit different patterns of movement. Payne and Krakauer (1997) have examined the effects of such sex-dependent dispersal on Fisher's runaway process by supposing that male dispersal rate increases when mating success is low. Under these conditions, spontaneous spatial patterns of mate preference evolve, even in the absence of environmental heterogeneity. Also, males with different phenotypes become localized in different regions of space due to independent, spatially localized runaway processes. This suggests that a much smaller degree of environmental heterogeneity is required to produce substantial changes in mate preference under such conditions than is required when male and female dispersal behavior is the same. It would be interesting to determine if such factors can enhance the level of costly female preference that evolves as well.

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APPENDIX 1

Here I derive the movement terms of equations (9) and (10). Similar equations have been presented before by several authors (Pease et al. 1989; García-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997) and are based on the results of Nagylaki (1975). Nagylaki provides the only published derivation that I know of and, because it is mathematically rigorous, it is difficult to read. My intention here is to provide a less rigorous but hopefully more user-friendly derivation. This derivation also provides a starting point for modeling alternative forms of individual movement in addition to diffusion.

Consider a one-dimensional spatial axis, x . Define $\kappa(y)$ to be the

dispersal kernel; $\kappa(y)\Delta y$ is the probability that a dispersing individual moves a distance y . I assume that this kernel is identical for both sexes and that it is independent of the spatial location of individuals. I will consider the effect of movement on the mean value of the male phenotype only because the effect on female preference will be identical. Letting μ be the probability that an individual disperses in a small interval of time and $c(z, x, t)$ be the density of individuals with trait value z at location x at time t (i.e., $c(z, x, t)\Delta x$ is the number of such individuals between x and $x + \Delta x$), we have

$$\frac{\partial c}{\partial t} = \mu \int_Y \kappa(y)[c(z, x - y, t) - c(z, x, t)] dy, \quad (A1)$$

where Y is the spatial domain (Murray 1993). With this I define the total density of individuals at location x at time t , $n(x, t)$, as

$$n(x, t) = \int_Z c(z, x, t) dz, \quad (A2)$$

where Z is the domain of the phenotypic axis. It satisfies differential equation

$$\begin{aligned} \frac{\partial n}{\partial t} &= \mu \int_Z \int_Y \kappa(y)[c(x - z, y, t) - c(z, x, t)] dy dz \\ &= \mu \int_Y \kappa(y)[n(x - y, t) - n(x, t)] dy. \end{aligned} \quad (A3)$$

This gives an equation for the population dynamics in models where it is necessary to keep track of both the phenotypes as well as the population density. Now I define the probability density of trait z at location x and time t as

$$q(z, x, t) = \frac{c(z, x, t)}{n(x, t)}. \quad (A4)$$

It obeys the differential equation

$$\begin{aligned} \frac{\partial q(z, x, t)}{\partial t} &= \frac{\partial c(z, x, t)}{\partial t} \frac{1}{n(x, t)} - q(z, x, t) \frac{\partial n(x, t)}{\partial t} \frac{1}{n(x, t)} \\ &= \frac{1}{n(x, t)} \left\{ \mu \int_Y \kappa(y)[c(z, x - y, t) - c(z, x, t)] dy \right\} \\ &\quad - \frac{q(z, x, t)}{n(x, t)} \left\{ \mu \int_Y \kappa(y)[n(x - y, t) - n(x, t)] dy \right\} \\ &= \mu \int_Y \kappa(y) \left[\frac{c(z, x - y, t)}{n(x - y, t)} \frac{n(x - y, t)}{n(x, t)} - q(z, x, t) \right] dy \\ &\quad - \mu \int_Y \kappa(y) q(z, x, t) \left[\frac{n(x - y, t)}{n(x, t)} - 1 \right] dy \\ &= \mu \int_Y \kappa(y) \left[q(z, x - y, t) \frac{n(x - y, t)}{n(x, t)} - q(z, x, t) \frac{n(x - y, t)}{n(x, t)} \right] dy \\ &= \mu \int_Y \kappa(y) \frac{n(x - y, t)}{n(x, t)} [q(z, x - y, t) - q(z, x, t)] dy. \end{aligned} \quad (A5)$$

Because $\bar{z}(x, t) = \int q(z, x, t)z dz$, an equation for the time dynamics of $\bar{z}(x, t)$ is then obtained as

$$\begin{aligned} \frac{\partial \bar{z}}{\partial t} &= \frac{\partial}{\partial t} \int_Z q(z, x, t)z dz \\ &= \int_Z \mu \int_Y \kappa(y) \frac{n(x - y, t)}{n(x, t)} [q(z, x - y, t) - q(z, x, t)] dyz dz \\ &= \mu \int_Y \kappa(y) \frac{n(x - y, t)}{n(x, t)} [\bar{z}(x - y, t) - \bar{z}(x, t)] dy. \end{aligned} \quad (A6)$$

