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# Evolution of a Mate Recognition System after Hybridization between Two *Drosophila* Species

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**ABSTRACT:** I investigated the genetic relationship between male and female components of the mate recognition system and how this relationship influenced the subsequent evolution of the two traits, in a series of replicate populations of interspecific hybrids. Thirty populations of hybrids between *Drosophila serrata* and *Drosophila birchii* were established and maintained for 24 generations. At the fifth generation after hybridization, the mating success of hybrid individuals with the *D. serrata* parent was determined. The genetic correlation between male and female components of the mate recognition system, as a consequence of pleiotropy or tight physical linkage, was found to be significant but low ( $r = 0.388$ ). This result suggested that pleiotropy may play only a minor role in the evolution of mate recognition in this system. At the twenty-fourth generation after hybridization, the mating success of the hybrids was again determined. The evolution of male and female components was investigated by analyzing the direction of evolution of each hybrid line with respect to its initial position in relation to the genetic regression. Male and female components appeared to converge on a single equilibrium point, rather than evolving along trajectories with slope equal to the genetic regression, toward a line of equilibria.

**Keywords:** sexual selection, genetic correlation, pleiotropy, hybridization, *Drosophila serrata*, *Drosophila birchii*.

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The importance of sexual selection in speciation remains to be determined (Endler and Houde 1995). In particular, we need to determine the association between genes that underlie male and female components of the mate recognition system (Butlin and Ritchie 1989; Boake 1991) and how these associations subsequently evolve (Lande 1981; Kirkpatrick 1982; Barton and Turelli 1991), if we are to understand the evolution of sexual isolation as a consequence of sexual selection.

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For sexual isolation between two populations to occur, a new mate recognition system needs to evolve in at least one of the populations. Mate recognition systems can be divided into male and female components (representing a range of “signals” and “responses” between the sexes), which ensure mating between similar types and avoidance of dissimilar types. Two alternatives have been proposed that allow mate recognition systems to diverge but that enable the male and female components to remain coordinated (Butlin and Ritchie 1989; Boake 1991). The male and female components may share the same genetic basis (pleiotropy); therefore, a change in one directly results in a change in the other. Alternatively, male and female components may have a different genetic basis, and coevolution through sexual selection may maintain coordination (Lande 1981; Kirkpatrick 1982).

The genetic relationship between male and female components can be represented by the genetic correlation between them. Genetic correlation can arise between two characters as a consequence of pleiotropy or linkage disequilibrium (involving genes that are physically linked or unlinked). If the same genes underlie male and female components, a genetic correlation as a consequence of pleiotropy will be apparent in most instances (but not all; see Kearsley and Pooni 1996). If sexual selection maintains coordination between male and female components within populations, a genetic correlation will be generated between male and female components through linkage disequilibrium (Lande 1981). A genetic correlation as a consequence of tight physical linkage is an alternative explanation for an observed genetic correlation that is often difficult to discount.

Two main approaches have been used to determine whether male and female components are genetically correlated. First, many studies have investigated whether the mating preference of  $F_2$  or backcross interspecific hybrids changes as recombination reduces any linkage disequilibrium between male and female components (reviewed in Butlin and Ritchie 1989). However, under these conditions, any lack of segregation after one generation of recombination may indicate physical linkage be-

tween genes rather than a genetic correlation between male and female components as a consequence of pleiotropy. Second, traditional quantitative genetic techniques have been used to estimate the genetic correlation between male and female components (reviews in Pomiankowski and Sheridan 1994; Bakker and Pomiankowski 1995). Selection experiments or traditional breeding designs are unable to distinguish between pleiotropy and linkage disequilibrium as causes of genetic correlation. Pleiotropy is usually discounted as a likely cause of genetic correlation in these instances (Pomiankowski and Sheridan 1994), presumably since different morphological (male trait) and neurological (female preference) characters are assumed to be involved in male and female components (Lande 1981; Boake 1991). In contrast, pleiotropy is considered the most likely cause of genetic correlation in general (Falconer 1981) and, in particular, between life-history traits (Simons and Roff 1996) that also have very different phenotypes. The importance of pleiotropy in genetic correlations between male and female components of mate recognition remains to be directly tested.

