EVOLUTION

THE EVOLUTION OF FEMALE MATING PREFERENCES: DIFFERENTIATION FROM SPECIES WITH PROMISCUOUS MALES CAN PROMOTE SPECIATION

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Abstract.—Females of many species are frequently courted by promiscuous males of their own and other closely related species. Such mating interactions may impose strong selection on female mating preferences to favor trait values in conspecific males that allow females to discriminate them from their heterospecific rivals. We explore the consequences of such selection in models of the evolution of female mating preferences when females must interact with heterospecific males from which they are completely postreproductively isolated. Specifically, we allow the values of both the most preferred male trait and the tolerance of females for males that deviate from this most preferred trait to evolve. Also, we consider situations in which females base their mating decisions on multiple male traits and must interact with males of multiple species. Females will rapidly differentiate in preference when they sometimes mistake heterospecific males for suitable mates, and the differentiation of female preference will select for conspecific male traits to differentiate as well. In most circumstances, this differentiation continues indefinitely, but slows substantially once females are differentiated enough to make mistakes rare. Populations of females with broader preference functions (i.e., broader tolerance for males with trait values that deviate from females' most preferred values) will evolve further to differentiate if the shape of the function cannot evolve. Also, the magnitude of separation that evolves is larger and achieved faster when conspecific males have lower relative abundance. The direction of differentiation is also very sensitive to initial conditions if females base their mate choices on multiple male traits. We discuss how these selection pressures on female mate choice may lead to speciation by generating differentiation among populations of a progenitor species that experiences different assemblages of heterospecifics. Opportunities for differentiation increase as the number of traits involved in mate choice increase and as the number of species involved increases. We suggest that this mode of speciation may have been particularly prevalent in response to the cycles of climatic change throughout the Quaternary that forced the assembly and disassembly of entire communities on a continentwide basis.

Key words.—Female mate preference, mate choice evolution, mate tolerance, premating isolating barrier, reinforcement selection, reproductive character displacement, sexual selection, species recognition system.

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Speciation is ultimately the outcome of processes that influence which males and females can and will successfully mate with one another. Myriad processes can generate such reproductive isolation, and many of these result from mating decisions that males and females make about one another (Dobzhansky 1937; Mayr 1942, 1963). In many species, males promiscuously attempt to mate with females, often without regard to whether those females are conspecifics or closely related heterospecifics. In these species, female mating decisions based on male phenotypes will define both mechanisms of intraspecific sexual selection and prezygotic mating boundaries among biological species. Thus, the evolution of female mating decisions can play a crucial role in the origins of new species (Paterson 1978, 1993; Lande 1981, 1982; Kirkpatrick 1982; West-Eberhard 1983; Lande and

Kirkpatrick 1988; Andersson 1994; Turner and Burrows 1995; Payne and Krakauer 1997; Parker and Partridge 1998; Boake 2000; Coyne and Orr 2004; Gavrilets 2004).

Several important models hypothesize that genetic drift plays a strong role in generating differentiation of female mating decisions across populations (e.g., Lande 1981; Kirkpatrick 1982; Anderson 1994; Gavrilets 2004). However, mating preferences for conspecifics may sometimes conflict with species recognition signals (Boake et al. 1997; Pfennig 1998). Specifically, females may often find themselves in demographic and social situations where discriminating between conspecifics and heterospecifics may impart strong selection on aspects of their mate choice. For example, when a species colonizes a new area that is already occupied by closely related species, females may initially be courted pri-

marily by heterospecific males and only rarely encounter a conspecific male because of their low relative abundance. In the laboratory, female acquiescence to mating with a heterospecific male is often seen in no-choice breeding experiments (Crapon de Caprona 1986; Seehausen et al. 1997; for a field example see also Lushai et al. 2005), and females often become less selective when males with preferred phenotypes are absent (Bakker and Milinski 1991; Backwell and Passmore 1996; Bateman et al. 2001; Luttbeg et al. 2001). Many females may acquiesce to heterospecific matings in this situation and produce fewer or less-viable offspring than females that secure matings with conspecifics. This process then has the potential to cause female mating preferences to evolve in ways that would increase their discriminatory power between conspecific and heterospecific males. Specifically, females may experience strong selection on their preference for the male phenotype they find most attractive and their willingness to accept males that deviate from that phenotype. This selection on female choice could, in turn, impart indirect selection on male phenotypes to track evolving female preferences (e.g., Lande 1981). The outcome could presumably be the reproductive differentiation of the colonizing species from the local collection of heterospecifics and as a consequence from other populations of its own lineage as well (e.g., Hoskin et al. 2005).

If this process were repeated across the landscape with different collections of heterospecifics, it could be a strong impetus for speciation. Many lines of evidence suggest that speciation via such a mechanism may be common. First, frequent observations of paraphyly and polyphyly in species-level molecular phylogenies due to the introgression of alleles across species boundaries suggest that mating attempts between heterospecifics are not particularly uncommon (Funk and Omland 2003; Chan and Levin 2005). Second, such introgression of genetic material between species has often been asymmetrical; such asymmetrical introgression, particularly of maternally inherited genetic material (i.e., mitochondrial or chloroplast DNA), is expected when females of one species are rare and cannot find suitable (i.e., conspecific) mates and eventually acquiesce to matings with heterospecifics (Hubbs 1955; Wirtz 1999; Randler 2002; Lushai et al. 2005; for analogous arguments about plant hybridization see also Rieseberg et al. 1996). Third, sexual selection is recognized as a pervasive cause of speciation that has contributed substantially to the diversification of many taxa (Barraclough et al. 1995; Seehausen et al. 1997; Møller and Cuervo 1998; Arnqvist et al. 2000; Stuart-Fox and Owen 2003). Fourth, speciation is frequently associated with lineages colonizing new areas. In fact, some of the best examples of dramatic radiations appear to have been driven by sexual selection as lineages colonized new areas (e.g., lineages on islands [Hawaiian *Drosophila*: Kaneshiro 1983, 1988, 1989; Kaneshiro and Boake 1987; Hawaiian spiders: Gillespie 2004; Hawaiian crickets: Mendelson and Shaw 2005; Caribbean lizards: Losos 1998], cichlid radiations in the African rift lakes following their drying and refilling [Seehausen et al. 1997; Kornfield and Smith 2000; Turner et al. 2001; Verheyen et al. 2003; Salzburger and Meyer 2004]). Recolonization of deglaciated areas during the interglacial periods of the Quaternary (reviewed in Hewitt 1999, 2004) may also

have provided substantial opportunities for such mechanisms to generate new species on continentwide bases. Finally, climate change throughout the Quaternary would have repeatedly placed many species in demographic and social settings that should have favored such speciation as species moved around the landscape in response to glacial advance and retreat.

Females should obviously discriminate against males who would sire fewer or less-viable offspring with them. This issue usually arises in the context of reinforcement of partially differentiated incipient species (e.g., Dobzhansky 1940; Butlin 1987; Howard 1993; Kirkpatrick and Servedio 1999; Kirkpatrick and Ravigné 2002; Servedio and Noor 2003). Reinforcement hypothesizes that prezygotic isolating barriers should evolve between sympatric incipient species if these new species produce less-viable offspring when they hybridize. However, reinforcement selection acts only after lineages begin to diversify, and thus cannot initiate speciation. The mechanism we describe and analyze here is different from reinforcement. Like in reinforcement, mating interactions with promiscuous heterospecific males generate reproductive differentiation through direct selection on female preferences. However in the scenario we model here, new species are created by various populations of one species differentiating from one another because each interacts with a different combination of heterospecific species. Speciation is simply an evolutionary by-product of local mating interactions with various combinations of other species across the landscape—the mating equivalent of Thompson's (2005) geographic mosaic selection.