The description of movement embodied in equations (9) and (10)

assumes that the dispersal kernel in (A1) corresponds to diffusion. This will be true whenever the dispersal kernel has a small variance. In this case, expanding $[n(x - y, t)]/[n(x, t)] [\bar{z}(x - y, t) - \bar{z}(x, t)]$ in equation (A6) in powers of y around $y = 0$ and neglecting terms of order 3 and higher gives the movement terms in equations (9) and (10), with D equal to $\mu/2$ times the variance of the dispersal kernel.

To determine the boundary conditions, first calculate $\partial q/\partial x$ at the boundaries;

$$\frac{\partial q}{\partial x} = \frac{\partial c}{\partial x} \frac{1}{n} - \frac{\partial n}{\partial x} \frac{c}{n^2} \tag{A7}$$

$$= q \left(\frac{\partial c/\partial x}{c} - \frac{\partial n/\partial x}{n} \right). \tag{A8}$$

In the text I assume that the flux of individuals across the boundaries is zero and therefore both terms in the parentheses of (A8) are zero at the boundaries. As a result $\partial q/\partial x = 0$ at the boundaries. Notice however that this will also be true whenever $(\partial c/\partial x)/c = (\partial n/\partial x)/n$ at the boundaries. In either case, the boundary conditions on \bar{z} are

$$\frac{\partial \bar{z}}{\partial x} = \frac{\partial}{\partial x} \int_Z q(z, x, t) z dz \tag{A9}$$

$$\frac{\partial \bar{z}}{\partial x} = \int_Z \frac{\partial q}{\partial x} z dz \tag{A10}$$

$$\frac{\partial \bar{z}}{\partial x} = 0 \tag{A11}$$

at the boundaries.

APPENDIX 2

Here I derive local stability conditions for the equilibrium. Because the system of PDEs is linear, it is also possible to obtain a formal solution (e.g., using techniques such as separation of variables; Boyce and DiPrima 1986). The solution does not provide any more insight into the model's behavior though (unpubl. results), and therefore I present only the local stability analysis.

Suppose $\hat{z}_s(x)$ and $\hat{p}_s(x)$ are equilibrium spatial patterns of male trait and female preference. Consider the dynamics of a small spatial perturbation to both $\hat{z}_s(x)$ and $\hat{p}_s(x)$ denoted by $\epsilon_z(x, t)$ and $\epsilon_p(x, t)$. From system (13) and (14) we have that $\bar{z}_s(x, t) = \hat{z}_s(x) + \epsilon_z(x, t)$ and $\bar{p}_s(x, t) = \hat{p}_s(x) + \epsilon_p(x, t)$ satisfy

$$\frac{\partial(\hat{z}_s + \epsilon_z)}{\partial t} = \frac{\partial^2(\hat{z}_s + \epsilon_z)}{\partial x^2} + 2 \frac{d \ln n}{dx} \frac{\partial(\hat{z}_s + \epsilon_z)}{\partial x} + \alpha_1[(\hat{z}_s + \epsilon_z) - \theta(x)] + \alpha_2(\hat{p}_s + \epsilon_p) \quad \text{and} \tag{A12}$$

$$\frac{\partial(\hat{p}_s + \epsilon_p)}{\partial t} = \frac{\partial^2(\hat{p}_s + \epsilon_p)}{\partial x^2} + 2 \frac{d \ln n}{dx} \frac{\partial(\hat{p}_s + \epsilon_p)}{\partial x} + \alpha_1[(\hat{z}_s + \epsilon_z) - \theta(x)] + \alpha_3(\hat{p}_s + \epsilon_p), \tag{A13}$$

which simplify to

$$\frac{\partial \epsilon_z}{\partial t} = \frac{\partial^2 \epsilon_z}{\partial x^2} + 2 \frac{d \ln n}{dx} \frac{\partial \epsilon_z}{\partial x} + \alpha_1 \epsilon_z + \alpha_2 \epsilon_p \quad \text{and} \tag{A14}$$

$$\frac{\partial \epsilon_p}{\partial t} = \frac{\partial^2 \epsilon_p}{\partial x^2} + 2 \frac{d \ln n}{dx} \frac{\partial \epsilon_p}{\partial x} + \alpha_1 \epsilon_z + \alpha_3 \epsilon_p. \tag{A15}$$