Much recent theoretical effort has been directed toward determining the consequences of sexual selection maintaining coordination between male and female components when pleiotropy is absent (Lande 1981; Kirkpatrick 1982; Barton and Turelli 1991; Pomiankowski et al. 1991; Pomiankowski and Iwasa 1993). These models are concerned with the interaction between sexual and natural selection in determining the existence of stable evolutionary points between male and female components. If natural selection operates only on male sexually selected characters and not on female preferences, coevolution of male and female components is predicted to proceed along lines of the ratio of the covariance of male/female components on the genetic variance of the male trait (i.e., the genetic regression). In addition, both two-locus and quantitative genetic models predict a line of equilibrium, although apparently not for the same reasons (Barton and Turelli 1991). If natural selection operates on female preferences as well, the genetic regression is no longer a good predictor of the direction of evolution, and a line of equilibrium may collapse to one or a few points (Lande 1981; Barton and Turelli 1991; Pomiankowski et al. 1991).

I report an estimate of the genetic correlation between male and female components of the mate recognition system, in hybrids between *Drosophila serrata* and *Drosophila birchii*, using an experimental design that allowed five generations of recombination to reduce any linkage disequilibrium present. A small but significant genetic correlation as a consequence of pleiotropy (or tight physical linkage) was found. I then investigated the evolution

of male and female components by analyzing the direction of evolution of each hybrid line with respect to its initial position in relation to the genetic regression (Lande 1981). I show that evolution of male and female components may be proceeding toward a single point of equilibrium, rather than a line of equilibrium, which suggests that female preference may be under selection in this system.

## Methods

### Generation of Hybrid Lines

*Drosophila serrata* and *Drosophila birchii* have very different, but overlapping, geographic distributions and habitat preferences along the east coast of Australia (Dobzhansky and Mather 1961; Ayala 1965). Females are morphologically identical, and males can only be reliably distinguished by a single bristle difference on the genital arch (Ayala 1965). They are strongly sexually isolated from each other, with <1% of females capable of being inseminated by males of the other species (Dobzhansky and Mather 1961; Ayala 1965). In contrast, postmating isolation is very weak, as hybrids of both sexes are viable and fertile (Ayala 1965).

Thirty replicate hybrid populations between *D. serrata* and *D. birchii* were established and maintained for 24 generations. The stocks used to create the interspecific hybrids were each founded by four field-caught females collected in April 1995 from areas in north Queensland where the two species are sympatric. Hybridizations were conducted in August 1995 by placing approximately 50 virgin females of either species in a culture bottle with 50 virgin males of the other species. After 5 d, females were placed singly into vials to check for inseminations. Of 973 *D. birchii* and 1,028 *D. serrata* females tested, only one female from each of the reciprocal crosses produced progeny. From each female, 15 F<sub>1</sub> female progeny were collected as virgins and sib-mated to a single male. Each pair founded an isofemale line, 30 lines in total, which were maintained to the F<sub>24</sub>, in one culture bottle each, at  $N \approx 100$ .

The generation of the hybrid isofemale lines in this manner had a number of consequences for the genetic constitution of the lines. First, only a single mating from each reciprocal cross was used as a consequence of the difficulty in generating successful interspecific matings. This may have resulted in a reduction in the levels of intraspecific genetic variation present in the lines, but this loss of genetic variation would be expected to be small compared with the addition of the genetic variation between the two species. Second, full-sib mating occurred in the first two generations after hybridization. Assuming infinite population size in the F<sub>3</sub> generation and after, the

genetic covariance of the isofemale lines will be  $6/8V_a + 1/8V_d + 36/64V_{aa} + 6/64V_{ad} + 1/64V_{dd}$  (following Falconer 1981, p. 143). This covariance is similar to that of full sibs but has a higher proportion of additive-to-non-additive (dominance and epistatic) variance than do full sibs. The between-line genetic correlations estimated later therefore fall between the traditionally defined narrow and broad-sense genetic correlations.