In this paper, we develop quantitative models that explore the dynamics of this scenario for one species that must interact with the promiscuous males of one or more closely related species. Our models elaborate previous work by Sved (1981a,b; see also Spencer et al. 1982) to explore the dynamics of evolution in both female preference for specific male phenotypes and female tolerance for males that deviate from the females' preferred male phenotype when females of a species must discriminate between conspecific and heterospecific males in making mating decisions. We find that female preference and tolerance rapidly evolve to permit discrimination between conspecific and heterospecific males, and as a result conspecific and heterospecific males will differentiate in the traits used by females to make mating decisions. If one species faced alternative species in multiple locations, this mechanism could rapidly generate reproductive isolation among these populations and thus lead to the rapid radiation of a lineage via sexual selection.

THE MODEL

Here, we consider the simultaneous evolution of male traits and female mating preferences for those traits. We consider a population of sexual diploid organisms with discrete, nonoverlapping generations. The population size is large enough to disregard the stochastic effects of random genetic drift. First, consider males that possess trait y, and females that base their mate choice decisions among males on the males' y values. The female trait x defines the male y value she most prefers. Each female has a function describing her preference

for a male's y trait; this function is given by ψ, such that the probability of a female with trait value x accepting a male with trait value y is proportional to ψ with a coefficient of proportionality being independent of x and y. We further assume that the tolerance of female discrimination among males is controlled by a second female trait α, which can also evolve. Trait α influences how rapidly a female's preference function ψ declines as the male trait deviates from her most preferred male type (i.e., x). A standard choice for ψ is a Gaussian function

$$\psi(x, y) = \exp[-\alpha(x - y)^2] \qquad (1)$$

(e.g., Sved 1981a,b; Lande 1981). Note that while x and y can take both positive and negative values, α is nonnegative. Smaller values of α imply larger female tolerances, whereas larger values of α imply stricter female mating preferences (Lande 1981). Note also that if the male and female traits differ by one unit, the female preference decreases by the factor $\exp(-\alpha)$. Another way to interpret α is to say that the difference between the male and female traits that reduces the probability of mating by the factor $1/e$ is equal to $1/\sqrt{\alpha}$. Throughout the paper we will refer to x as the female's preference and α as the female's tolerance.

This model postulates that premating reproductive isolating barriers can evolve among populations within a species because this species engages in local reproductive interactions with other species from which it is reproductively isolated by postmating barriers. That is, we consider "reproductive character displacement" in the terminology of Butlin (1987). Hereafter, we refer to the "focal" species—the species whose evolution we are tracking—and the "background" species—those species with which the focal species interacts. For simplicity, we do not allow the background species to evolve.

Consider a patch that supports populations of the focal species and one background species. The background species' males have distribution $F(y)$ for trait y, with mean Y and variance V. The focal species' males have distribution $f(y)$ for trait y, with mean $\bar{y}$ and variance G_y. We define p as the frequency of focal males among all males in the patch and $q = 1 - p$ as the frequency of background males. The frequency of males with trait value y among all males is then $pf(y) + qF(y)$, and the frequency of focal males having trait value y among all males is $pf(y)$. Let $g(x)$ be the distribution of the female trait x with mean $\bar{x}$ and variance G_x, and let $h(\alpha)$ be the distribution of the female trait α with mean $\bar{\alpha}$ and variance G_α. For simplicity, we assume that trait variances include only additive genetic components.

We assume that females accept males on the basis of their trait value y without regard to whether they are focal or background species. All females attempt to mate, but if a female chooses a background male, no offspring are produced and so her fitness is zero. The probability that a female with trait values x and α chooses a focal male is then

$$P(x, \alpha) = \frac{\displaystyle\int \psi(x, y, \alpha)pf(y)\, dy}{\displaystyle\int \psi(x, y, \alpha)pf(y)\, dy + \int \psi(x, y, \alpha)qF(y)\, dy}$$

$$\approx \frac{p\psi(x, \bar{y}, \alpha)}{p\psi(x, \bar{y}, \alpha) + q\psi(x, Y, \alpha)}, \qquad (2)$$

where the approximation assumes that the mating preferences are weak, so that ψ changes slowly over the range of possible trait values (simulation results show that this assumption of weak preferences is not critical). We assume that up to a common multiplier female fitness is

$$w_f(x, \alpha) = P(x, \alpha). \qquad (3)$$

This equation is justified if all females mate only once and the number of offspring produced by conspecific matings is the same for all females. Equation (3) is also compatible with multiple mating so long as fertilization by nonfocal male sperm is in proportion to mating frequency and results in inviability of that zygote. We also considered more elaborate mating models (e.g., sequential mate choice), but these also had little effect on the evolutionary dynamics and so are not presented (M. A. McPeek and S. Gavrilets, unpubl. results).

For a male of the focal species with trait value y, his fitness is the probability that he is chosen by a conspecific female:

$$w_m(y) = \iint \psi(x, y, \alpha)g(x)h(\alpha)\, dx\, d\alpha \approx \psi(\bar{x}, y, \bar{\alpha}). \qquad (4)$$

Assuming that the genetic variances G_x, G_y, and G_α remain constant and that the male and female traits are controlled by independent and unlinked loci, the dynamics of the mean trait values $\bar{x}$, $\bar{y}$, and $\bar{\alpha}$ can be approximated by Lande's (1976; see also Iwasa et al. 1991; Abrams et al. 1993) equations

$$\Delta\bar{x} = \frac{1}{2}G_s\left[\frac{d \ln w_f(x)}{dx}\right], \qquad (5a)$$

$$\Delta\bar{y} = \frac{1}{2}G_y\left[\frac{d \ln w_m(y)}{dy}\right], \quad \text{and} \qquad (5b)$$

$$\Delta\bar{\alpha} = \frac{1}{2}G_\alpha\left[\frac{d \ln w_f(\alpha)}{d\alpha}\right], \qquad (5c)$$

where the derivatives are evaluated at $x = \bar{x}$, $y = \bar{y}$, and $\alpha = \bar{\alpha}$. We will analyze these dynamical equations starting with the simplest case.

No Evolution in Female Tolerance

If female mating tolerance does not evolve (which is the case if for example genetic variation in α is absent, that is, if $G_\alpha = 0$), the dynamics of the mean trait values $\bar{x}$ and $\bar{y}$ are described by

$$\Delta\bar{x} = \alpha G_x(\bar{y} - \bar{Y})Q(\bar{x}, \alpha) \quad \text{and} \qquad (6a)$$

$$\Delta\bar{y} = \alpha G_y(\bar{x} - \bar{y}), \qquad (6b)$$

where $Q(\bar{x}, \alpha) = 1 - P(\bar{x}, \alpha)$ is the probability that an average female mates with a background male and $P(\cdot, \cdot)$ is defined by equation (2). Note that the rate of change of the female trait is larger when Q is larger (i.e., when females are interacting mostly with background males). Analysis of equations (6a,b) shows that the male trait evolves to match the female trait (so that $\bar{x} = \bar{y}$). If $\bar{x} \approx \bar{y}$, the difference between the focal species traits and the background male trait (i.e., $d = \bar{x} - \bar{Y}$) changes according to the equation

$$\Delta d = \alpha G_x \frac{d}{1 + \dfrac{p}{q} \exp(\alpha d^2)}. \qquad (7)$$

Equation (7) implies that the focal species' traits will continuously diverge from the background species, because d and Δd will always be the same sign. In other words, no equilibrium level of divergence exists. Also, the change in Δd will decelerate as the species diverge, because the magnitude of the denominator increases faster than the magnitude of the numerator with increasing $|d|$ in equation (7). One can find an approximate solution of equation (7). Specifically, using a rescaled dependent variable $u = \sqrt{\alpha}\, d$ and rescaled time $\tau = \sqrt{\alpha}\, G_x t$, the time to reach a prespecified value u is

$$\tau = \ln(u/u_0) - p/(2q)[Ei(1, -u^2) - Ei(1, -u_0^2)], \qquad (8)$$

where u_0 is the initial value of u and $Ei(a, b)$ is the exponential integral (Abramowitz and Stegan 1965). This equation shows that τ depends linearly on p and is sensitive to both α and G_x and to initial conditions. Numerical simulations starting with $\bar{x} \approx \bar{y}$ show two different phases in the dynamics of the system (Fig. 1). Initially, the female preference trait $\bar{x}$ rapidly diverges from Y, the average background male trait value, and this divergence in the female trait causes the focal male trait $\bar{y}$ to diverge from the background males as well. When the average female preference for the background males has dropped to near zero, the rate of divergence of female preference from the background male trait value then rapidly slows, but continues to diverge (Fig. 1).