Letting $\underline{\epsilon}(x, t) = [\epsilon_z(x, t), \epsilon_p(x, t)]^T$ be a vector of the male and female perturbations (T denotes transpose), equations (A14) and (A15) can be written as

$$\frac{\partial \underline{\epsilon}}{\partial t} = L[\underline{\epsilon}] + \mathbf{A}\underline{\epsilon}, \tag{A16}$$

where

$$\mathbf{A} = \begin{bmatrix} \alpha_1 & \alpha_2 \\ \alpha_1 & \alpha_3 \end{bmatrix} \tag{A17}$$

and $L[\cdot]$ is the linear differential operator

$$L[y] = \frac{\partial^2 y}{\partial x^2} + 2 \frac{d \ln n}{dx} \frac{\partial y}{\partial x}. \tag{A18}$$

If the equilibrium is locally stable, then the perturbation vector $\underline{\epsilon}$ must decay as $t \rightarrow \infty$. The fate of $\underline{\epsilon}$ can be determined by solving the system of PDEs (eq. A16)

The boundary value problem defined by

$$L[\phi(x)] = \lambda \phi(x), \tag{A19}$$

where λ is a constant, together with zero-flux boundary conditions, is a Sturm-Liouville eigenvalue problem (Birkhoff and Rota 1989). Writing it in Sturm-Liouville form gives

$$\frac{d}{dx} \left[n^2 \frac{d\phi}{dx} \right] = \lambda n^2 \phi. \tag{A20}$$

Therefore, all eigenvalues of the operator $L[\cdot]$ are real and discrete and they form an infinite sequence (Birkhoff and Rota 1989). Thus, a formal solution to equation (A16) has the form

$$\underline{\epsilon}(x, t) = \sum_{j=0}^{\infty} \underline{v}_j(t) \phi_j(x), \tag{A21}$$

where $\phi_j(x)$ and λ_j are the eigenfunctions and eigenvalues of the operator (A18) (i.e., they satisfy A19), and $\underline{v}_j(t)$ is a time-dependent vector satisfying

$$\frac{d \underline{v}_j}{dt} = (\mathbf{A} + \lambda_j \mathbf{I}) \underline{v}_j. \tag{A22}$$

Therefore, from equation (A21), the equilibrium will be stable to all small perturbations if and only if all of the functions \underline{v}_j decay to zero. For this to happen, we require that the largest eigenvalue of the matrix $\mathbf{A} + \lambda_j \mathbf{I}$ (denoted ρ_j^*) has negative real part for each j . To obtain simple conditions under which this will be true, I first show that $\lambda = 0$ is the largest eigenvalue of the differential operator (A19). Therefore, we simply require that the largest eigenvalue of \mathbf{A} has negative real part to guarantee stability against all small perturbations.

First, multiply both sides of equation (A20) by ϕ and integrate over the spatial domain to get

$$- \int_{\omega_1}^{\omega_2} n^2 \left(\frac{d\phi}{dx} \right)^2 dx = \lambda \int_{\omega_1}^{\omega_2} n^2 \phi^2 dx. \tag{A23}$$

Because the integral on the right side of (A23) is positive and that on the left side is nonnegative, the largest eigenvalue of the operator (A19) must be zero (and its eigenfunction is a constant). The remaining eigenvalues are negative, and therefore, all the eigenvalues can be ordered as $\dots \lambda_j < \dots \lambda_1 < \lambda_0 = 0$. Consequently, ρ_0^* (which is the largest eigenvalue of the matrix \mathbf{A}) is the largest eigenvalue all the $\mathbf{A} + \lambda_j \mathbf{I}$. This means that the equilibrium will be stable to all small spatial perturbations if and only if ρ_0^* has negative real part. This eigenvalue is given by

$$\rho_0^* = \frac{1}{2} (\alpha_1 + \alpha_3 + \sqrt{(\alpha_1 - \alpha_3)^2 + 4\alpha_1\alpha_2}). \tag{A24}$$

What is of most interest is the case where b is small because selection against the female preference is likely to be weak. In this case a first-order approximation of equation (A24) shows that \hat{z}_s, \hat{p}_s is a stable equilibrium if $B/G_z < 2c/a$.