#### *Measurement of Mating Success*

At the fifth generation, the mating success between male and female hybrids (H) and the parental species, *D. serrata* (S) and *D. birchii* (B), was determined. Mating success was measured as the proportion of five females inseminated by a single male in a vial. For each of the 30 lines, four test crosses were set up in this fashion (S female  $\times$  H male, H female  $\times$  S male, B female  $\times$  H male, and H female  $\times$  B male). For each test cross, eight replicate vials for each line were set up, resulting in 960 vials in total. The vials, each containing five virgin females and one virgin male, were placed at 25°C for 4 d. At the end of this period, each individual was placed in a well of a 24-well tissue culture plate that was half filled with medium. Plates were left at 25°C for a further 3 d and then scored for the presence of larval activity. At the twenty-fourth generation, the mating success of male and female hybrids with the *D. serrata* parent species was determined in the same way as in generation 5.

This measure of mating success has the advantage of not relying on a single behavioral mechanism that is thought to be associated with preference. Such behaviors are often labile (Wu et al. 1995) and do not describe the preference in toto. The disadvantage of this measure is that traits other than those involved in mate preference may contribute to it. For instance, mating success measured in this way may contain a component of larval viability, especially as interspecific hybrids are involved. To determine the impact of viability on the measure of mating success, the viability of lines was determined at the  $F_8$  generation by placing five eggs in each of nine vials for each isofemale line. The correlations between the line means for viability and the line means for mating success (representing genetic correlations) were not significant for both male and female components ( $r = 0.013$ ,  $P = .946$ ,  $N = 29$  and  $r = 0.154$ ,  $P = .424$ ,  $N = 29$ , respectively). This demonstrated that viability was not confounded with the mating success measure. Still other traits genetically correlated with mating success, which have not been investigated, may be confounded with the measure, such as sterility or other aspects of fertilization. Since the frequency of hybridization between the two parental species, as measured by the presence of sperm in

female reproductive tracts (Ayala 1965), is similar to that found when the hybrid lines were generated, immobilization of sperm or other fertilization or developmental problems before egg hatch do not appear to be important in this system. Sterility in hybrid individuals, however, cannot be discounted as a contributing factor to the mating success measure.

## Results

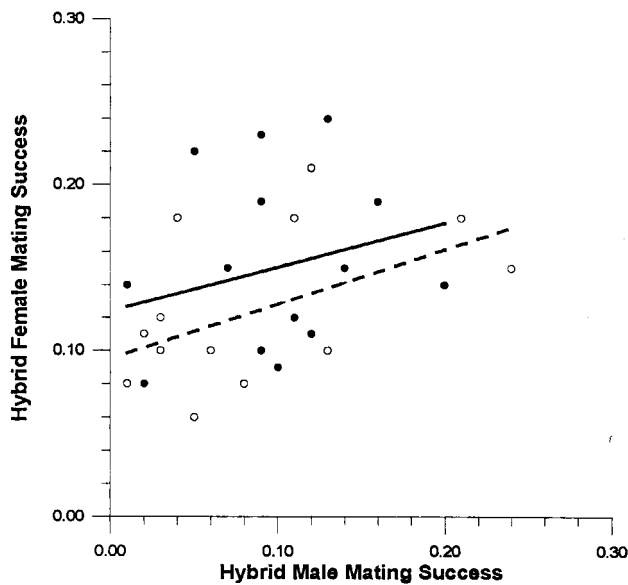
#### *Genetic Correlation between Male and Female Components*

The ability of the  $F_5$  hybrids to mate back to the parental species was highly asymmetric; only one female of 2,400 in the four test crosses involving matings with *Drosophila birchii* was inseminated. All subsequent analyses deal with the matings between the hybrids and the *Drosophila serrata* parent only. The means and variances of the isofemale lines for the proportion of the five females inseminated, based on the eight replicates for each treatment, were correlated, so all data were log-transformed using  $x' = \log_{10}(x + 1)$ , which removed the correlation. The male component of the mate recognition system, represented by the test cross S female  $\times$  H male, and the female component (H female  $\times$  S male), were tested for the presence of genetic variation by two nested ANOVAs (lines nested within reciprocal cross). The between-line component of variance was significant for both the male component ( $F = 5.46$ ,  $df = 28, 210$ ,  $P < .001$ ) and the female component ( $F = 3.08$ ,  $df = 28, 202$ ,  $P < .001$ ).