Two of the most important parameters influencing the magnitude and rate of divergence are female tolerance (α) and focal male frequency (p). Broader female tolerance (i.e., smaller α, which produces a broader preference function $\psi(x, y, \alpha)$) results in greater differentiation between the focal and background species, but the dynamics of differentiation are slower (Fig. 2). Broader female tolerance means that females are more willing to accept males—focal or background—that deviate from their preferred phenotype. Therefore, with broader female tolerances, the focal species must differentiate to a greater extent from the background species to decrease the likelihood that focal females will choose background males as mates. However, broader tolerance slows this differentiation process because females of all phenotypes are making more mating mistakes until the species are somewhat differentiated.

If focal males are rarer (i.e., smaller p), reproductive differentiation of the focal species from the background species progresses farther and more rapidly (Fig. 2). Having a lower frequency of focal males in the population means that fewer females overall will choose mating partners with which they can produce offspring, but the difference in the likelihood that females with extreme preferences will choose focal males as compared to females with preferences nearer the background males' phenotypes increases as p decreases. Lower p thus speeds the rate of evolution, because females with extreme preferences will contribute relatively more offspring each generation. This pushes the focal species farther away from the background species, because the greater difference in female preference ($\bar{x}$) and the background male phenotype
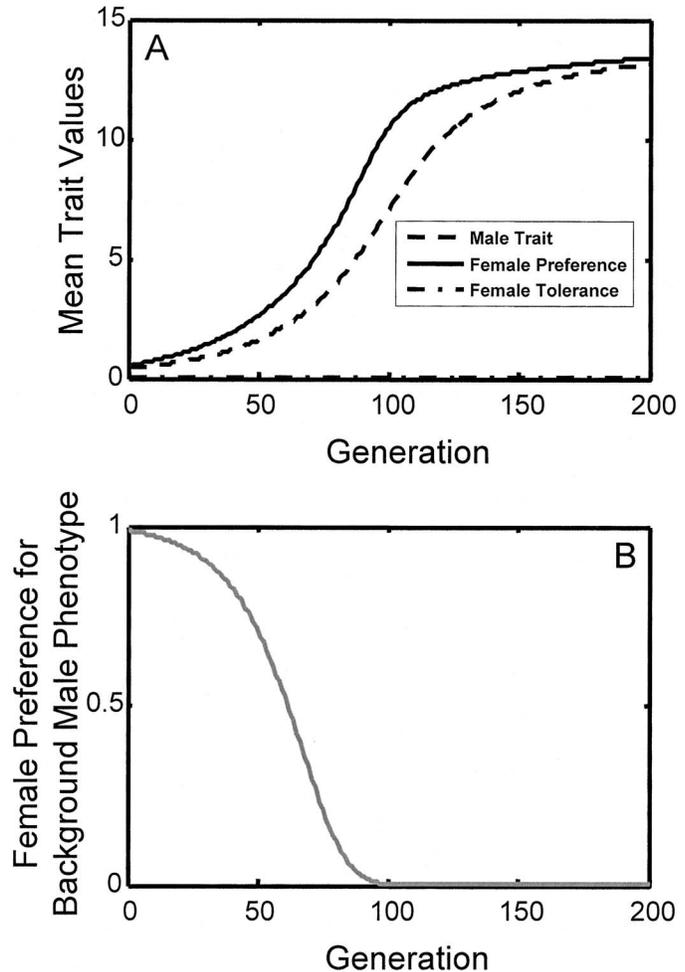

FIG. 1. Dynamics of the female preference trait x, the male trait y (A) and the preference of the average focal female for background males (B) over 300 iterations of the model specified by equations (6a,b) when the female tolerance trait α is not allowed to evolve (by setting $G_\alpha = 0$). For this simulation, the female tolerance trait $\alpha = 0.05$ throughout, the genetic variances $G_x = G_y = 1.0$, the frequency of focal males $p = 0.01$ throughout, and the background males have $Y = 0.0$.

(Y) is needed to offset the likelihood of encountering a focal male.

Changing Population Size

The relative frequency of a species is unlikely to remain constant over many generations, particularly when a species colonizes and becomes established in a patch. To explore this population dynamic process, we also considered situations in which p increased over generations. For simulations, we assumed that p changed in a logistic fashion using the Beverton-Holt model (Turchin 2003):

$$p_{t+1} = \lambda p_t[1 + p_t(\lambda - 1)/p_\infty], \qquad (9)$$

where λ is the rate of increase in p, and p_∞ is the maximal p value. This assumes that the abundance of the background species remains constant through time. Allowing p to change introduces no new dynamics into the problem; it merely influences whether the focal species will be evolving more at
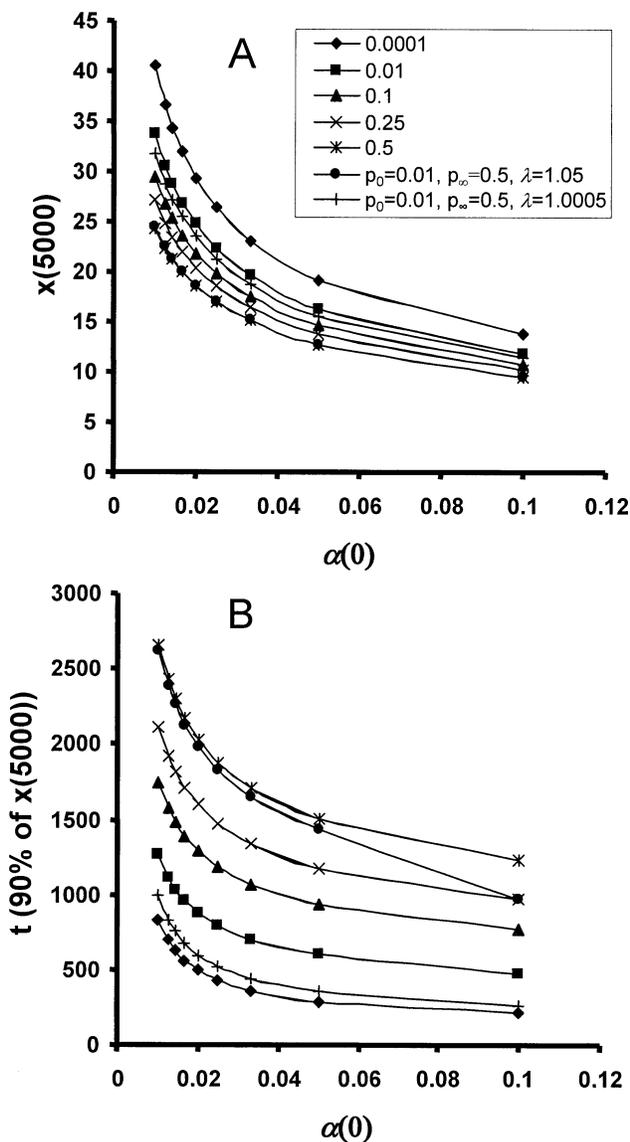
FIG. 2. Results of numerical simulations showing the magnitude and rate of differentiation between the focal and background species when female tolerance is not allowed to evolve. (A) The value of the female trait x after 5000 iterations for different frequencies of focal males (see legend: note that the last two parameter sets identify results from simulations in which p increases according to the Beverton-Holt model) and different values of female tolerance α (x axis). (B) The iteration in which female preference x reaches 90% of the value it will have after 5000 iterations. This value scales with the transition from rapid divergence to slow divergence seen in Figure 1.

FIG. 3. Dynamics of the female preference trait x, female tolerance trait z, and the male trait y (A), and the preference of the average focal female for background males (B) over 200 iterations of the model specified by equations (6a,b,c) when the female tolerance trait z is allowed to evolve. For this simulation, the same parameters were used as in Figure 1, except that $G_\alpha = 0.01$.

low or high relative frequency. When p increases slowly, results of simulations are similar to those with constant and low p values; and when p increases more rapidly, results are more similar to those with constant and high p values (Fig. 2). Thus, a species that colonizes a patch and increases slowly in abundance will differentiate faster and to a greater degree from a species that is already present than will a species that increases rapidly in abundance after colonization.