APPENDIX 3

Here I derive equation (24) of the text. At equilibrium and with uniform population density, equation (13) can be subtracted from equation (14) to give

$$\frac{d^2 \hat{p}_s}{dx^2} - (\alpha_2 - \alpha_3) \hat{p}_s(x) = \frac{d^2 \hat{z}_s}{dx^2}. \tag{A25}$$

We can multiply both sides of (A25) by any function and integrate while still retaining the equality, and therefore

$$\int_{\omega_1}^{\omega_2} \left\{ \frac{d^2 \hat{p}_s}{d\xi^2} - (\alpha_2 - \alpha_3) \hat{p}_s(\xi) \right\} g(\xi, x) d\xi = \int_{\omega_1}^{\omega_2} \frac{d^2 \hat{z}_s}{d\xi^2} g(\xi, x) d\xi. \tag{A26}$$

Here the integration is over the spatial domain, the dummy variable of integration is ξ , and $g(\xi, x)$ is a two-variable function that will be chosen in such a way as to give a useful result. To simplify notation, define

$$k = \alpha_2 - \alpha_3 \tag{A27}$$

$$k = \frac{G_z}{D} \left(\frac{G_p}{G_z} - \frac{B^2}{G_z^2} \right) b, \tag{A28}$$

which is positive. Before choosing $g(\xi, x)$, I first evaluate equation (A26) more explicitly by integrating by parts and using the boundary conditions to get

$$-\hat{p}_s \frac{\partial g}{\partial \xi} \Big|_{\omega_1}^{\omega_2} + \int_{\omega_1}^{\omega_2} \left[\frac{\partial^2 g}{\partial \xi^2} - kg \right] \hat{p}_s d\xi = -\hat{z}_s \frac{\partial g}{\partial \xi} \Big|_{\omega_1}^{\omega_2} + \int_{\omega_1}^{\omega_2} \frac{\partial^2 g}{\partial \xi^2} \hat{z}_s d\xi. \tag{A29}$$

Now if we choose $g(\xi, x)$ so that it satisfies both

$$\frac{\partial g}{\partial \xi} \Big|_{\omega_1, \omega_2} = 0, \quad \text{and} \tag{A30}$$

$$\frac{\partial^2 g}{\partial \xi^2} - kg = \delta(\xi - x), \tag{A31}$$

where $\delta(\xi - x)$ is the Dirac delta function, (A29) then becomes (Greenberg 1971):

$$\hat{p}_s(x) = \int_{\omega_1}^{\omega_2} \{ \delta(\xi - x) + kg \} \hat{z}_s d\xi \tag{A32}$$

$$\hat{p}_s(x) = \hat{z}_s(x) + k \int_{\omega_1}^{\omega_2} g(\xi, x) \hat{z}_s(\xi) d\xi. \tag{A33}$$

Therefore, to get equation (24) of the text, we simply need to calculate $g(\xi, x)$ and show that $\psi(\xi, x) = -k \cdot g(\xi, x)$ is a probability density.

The function $g(\xi, x)$ is found by treating the cases $\xi < x$ and $x < \xi$ separately, and requiring that $g(\xi, x)$ be continuous in ξ at $\xi = x$. The boundary conditions (A30) along with this continuity condition at $\xi = x$ determine three of the four constants of integration. The fourth constant is determined by integrating equation (A31) from ‘‘just below’’, to ‘‘just above’’ x :

$$\int_{x-0}^{x+0} \left[\frac{\partial^2 g}{\partial \xi^2} - kg \right] d\xi = \int_{x-0}^{x+0} \delta(\xi - x) d\xi. \tag{A34}$$

‘‘Just below’’ (i.e., $x - 0$) and ‘‘just above’’ (i.e., $x + 0$) mean the limit as $\xi \rightarrow x$ from below and from above. Using the fact that g is continuous at $\xi = x$, equation (A34) evaluates to

$$\frac{\partial g}{\partial \xi} \Big|_{x-0}^{x+0} = 1, \tag{A35}$$

which gives the fourth condition required to determine g . Multiplying by $-k$ then gives ψ :

$$\psi(\xi, x) = \begin{cases} \frac{\sqrt{k} e^{-\sqrt{k}(x-\xi)} (e^{2\sqrt{k}(\omega_1-\xi)} + 1)(e^{2\omega_2\sqrt{k}} + e^{2x\sqrt{k}})}{2(e^{2\omega_2\sqrt{k}} - e^{2\omega_1\sqrt{k}})} & \text{if } \xi < x \\ \frac{\sqrt{k} e^{-\sqrt{k}(\xi-x)} (e^{2\sqrt{k}(\omega_1-x)} + 1)(e^{2\omega_2\sqrt{k}} + e^{2\xi\sqrt{k}})}{2(e^{2\omega_2\sqrt{k}} - e^{2\omega_1\sqrt{k}})} & \text{if } x < \xi \end{cases} \tag{A36}$$