An approximation of the genetic correlation at the  $F_5$  generation, between male and female components, may be estimated by the product-moment correlation between the line means for S female  $\times$  H male and H female  $\times$  S male (Via 1984; fig. 1). Combining the data from the two interspecific reciprocal crosses gives  $r = 0.388$  ( $N = 29$ ,  $P = .038$ ), indicating that only 15.1% of the genetic variation in mating success, between the hybrids and *D. serrata*, is common between male and female components.

#### *Evolution of the Mate Recognition System*

The low genetic correlation between male and female components provided the opportunity to determine how coevolution would realign male and female components in subsequent generations when the contribution of pleiotropy was small. The positions of the hybrid populations at the twenty-fourth generation, relative to their initial positions at the fifth generation, are shown in figure 2A and B. The mean angle of the evolutionary trajectories for those lines that were initially below the  $F_5$  genetic regression (fig. 2A) was 26.1°, with a mean vector



**Figure 1:** The genetic relationship between the male and female components of the mate recognition system. The isofemale line means, on the transformed scale, for S female  $\times$  H male and H female  $\times$  S male, are plotted separately for the two interspecific reciprocal crosses; B female  $\times$  S male is indicated by solid circle/solid line; S female  $\times$  B male, open circle/dashed line. Only 29 of the 30 hybrid lines appear in this analysis, and two points are completely obscured by two other points in the figure (see fig. 2A for their position). ANCOVA indicated that the slopes of the two genetic regressions were not different (interspecific cross  $\times$  test cross interaction,  $F = 0.79$ ,  $df = 1$ ,  $26$ ,  $P = .382$ ), indicating that there is no sex-linked effect on this relationship.