As expected, greater genetic variance in female preference (i.e., greater G_x) increases the rate of species differentiation,
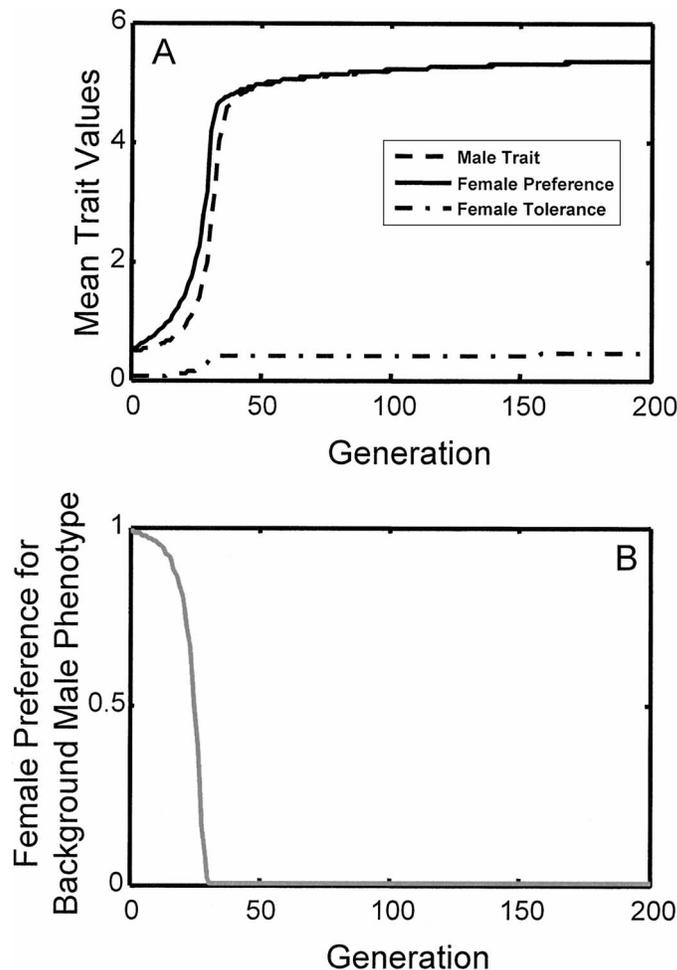
but it has little effect on the magnitude of differentiation. Also, as is evident from equations (6a,b) and (7), the genetic variance in the male trait y (i.e., G_y) directly controls the rate of change in the focal male's phenotype, but it has negligible effects on the magnitude of differentiation or rate of evolution of the female trait. The initial degree of differentiation between the focal and background species was also unimportant to the magnitude of differentiation achieved.

Evolving Female Tolerance

When female tolerance α is allowed to evolve, its dynamics are described by

$$\Delta\bar{\alpha} = G_\alpha(\bar{y} - Y)\left(\bar{x} - \frac{\bar{y} + Y}{2}\right)Q(x). \qquad (10)$$

The dynamics of $\bar{x}$ and $\bar{y}$ are defined by the same equations as before (i.e., eqs. 6a,b). This system of dynamic equations behaves the same as when α cannot evolve but differentiation occurs much more rapidly (Fig. 3). Again, the change in the
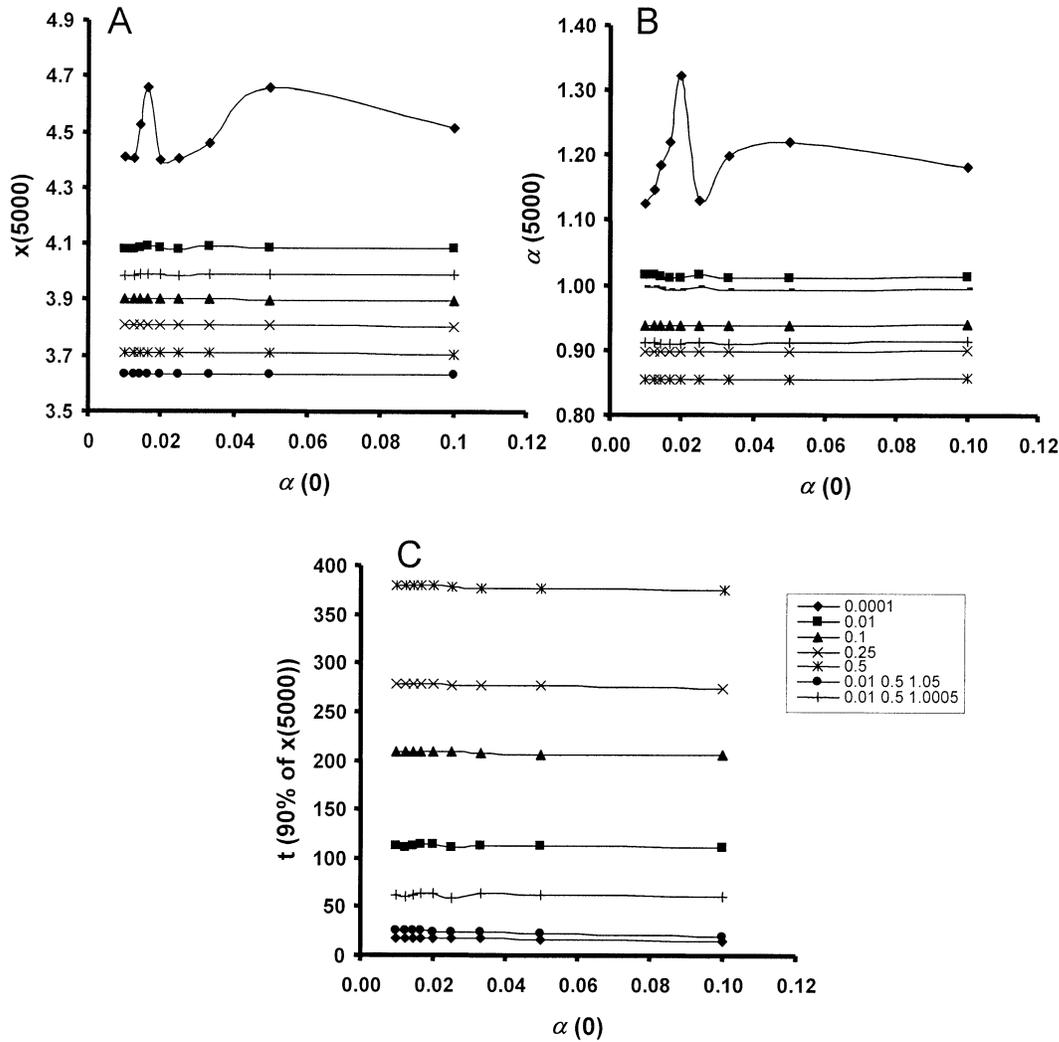
Fig. 4. Results of numerical simulations showing the magnitude and rate of differentiation between the focal and background species when female tolerance is allowed to evolve. (A) The value of the female trait x after 5000 iterations for different frequencies of focal males (see legend in B: note that the last two parameter sets give the values p_0 to p_∞ at a rate of λ, which describe the increase in p over the simulation according to the logistic function from p_0 to p_∞ at a rate of λ) and different values of initial female tolerance $\alpha(0)$ (x-axis). (B) The values of the female tolerance trait α after 5000 iterations. (C) The iteration in which female preference x reaches 90% of the value it will have after 5000 iterations. This value scales with the transition from rapid divergence to slow divergence seen in Figure 3.

female preference trait $\bar{x}$ is initially a rapid divergence from the background species' male mean trait Y until the preference of the average focal female for the background males is almost zero, with slow divergence thereafter (Fig. 3). Female tolerance changes slowly when the average female preference is near the background male trait, and the evolutionary rate of change in $\bar{\alpha}$ increases as the focal species diverges from the background species. Throughout, $\bar{\alpha}$ evolves to increase, which narrows the width of the average female tolerance function $\psi(\bar{x}, y, \bar{\alpha})$ and thus decreases female tolerance for males away from $\bar{x}$ (Fig. 3). As the average female's preference for background males approaches zero, change in female tolerance also slows appreciably (Fig. 3). Thus, the focal species reproductively differentiates from the background species by females evolving mating preferences that shift away from background males and being less tolerant of males

that deviate from their preference (i.e., more choosy in their mating preferences), and by focal males evolving to differentiate from background males because of the change in focal female preference.