It is easiest to interpret these expressions in the case where the boundaries are far enough apart that they do not have any effect ($\omega_1 \rightarrow -\infty$ and $\omega_2 \rightarrow \infty$). In this case we get

$$\psi(\xi, x) \approx \frac{\sqrt{k} \exp(-\sqrt{k}|x - \xi|)}{2}. \tag{A37}$$

APPENDIX 4

The particular form of sexual selection used in the text is one of several possibilities. Here I consider two alternatives and dem-

onstrate that most of the conclusions of the paper remain unchanged.

The model of the text assumes that the optimal female preference is zero. In many species it is probably more reasonable to assume that the female’s sensory system is such that the optimum preference is nonzero (Kirkpatrick and Ryan 1991). This can be modeled by changing equation (4) to

$$W_f(p) = -b(p - \gamma)^2, \tag{A38}$$

where γ is the optimal female preference resulting from natural selection. The selection gradient is then

$$-b(\bar{p} - \gamma). \tag{A39}$$

Using this it can be shown that system (13, 14) is unaltered except that α_4 is added to equation (13) and α_5 is added to equation (14), where

$$\alpha_4 = bB\gamma/D \quad \text{and} \tag{A40}$$

$$\alpha_5 = bG_p G_z \gamma / DB. \tag{A41}$$

Using these equations it can be shown that there is no $\theta(x)$ for which the equilibrium female preference is optimal everywhere (\bar{p}_s is never identically equal to γ). Also, the average preference over space at equilibrium (in terms of the nondimensional variables) is now $(\alpha_5 - \alpha_4)/(\alpha_2 - \alpha_3) = G_z \gamma / B$, and the average male maladaptation is $(\alpha_3 \alpha_4 - \alpha_2 \alpha_5)/(\alpha_1 \alpha_2 - \alpha_1 \alpha_3) = a\gamma / 2c$. The stability conditions for equilibrium remain unchanged. Lastly, we can calculate the expression for the equilibrium female preference. In terms of the nondimensional variables, it is

$$\hat{p}_s(x) - \gamma \frac{G_z}{B} = \hat{z}_s(x) - \int_{\omega_1}^{\omega_2} \psi(\xi, x) \hat{z}_s(\xi) d\xi. \tag{A42}$$

This shows that the quantitative conclusions of the text remain valid if the equilibrium female preference is measured as a deviation from its optimum. Notice, however, that the equilibrium male trait will now be different due to the additional strength of sexual selection that results from the females having a nonzero optimal preference. Consequently, although the relationship between female preference and male trait are the same (when preference is measured as a deviation from the optimum), the absolute pattern of preference may now be different. In particular, for small cost of female preference, expressions (29) and (30) are now

$$\hat{z}_s(x) \approx \frac{G_z c}{G_z c - aB} \int_{\omega_1}^{\omega_2} \tilde{\psi}(\xi, x) \tilde{\theta}(\xi) d\xi + \theta^* + \frac{a}{2c} \gamma \quad \text{and} \tag{A43}$$

$$\hat{p}_s(x) \approx \frac{G_z c}{G_z c - \frac{aB}{2}} \int_{\omega_1}^{\omega_2} \tilde{\psi}(\xi, x) \tilde{\theta}(\xi) d\xi + \frac{G_z}{B} \gamma. \tag{A44}$$

The model of the text also assumes an open-ended preference for more extreme traits. An alternative scenario is that there is an absolute preference by the females and that males that deviate from this phenotype do less well in the competition for mates. This can be modeled by changing equation (3) to

$$W_m(z; \bar{z}, \bar{p}) = -a(z - \bar{p})^2 - c(z - \theta)^2. \tag{A45}$$

The selection gradient is then

$$-a(\bar{z} - \bar{p}) - c(\bar{z} - \theta). \tag{A46}$$

In this case it is possible to show that the system of PDEs has the exact same form as equations (9) and (10), except with c replaced by \bar{c} , a replaced by \bar{a} , and $\theta(x)$ replaced by $\tilde{\theta}(x)$, where

$$\bar{c} = c + a, \tag{A47}$$

$$\bar{a} = 2a, \quad \text{and} \tag{A48}$$

$$\tilde{\theta}(x) = \frac{c}{c + a} \theta(x). \tag{A49}$$

Therefore, all conclusions remain the same, but with altered parameter values. It is possible to construct a model with both of the above alterations as well.