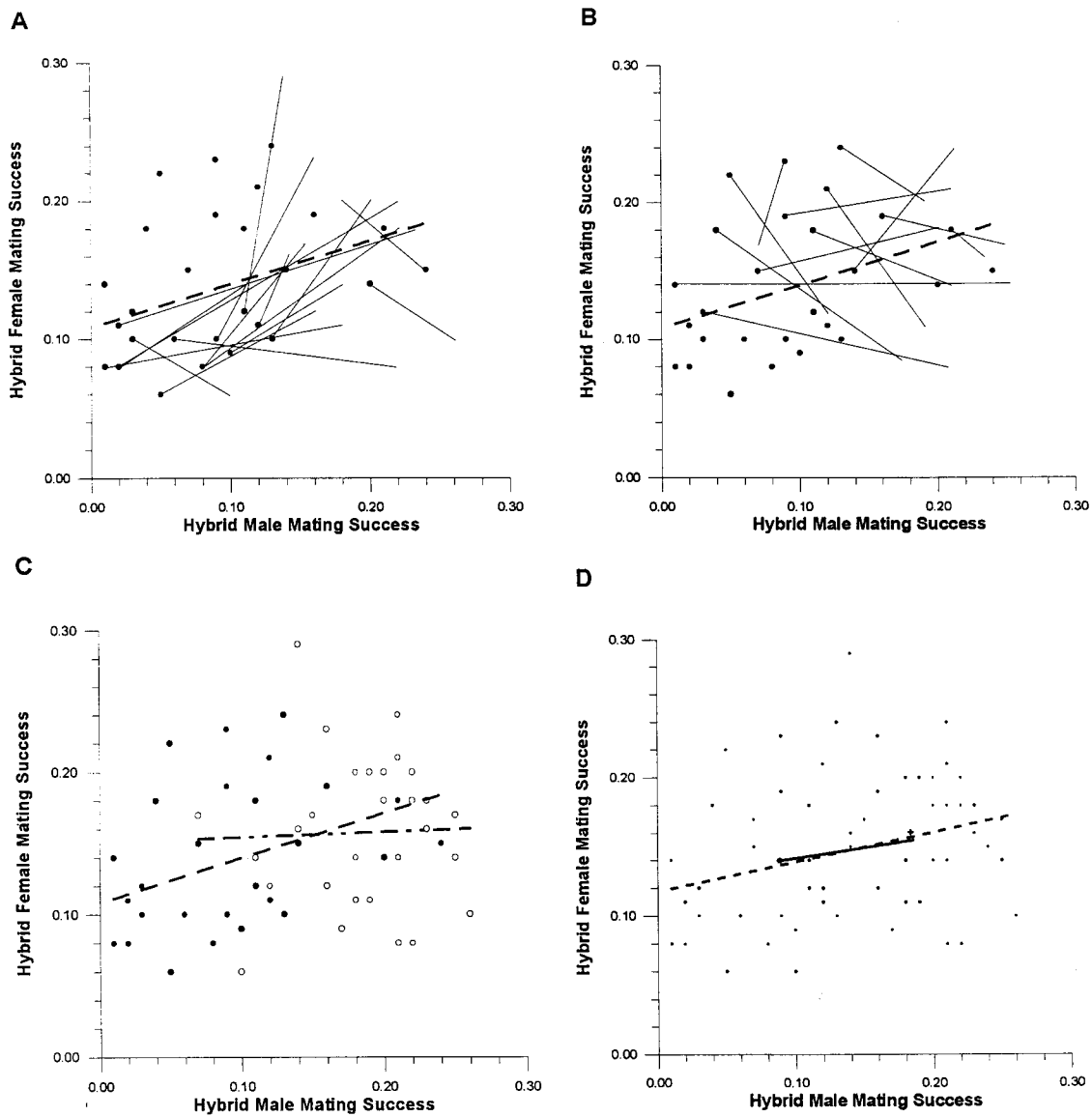
length of  $r = 0.82$ , and represented a significant mean direction (Rayleigh  $z$ -test,  $N = 16$ ,  $z = 10.76$ ,  $P < .001$ ). The mean angle of the evolutionary trajectories for those lines that were initially above the  $F_5$  genetic regression (fig. 2B) was  $-13.2^\circ$ , with a mean vector length of  $r = 0.80$ , and represented a significant mean direction ( $N = 13$ ,  $z = 8.32$ ,  $P < .001$ ). These two angles were significantly different (Watson-Williams test,  $F = 5.63$ ,  $df = 1$ ,  $27$ ,  $P < .02$ ), suggesting that female mating success was converging toward the  $F_5$  genetic regression. To ensure that this convergence was not simply a consequence of the tendency of a second sample to regress toward the mean, a two-sample  $t$ -test was conducted for each line to test for a difference in female mating success between the two generations. The combined probability (Sokal and Rohlf 1981) of these 29 tests ( $\chi^2 = 120.48$ ,  $df = 58$ ,  $P < .001$ ) indicated that female mating success significantly changed between the two generations; therefore, the convergence cannot be attributed solely to this tendency.

Before the similarity between the mean evolutionary

trajectory and the genetic regression could be investigated, the consistency of the genetic regression between the two generations needed to be determined (fig. 2C). ANCOVA indicated that the slopes of the two lines were not different (generation  $\times$  hybrid male mating success interaction term,  $F = 1.21$ ,  $df = 1$ ,  $54$ ,  $P = .275$ ). Since no evidence was found for the genetic regression varying between the  $F_5$  and  $F_{24}$  generations, the mean evolutionary trajectory was compared with the mean genetic regression (fig. 2D). The mean evolutionary trajectory, with a mean angle ( $\pm 95\%$  confidence limits) of  $8.9^\circ \pm 16^\circ$  and a mean vector length of  $r = 0.76$ , represented a significant mean direction (Rayleigh  $z$ -test,  $N = 29$ ,  $z = 16.75$ ,  $P < .001$ ). The angle of the mean genetic regression,  $12.8^\circ$ , lay within the 95% confidence interval of the angle of the mean evolutionary trajectory.