When female tolerance can evolve, the focal species' traits do not differentiate from the background species as much as when tolerance is fixed, and the time required for differentiation is much shorter (cf. Figs. 2 and 4). Moreover, the degree and time required for differentiation is largely independent of the initial level of female tolerance (Fig. 4). As when female tolerances cannot evolve, decreasing the frequency of focal males increases the magnitude and pace of differentiation (Fig. 4). As expected, the relative magnitudes of the genetic variances in female preference and tolerance influence the magnitudes of change in these characters, but the degree of genetic variance in the male trait does not.

Two Background Species

Adding a second background species to the system can change the dynamics of the system appreciably. Assume that the males of the two background species have male trait distributions $F(y)$, with mean trait values Y_1 and Y_2 and their frequencies among all males are q and r, respectively, where $p + q + r = 1$. From this, the focal female preference function becomes

$$P(x) \approx \frac{p\psi(x, \bar{y}, \bar{\alpha})}{p\psi(x, \bar{y}, \bar{\alpha}) + q\psi(x, Y_1, \bar{\alpha}) + r\psi(x, Y_2, \bar{\alpha})}, \quad (11)$$

Let Q_1 and Q_2 be the probabilities that the average focal female mates with the average male from the first and second background species, respectively. These probabilities can be approximated as

$$Q_1 = \frac{q\psi(\bar{x}, Y, \bar{\alpha})}{p\psi(\bar{x}, \bar{y}, \bar{\alpha}) + q\psi(\bar{x}, Y_1, \bar{\alpha}) + r\psi(\bar{x}, Y_2, \bar{\alpha})} \quad \text{and} \quad (12a)$$

$$Q_2 = \frac{r\psi(\bar{x}, Y_2, \bar{\alpha})}{p\psi(\bar{x}, \bar{y}, \bar{\alpha}) + q\psi(\bar{x}, Y_2, \bar{\alpha}) + r\psi(\bar{x}, Y_2, \bar{\alpha})}. \quad (12b)$$

The traits in the focal species will then evolve according to

$$\Delta\bar{x} = \bar{\alpha}G_x[Q_1(\bar{y} - Y_1) + Q_2(\bar{y} - Y_2)], \quad (13a)$$

$$\Delta\bar{y} = \bar{\alpha}G_y(\bar{x} - \bar{y}), \quad \text{and} \quad (13b)$$

$$\Delta\bar{\alpha} = G_\alpha\left[Q_1(\bar{y} - Y_1)\left(\bar{x} - \frac{\bar{y} + Y_1}{2}\right) \right.$$
$$\left. + Q_2(\bar{y} - Y_1)\left(\bar{x} - \frac{\bar{y} + Y_1}{2}\right) \right]. \quad (13c)$$

Note that the rate of change in $\bar{x}$ and $\bar{\alpha}$ increase with increasing chances of mating with a background male (i.e., increasing Q_1 and Q_2). Equations (13a–c) define a dynamical system that does have equilibrium values for $\bar{x}$ and $\bar{y}$ at approximately:

$$\bar{x}^* = \bar{y}^* \approx \frac{qY_1 + rY_2}{q + r}, \quad (14)$$

which is the weighted average of the background male trait means. Numerical simulations show that this approximation is good when q and r are not too different. Simulations also show that this focal species' equilibrium is locally stable, with a domain of attraction that is often smaller than the interval (Y_1, Y_2) (Fig. 5). The degree of symmetry in the domain is defined by the relative abundances of the two background species, and the overall width of the attraction domain decreases with increasing female tolerance. The rate of approach to this equilibrium from within the domain of attraction depends on the distance between the background species' traits and female tolerance. If the background species' traits are relatively close to one another, the focal species will rapidly converge to the equilibrium. If they are far apart, the focal species may initially rapidly diverge from the nearer background species, and then slowly approach the equilibrium thereafter (i.e., with dynamics similar to the one background species case but slowly approaching an equilibrium).
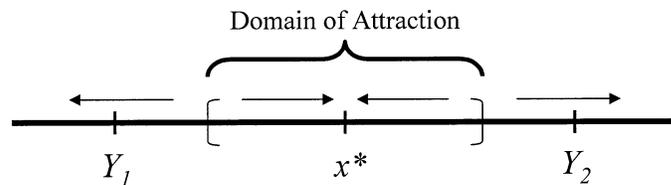

FIG. 5. Graphical representation of the equilibrium trait value for female preference when two background species are present in the system. Y_1 and Y_2 are the mean male trait values for background species 1 and 2, respectively. x^*, the locally stable equilibrium trait value for the focal female is located approximately at the weighted average of the background species traits. The boundaries of the domain of attraction are always closer to x^* than are Y_1 and Y_2, and the width of this attraction domain becomes narrower as female tolerance increases (i.e., α decreases).

The focal species evolves more quickly to the equilibrium when female tolerance is lower (i.e., α is larger).

Not surprisingly, if the focal species begins somewhere outside of the interval (Y_1, Y_2), it evolves away from the nearer background species with the same dynamics as if that were the only background species. Because the attraction domain is not coincident with the interval (Y_1, Y_2), two other areas exist in which the focal species may start between the two background species, but move away from the equilibrium (Fig. 5). In these areas, the focal species will initially evolve to become more similar to the nearer background species. These dynamics result from the differential abilities of focal females to discriminate among focal males and the two background males. Within the attraction domain and with $\bar{x} \approx \bar{y}$, focal females are able to discriminate among focal and both background males to some degree. In contrast, when the focal species is outside the attraction domain but still within the interval (Y_1, Y_2), focal females can much more easily discriminate focal males from the males of the distant background species, but males of the nearer background species are very similar in phenotype to focal males. As a result, selection on female preference, x, is dominated by the focal females' abilities to discriminate focal males from the distant background males. The focal species, therefore, initially evolves to become more similar to the nearer background species. As the focal species approaches the nearer background species, focal females become even less able to discriminate those males from focal males, which makes the repulsion by the distant background species relatively stronger. After the focal species passes the nearer background males to move outside (Y_1, Y_2), focal females experience selection to evolve in the same direction from interactions with both background species (i.e., away from both), and so the focal species then evolves as though it were evolving only in response to the nearer background species.

The evolution of female tolerance also has little effect on these dynamics. Female tolerance, α, always evolves to narrow the female preference function and follows dynamics similar to those seen in the one-background species case when the focal species is moving away from x^*. So, for example, when the focal species evolves to move out of (Y_1, Y_2), α does not change substantially until the focal species is past and rapidly differentiating from the nearer background spe-

cies. Within the domain of attraction, α also initially evolves to rapidly decrease, until focal females can effectively discriminate among focal males and both background males. After this, female tolerance continues to decrease at a very slow rate. This is true even after female preference reaches $\bar{x}^*$, because $\Delta\bar{\alpha} \neq 0$ at $\bar{x}^*$ (cf. eqs. 13a and 13c).

Multiple Correlated Traits

So far we have considered a single trait per individual and assumed that the traits expressed in males and females were not genetically correlated. However, females may base their mate choice decisions on more than one male trait. Such female mating decisions may consider traits that are largely independent both phenotypically and genetically (e.g., female birds may choose among males based on body size and wing color) or on multiple traits associated with one structure (e.g., females often base their mate choices on more than one aspect of a male's call or song; Ritchie et al. 2001; Gerhardt 2005). Using matrix notation, our approach can be generalized in a straightforward fashion for the case of multiple, genetically correlated characters.

Assume that mating probabilities depend on k male and k female characters. Let $\mathbf{x} = (x_1, \ldots, x_k)^T$ and $\mathbf{y} = (y_1, \ldots, y_k)^T$ be the vectors of female and male characters in the focal species, respectively. Let $\bar{\mathbf{x}}$ and $\bar{\mathbf{y}}$ be the vectors of the corresponding average values, and let $\mathbf{Y}$ be the vector of average male characters in the background species. The $2k \times 2k$ matrix of genetic covariances in the focal species can be written as

$$\mathbf{C} = \begin{pmatrix} \mathbf{C_{xx}} & \mathbf{C_{xy}} \\ \mathbf{C_{xy}} & \mathbf{C_{yy}} \end{pmatrix}, \tag{15}$$

where $\mathbf{C_{xx}}$ is a $k \times k$ matrix of covariances between female traits, $\mathbf{C_{yy}}$ is a $k \times k$ matrix of covariances among males traits, and $\mathbf{C_{xy}}$ is a $k \times k$ matrix of covariances among female and males traits. In the cases with $k = 1$ considered above, genetic variance in females G_x corresponded to $\mathbf{C_{xx}}$, and genetic variance in males G_y corresponded to $\mathbf{C_{yy}}$.

We assume that the preference function is given by a multidimensional generalization of equation (1), which we write as

$$\boldsymbol{\psi}(\mathbf{x}, \mathbf{y}, \boldsymbol{\alpha}) \sim \exp[-(\mathbf{x} - \mathbf{y})^T \boldsymbol{\alpha}(\mathbf{x} - \mathbf{y})]. \tag{16}$$

The symmetric, $k \times k$ matrix $\boldsymbol{\alpha}$ characterizes female mating tolerance. If the matrix $\boldsymbol{\alpha}$ is diagonal, different pairs of male and female traits contribute to $\boldsymbol{\psi}$ multiplicatively. Nondiagonal elements of $\boldsymbol{\alpha}$ control the degree to which different pairs of traits interact. With $k > 1$, we must postulate $k(k - 1)/2$ such traits (i.e., cells in $\boldsymbol{\alpha}$) scaling female tolerances for the various male traits. One way to interpret the multitrait function $\boldsymbol{\psi}$ is as fitness of potential mating pairs (Gavrilets 2004, ch. 2). Here, fitness depends on $\mathbf{x}$ and $\mathbf{y}$ only through their difference $\mathbf{d} = \mathbf{x} - \mathbf{y}$. Equation (16) defines a single peak fitness landscape with a maximum at $\mathbf{d} = 0$. The diagonal elements of $\boldsymbol{\alpha}$ define how quickly fitness falls off with a deviation from $\mathbf{d} = 0$ in the corresponding direction whereas the nondiagonal elements define the shape of slopes around $\mathbf{d} = 0$.

Using the same approach as above in the one-dimensional

case and for simplicity assuming no evolution in $\boldsymbol{\alpha}$ and all $\mathbf{C_{xy}} = 0$, we find that the changes in the vectors of average female and male trait values per generation are

$$\begin{pmatrix} \Delta\bar{\mathbf{x}} \\ \Delta\bar{\mathbf{y}} \end{pmatrix} = \begin{pmatrix} \mathbf{C_{xx}} & \mathbf{C_{xy}} \\ \mathbf{C_{xy}} & \mathbf{C_{yy}} \end{pmatrix} \begin{bmatrix} \boldsymbol{\alpha}(\bar{\mathbf{y}} - \mathbf{Y})Q \\ \boldsymbol{\alpha}(\bar{\mathbf{x}} - \bar{\mathbf{y}}) \end{bmatrix}, \tag{17a}$$

where

$$Q = \frac{q\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}, \boldsymbol{\alpha})}{p\boldsymbol{\psi}(\bar{\mathbf{x}}, \bar{\mathbf{y}}, \boldsymbol{\alpha}) + q\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}, \boldsymbol{\alpha})} \tag{17b}$$

is the probability that an average focal female mates with the average background male (cf. eqs. 17b and 6a).

The dynamics in the multidimensional case are qualitatively identical to those in the one-dimensional case. That is, male traits will evolve to match female traits, whereas female traits will evolve to move away from the trait values of background males. Also, as in the one-dimensional case, increasing Q, by either increasing the relative frequency of the focal males or increasing the likelihood that focal females will choose focal males over background males, slows the rates of evolution of both $\mathbf{x}$ and $\mathbf{y}$.

One interesting feature of the dynamics is that very small initial differences between the focal and background species have profound differences on the outcome of differentiation. For example, Figure 6 shows the results of several simulations all with identical parameters, but slightly different initial conditions. In each of these simulations, the focal species diverged from the background species to the same degree, but the direction of differentiation is based along the initial angle of difference between the focal and background species.

Multiple Traits and Multiple Background Species

Combining the above approaches, we can now write a two-trait/two-background species model:

$$\begin{pmatrix} \Delta\bar{\mathbf{x}} \\ \Delta\bar{\mathbf{y}} \end{pmatrix} = \begin{pmatrix} \mathbf{C_{xx}} & \mathbf{C_{xy}} \\ \mathbf{C_{xy}} & \mathbf{C_{yy}} \end{pmatrix} \begin{Bmatrix} \boldsymbol{\alpha}[(\bar{\mathbf{y}} - \mathbf{Y}_1)Q_1 + (\bar{\mathbf{y}} - \mathbf{Y}_2)Q_2] \\ \boldsymbol{\alpha}(\bar{\mathbf{x}} - \bar{\mathbf{y}}) \end{Bmatrix}, \tag{18a}$$

where

$$Q_1 = \frac{q\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}_1, \boldsymbol{\alpha})}{p\boldsymbol{\psi}(\bar{\mathbf{x}}, \bar{\mathbf{y}}, \boldsymbol{\alpha}) + q\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}_1, \boldsymbol{\alpha}) + r\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}_2, \boldsymbol{\alpha})} \tag{18b}$$

and

$$Q_2 = \frac{r\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}_2, \boldsymbol{\alpha})}{p\boldsymbol{\psi}(\bar{\mathbf{x}}, \bar{\mathbf{y}}, \boldsymbol{\alpha}) + q\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}_1, \boldsymbol{\alpha}) + r\boldsymbol{\psi}(\bar{\mathbf{x}}, \mathbf{Y}_2, \boldsymbol{\alpha})}. \tag{18c}$$