To determine whether an equilibrium position existed, the trajectory length of each population was compared with the distance of its initial starting point from the mean end point by linear regression. As populations started closer to the mean end point by chance, the trajectory length significantly decreased (linear regression,  $r^2 = 0.404$ ,  $F = 18.33$ ,  $df = 1$ ,  $27$ ,  $P < .001$ ). This indicated that the rate of evolution slowed as the populations approached the mean end point, suggesting an equilibrium position.

Although the evolutionary trajectories are represented as linear in figure 2, if female preference is under selection (as I have previously suggested), the direction of evolution may first follow the genetic regression until the line of equilibrium is approached, and then proceed along this line to the equilibrium point (Pomiankowski et al. 1991). Without data from multiple generations it is not possible to observe the evolution of the populations under this model. However, it is possible to determine whether the observed evolutionary trajectories resemble the genetic regression more closely than a trajectory of the resultant vector that this process would produce. To test whether the evolutionary trajectories were approaching a single point rather than a number of points along parallel lines with slope equal to the genetic regression, a comparison of the angular distances between the angle of each observed trajectory and the angle to the mean end point, with the angular distances between the angle of each trajectory and the angle of the slope of the genetic regression, was conducted. This analysis is represented in figure 3 by a comparison of the angular distances between the observed trajectory and trajectory 1, and the observed trajectory and trajectory 2. This analysis indicated that the angle of the evolutionary trajectory for each line was more similar to the angle to the mean end point than to the angle of the genetic regression (two-tailed Mann-Whitney  $U$ -test,  $U = 297$ ,  $df = 29$ ,  $29$ ,



**Figure 2:** Evolutionary trajectories of the hybrid populations. Those trajectories with initial points falling below the  $F_5$  genetic regression (A) and those falling above this line (B) are displayed separately for clarity. The initial position of each hybrid population ( $F_5$  generation) is indicated by a solid circle, and the final position ( $F_{24}$  generation) is indicated by the end of the vector, on the log-transformed scale. The genetic regressions for both generation  $F_5$  and  $F_{24}$  are displayed in C;  $F_5$  is indicated by solid circles/dashed line ( $y = 0.323x + 0.107$ ,  $F = 4.77$ ,  $df = 1, 27$ ,  $P = .038$ );  $F_{24}$ , open circles/dashed-dotted line ( $y = 0.040x + 0.150$ ,  $F = 0.04$ ,  $df = 1, 27$ ,  $P = .852$ ). The mean evolutionary trajectory, calculated as the mean angle of all population trajectories and originating from the mean initial point (*large solid circle*), and the mean genetic regression ( $y = 0.221x + 0.117$ ,  $F = 5.69$ ,  $df = 1, 56$ ,  $P = 0.020$ ) are shown in D. The mean end point is indicated by a cross.

$P = .055$ ). Therefore, if the direction of evolution was in the first instance along the genetic regression and then parallel to the line of equilibrium, these populations must have been well into this second phase to produce observed trajectories that are significantly different from the genetic regression.

## Discussion

### *Genetic Correlation between Male and Female Components*

The low but significant genetic correlation between male and female components of the mate recognition system