Numerical simulations of simple cases (e.g., no genetic correlations among traits, and off-diagonal elements of $\boldsymbol{\alpha} \approx 0$) show that the dynamics of this more complicated model are fundamentally the same as those of the simpler versions. An equilibrium exists on the line running between the two background species' phenotypes and at approximately the weighted average of their phenotypes, but in this case the equilibrium is unstable (Fig. 7). Altering the relative frequencies of the two background species moves the position of the equilibrium along the line. Again, a domain of attraction exists on this line between the background species and, if the focal species begins on this line and within the attraction domain, it will move to the equilibrium. Outside the attraction domain,
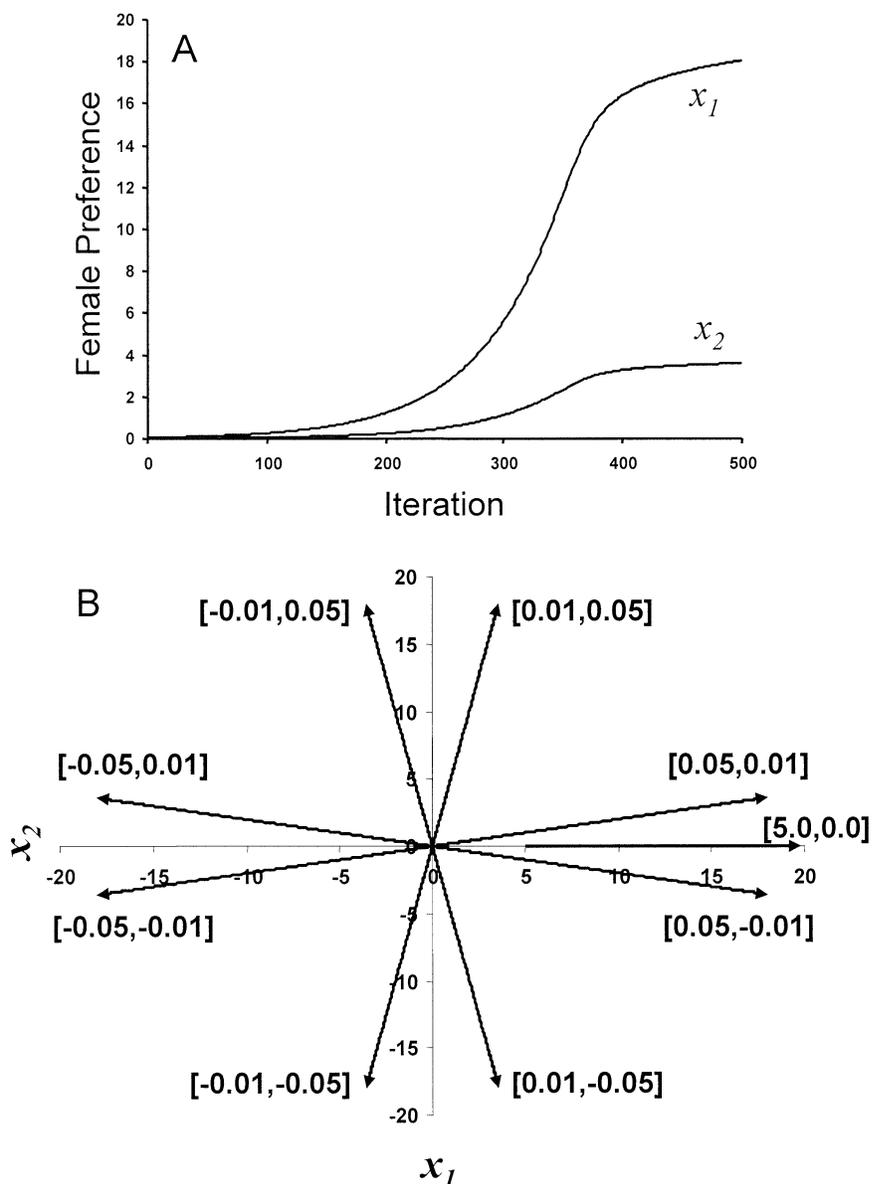
FIG. 6. The effects of initial conditions on the evolutionary trajectories of female preferences for the case where females base their mating decisions on two male traits. (A) The dynamics over 500 iterations of one simulation with initial conditions of [0.05, 0.01] for the x_1 and x_2 female preference traits. In (B) each line traces the trajectory for 500 iterations of a simulation where the starting conditions for the female preference traits are given in brackets next to the line. For these simulations, female tolerances were set at 5.0 for each character, genetic variances = 1.0 and covariances = 0.0 for male traits and female preferences, the relative frequency of the focal species was held constant at 0.01, and the background males had mean traits of [0.0, 0.0].

the focal species will evolve toward and then past the nearer background species, as in the one-trait case.

If the focal species' phenotype starts off the line connecting the two background species' phenotypes, it will diverge from the two background species, and its evolutionary trajectory will depend on its initial position (Fig. 7). The focal species will initially diverge from the nearer background species. If this initial trajectory approaches the line passing through the equilibrium and running perpendicular to the line connecting the background species' phenotypes, the trajectory will turn to asymptotically approach this line in the direction moving away from the equilibrium (Fig. 7). Otherwise, the focal spe-

cies will continue to diverge directly from the nearer background species.

DISCUSSION

For taxa in which promiscuous males of many species may attempt to mate with any given female, female discrimination among males has a high selective value. Females will be continuously harassed by males of many closely related species, and females must choose mates correctly to produce viable offspring. Our analyses indicate that equilibrium levels of differentiation only exist in special cases (e.g., in some
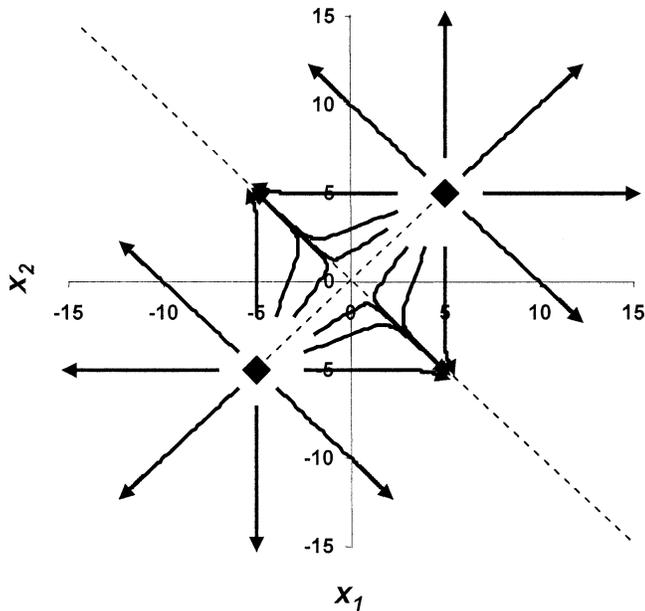
FIG. 7. The effects of initial conditions on the evolutionary trajectories of female preferences for the case where females base their mating decisions on two male traits and two background species are present. The diamonds identify the positions of the two background species phenotypes. Arrows show the dynamics of the two female preference traits (x_1 and x_2) over 500 iterations of one simulation from various initial phenotypes. For these simulations, female tolerances were set at 5.0 for each character, genetic variances = 1.0 and covariances = 0.0 for male traits and female preferences, the relative frequency of the focal species was held constant at 0.01, and the relative frequencies of the two background species were each 0.495.

cases when females base their mating decision on only one male trait), and so differentiation of species recognition systems (Paterson 1993) should usually be a continuous process among most species that are already postzygotically reproductively isolated from one another. When the distribution of heterospecific male traits overlaps significantly with females' preference functions and females will thus sometimes make mistakes, selection on both female preference and tolerance is intense because of the direct fitness consequences of mating mistakes, and differentiation of both female preference functions and male traits thus proceeds extremely rapidly. However, even when female preferences and heterospecific male traits are well differentiated, weak selection still acts on the position and shape of female preference functions to push them even further apart. Whether this weak selection after they are well differentiated will result in any appreciable evolution will depend on many other features of the biology of the species (e.g., other functions of the traits, genetic correlations with other traits, population size).

Our work builds on a model of reproductive character displacement introduced by Sved (1981a). In Sved's model, each individual is characterized by a single sex-specific quantitative character controlling the probability of mating with an individual of the opposite sex, and mating between individuals of different species is assumed to result in inviable offspring. We have generalized Sved's model by explicitly con-

sidering growing populations and the evolution of the male traits and by introducing multiple background species and multiple traits including those that control mating tolerance. Following Sved (1981a,b) and many others, we used the standard quantitative genetic approach assuming weak selection (e.g., Iwasa et al. 1991; Gavrilets 2000) and the constancy of relevant genetic variances (e.g., Lande 1981). The great advantage of this approach over alternatives (e.g., Liou and Price 1994; Kelly and Noor 1996; Servedio and Kirkpatrick 1997; Kirkpatrick and Servedio 1999; Kirkpatrick 2000, 2001; Servedio 2000; Pfennig and Ryan 2006) is its mathematical simplicity. Given the intuitive nature of our results on the evolutionary dynamics of the system studied and the rapidity of observed changes, we expect our results to be robust. This expectation is supported by a close correspondence of predictions based on analogous approximations and of individual-based simulations in related models of divergence driven by within-species between-sexes interactions (Gavrilets 2000; Gavrilets and Hayashi 2005). In addition, our general conclusions are completely consistent with those from a theoretical study of frog mate calling evolution using the framework of artificial neural networks (Pfennig and Ryan 2006).

During the rapid divergence phase, many features of the interacting species influence the rate, magnitude and direction of divergence. The primary feature is the degree of overlap of female preference functions with the phenotypes of heterospecific males they encounter. Assuming that the conspecific males' trait distribution tracks female preferences in the population, the degree of overlap between female preferences and heterospecific male traits defines the shape of the fitness function for females. Females with preferences in the tail of the distribution farthest from heterospecific males will make the fewest mistakes and so will have the highest fitness. With substantial overlap, the strength of selection will initially increase as the species diverge and the frequency of females making correct choices increases. As the population responds to this selection and more females can discriminate, the strength of selection then decreases and the rate of divergence slows (Figs. 1, 3). In this response, selection acts to push female preferences in the direction most directly away from heterospecific males and decrease female tolerances for more extreme male trait values. Obviously, genetic correlations among female traits describing their preference function or among male and female traits will deflect the response from this most direct path of differentiation (M. A. McPeek and S. Gavrilets, unpubl. data; Via and Lande 1985).

The magnitude of differentiation that will result depends critically on the initial female tolerance values and the degree to which female tolerance can evolve. With greater initial tolerance and if tolerance cannot evolve, the female preference function must evolve farther to achieve high success in female discrimination among conspecific and heterospecific males (Fig. 2). If female tolerance can evolve, much less differentiation is needed to achieve high discrimination success because female tolerance is narrowing as preference is differentiating (cf. Figs. 2 and 4 and note differences in abscissa scale). These results imply clear predictions about the degree of phenotypic diversity among species in reproductive characteristics for species that differ in the degree of female

mating tolerances: males of different species should be more differentiated from one another if females have broader intraspecific tolerances for males with various trait values.

The speed and magnitude of differentiation also depends on the relative frequency of conspecific males (Figs. 2, 4). When conspecific males are rare, fewer females will encounter conspecific males, let alone choose a conspecific as a mate. However, those few that do will have a substantial fitness advantage, and those with more extreme preferences are more likely to make correct choices. Thus, the relative frequency of conspecifics also influences the strength of the selection gradients on female preference and tolerance, with the strength of these gradients increasing as the relative frequencies of conspecific males decrease. This is a prime reason why this mode of reproductive differentiation should be most prevalent as a species colonizes new areas.

These results have direct implications for the rapid generation of reproductive isolation and thus the generation of new species by selection via the fitness consequences of female choice. As a species colonizes a new area with a new set of interacting species, differentiation from the local heterospecific assemblage may result in enough change to generate reproductive isolation from formerly conspecific populations in its ancestral area as well. Moreover, different populations of this colonizing species may differentiate in various phenotypic directions in different isolated patches across the new area, resulting in multiple new species. This may happen for two reasons: First, selection may push the focal species in different directions because it encounters different species assemblages in different patches across the new area. In addition, genetic drift during colonization may start populations of the focal species at slightly different positions in phenotype space, and small differences in initial conditions can have substantial consequences for the direction of differentiation (Fig. 6B). Thus, colonization of new areas may present lineages with substantial opportunities to radiate via the mechanism explored in these models.

A recent study of frogs illustrates the efficacy of the mechanism we have explored in initiating speciation. In a study of a hybrid zone between two hylid frog lineages, reinforcement selection in the contact zone between two partially postzygotically isolated lineages caused evolutionary changes in the calls used by males to attract females (Hoskin et al. 2005). Presumably, these changes in male calls were the result of strong selection on female preference functions to discriminate among males with which they would and would not produce many viable offspring. Differentiation in male calls in the contact zone also caused a substantial level of premating isolation from the ancestral lineages outside the contact zone (Hoskin et al. 2005). As well, differentiation of two spadefoot toad species in sympatry in the southwestern United States may also have been caused in part by such reproductive character displacement, but the degree to which this differentiation has affected reproductive isolation with allopatric populations is unclear (Pfennig and Pfennig 2005).

Indicators of sexual selection are generally associated with greater diversity in many animal clades (Barraclough et al. 1995; Seehausen et al. 1997; Møller and Cuervo 1998; Arnqvist et al. 2000; Stuart-Fox and Owen 2003). Moreover, many of the most spectacular radiations have occurred when taxa have colonized islands, and many of these radiations have been driven by sexual selection to diversify mate recognition systems. For example, sexual selection has played a substantial role in the radiations of several arthropod groups after they colonized Hawaii (*Drosphila*: Kaneshiro and Boake 1987; Kaneshiro 1988; crickets: Mendelson and Shaw 2005; spiders: Gillespie 2004). Sexual selection also appears to have strongly contributed to the radiation of cichlids after recolonizing the refilling African rift lakes about 20,000 years ago (Seehausen et al. 1997; Turner et al. 2001; Allender et al. 2003; Sturmbauer et al. 2003). For interactions with promiscuous, heterospecific males to have played a role in these radiations, multiple reproductively isolated lineages would have had to colonize these islands.

Although this mechanism is a possible contributor to these island radiations, the ecological and biogeographic conditions on continents throughout the Quaternary period would have been ideal for the operation of this mechanism. Over the past 1.8 million years, glaciers advanced and retreated on an approximately 100,00-year cycle (Lisiecki and Raymo 2005), and the associated global cyclical climate change must have repeatedly forced major range shifts in many species. These range shifts would have been most severe at higher latitudes, where each glacial advance denuded large swaths of the landscape and forced surviving species into isolated refuges surrounded by glaciers or to lower latitudes. Then when the glaciers receded, species would have followed the changing climate into higher latitudes to recolonize the empty landscape (e.g., Davis 1986; Delcourt and Delcourt 1991; Overpeck et al. 1992). Even at lower latitudes, glacial cycles caused climate change that forced range shifts in many species (e.g., McAuliffe and Van Devender 1998). The signatures of the latest range shifts can be found in the genetic population structures of many extant species (reviewed in Hewitt 1999, 2005). The paleontological record also shows that communities of species did not move en masse and intact. Rather, communities were being continually disassembled and reassembled into new constellations of species (Coope 1995, 2004; Graham et al. 1996). As a result, new sets of interacting species may have been continually thrown together, and those species would have had to adjust evolutionarily to the new selection pressures these interactions engendered. Sequential colonization of large areas of the continent would have provided ideal conditions for the interaction of multiple, reproductively isolated species within a lineage that may have been experiencing one another for the first time.

Many taxa also appear to have radiated during the Pleistocene (reviewed in Hewitt 2004). Ecological differentiation clearly played a substantial role in many of the speciation events in these radiations (e.g., McPeek and Brown 2000; Rundle et al. 2000), but sexual selection and mate recognition played a substantial role in many as well. For example, *Chrysoperla* lacewings speciated across North America and Eurasia, and this recent radiation appears to have been driven primarily by differentiation in courtship songs and little else (Henry et al. 1999). Males and females show strong mating fidelity to individuals of the opposite sex that sing the same song as they do, and many species in the radiation are identifiable only by their courtship song (Henry et al. 1999) Two

lineages of *Enallagma* damselflies also explosively radiated over the past 250,000 years to produce 18 extant species in eastern North America. Ecological differentiation can account for a few of these speciation events, but the ecological similarity of most extant *Enallagma* species suggests that differentiation in mate recognition was a prime mechanism generating new species (McPeek and Brown 2000; Turgeon et al. 2005). Likewise, Price et al. (2000) postulated that the radiation of *Dendroica* warblers in North America was driven mainly by sexual selection to produce many ecologically similar species. Breeding interactions during the repeated cycles of community assembly and disassembly may have put tremendous selection pressures on the mating preferences of colonizing females.

The processes that have created the biodiversity we study today did not operate on a static landscape, and that landscape continues to change. Heightened speciation rates and heightened extinction rates were the result of Quaternary climate change for many taxa as they were forced to migrate as their ecological surroundings changed. Human-mediated movement of species around the globe today may also be speeding both the extinction rates of local biotas due to these invasive species, but also imparting new evolutionary dynamics on both the natives and introduced species (Mooney and Cleland 2001; Strauss et al. 2006). Ecological adjustments are surely underway, but evolutionary adjustments in mating decisions may also be a necessary outcome as closely related species are brought into contact with one another. To study the past action of the mechanisms we explore in these models, we will have to rely primarily on indirect evidence, such as asymmetrical introgression, biogeographic reconstructions of speciation events, and short-term experiments of mate choice. However, the evolution of reproductive decisions in invasive species may offer new opportunities to test the mechanisms postulated here in real time.

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