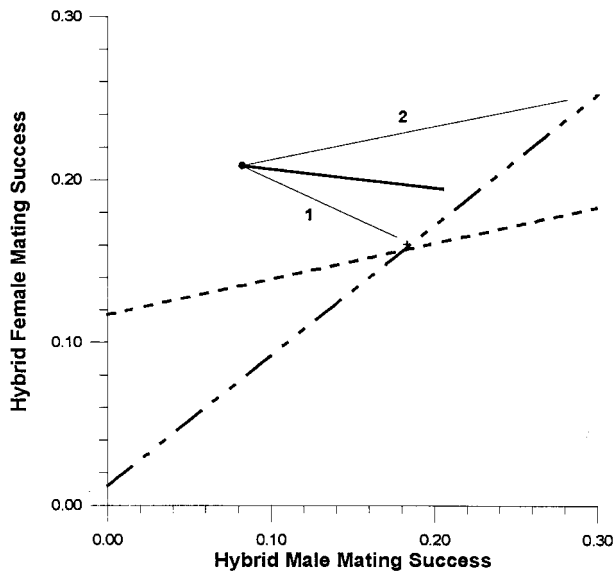


Figure 3: Schematic representation of the determination of a point of equilibrium. The thick dashed line is the genetic regression, and the mean end point is represented by a cross as in figure 2D. The thick dashed/dotted line represents an imaginary line of equilibria (Lande 1981), which passes through the mean end point. The thick solid line from the solid circle represents the evolutionary trajectory of a line from its initial starting point at generation 5. If no selection acts on female preference, the population may evolve along trajectory 2, with slope equal to the genetic regression. If female preference is under selection, the population may evolve along a resultant vector represented by trajectory 1, assuming the mean end point represents the equilibrium point. See the text for an analysis investigating the association between the observed evolutionary trajectories and trajectories 1 and 2.

suggests that pleiotropy may play only a minor role in the evolution of mate recognition in this system. Pleiotropy between male and female components has been assumed to be unlikely since different morphological and neurological characters may be involved in the two traits (Lande 1981; Boake 1991). Pleiotropy has been shown here to be relatively unimportant even though both male and female components are highly genetically correlated (on average, a genetic correlation of 0.84) with the same mechanism, cuticular hydrocarbons (M. W. Blows and R. A. Allan, unpublished manuscript). Therefore, even when the same mechanism may be involved in determining mate choice in both sexes, different genes may underlie the expression of the mechanism in males and females.

The presence of pleiotropy between male and female components, although minor, raises a complication for studies of the genetic basis of sexual selection. If pleiotropy is present, this may change the general expectation

of finding a positive genetic correlation between male and female components as a consequence of sexual selection. Alleles affecting two life-history traits in a positive fashion are expected to have a greater rate of fixation than alleles displaying positive effects on one trait and negative effects on the other, resulting in the evolution of antagonistic pleiotropy (Roff 1996). The evolution of antagonistic pleiotropy may also occur when the same alleles affect male and female mating success. The generation of positive genetic covariance through linkage disequilibrium (Lande 1981) may therefore be accompanied by negative covariance as a consequence of antagonistic pleiotropy. This argument does not apply to the estimate of genetic correlation from this experiment as it is a product of hybridization between two species; therefore, the alleles contributing to both traits have not evolved together for a sufficient time for this process to occur. It will, however, apply to estimates of genetic correlation made within populations using traditional breeding designs if pleiotropy is present between the two traits under consideration.

#### Evolution of the Mate Recognition System

The rate of evolution, and therefore the strength of selection, was greater in lines that at the  $F_5$  generation occurred farther away from the position of the grand mean of all lines at generation 24 (i.e., the mean end point). In addition, the angle of a line's trajectory was more similar, on average, to the angle of a line drawn from a line's  $F_5$  position to the mean end point than to the angle of the genetic regression. These results suggest that the mate recognition systems in the hybrid populations have evolved toward a single equilibrium point. I am unable to distinguish from these experiments whether the hybrid populations are evolving toward the equilibrium point that represents the *D. serrata* mate recognition system or a novel system combining components of both parental recognition systems (Wallace et al. 1983).

Models of sexual selection that predict single equilibrium points involve a cost to female preference (Lande 1981; Barton and Turelli 1991; Pomiankowski et al. 1991). Although selection on female preference may destroy the relationship between the direction of evolution and the genetic regression within populations, the mean direction of evolution between male and female components has been along the genetic regression between populations. The relationship between the mean evolutionary trajectory and the genetic regression is a consequence of the equilibrium point being close to the genetic regression. It is not clear at this stage whether the position of the equilibrium point is constrained to be close to the ge-

netic regression as a result of the hybridization process or whether this is a consequence of chance. One way to test this matter would be to change the selective optimum of the system. Given the involvement of cuticular hydrocarbons in the mate recognition system (M. W. Blows and R. A. Allan, unpublished manuscript), changing the temperature and humidity may alter the influence of natural selection, since cuticular hydrocarbons in *Drosophila* have been associated with the evolution of stress resistance in the laboratory (Toolson and Kuper-Simbron 1989). This may produce a new equilibrium position in the space described by figure 2.

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