A TEST FOR RARE MALE MATING ADVANTAGE WITH 
DROSOPHILA PSEUDOOBSCURA KARYOTYPES

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Manuscript received March 11, 1983
Revised copy accepted March 28, 1984

ABSTRACT

Recent work has called into question the reality of the rare male mating advantage, pointing out that it could be a statistical artifact of marking flies for behavioral observation or of experimental bias in collecting males. We designed an experiment to test for rare male mating advantage that avoids these sources of bias. Large numbers of males of three Drosophila pseudoobscura karyotypes were allowed to mate with females of one karyotype in population cages. The females were then isolated before multiple mating occurred and their progeny used to diagnose the males that mated them. Populations were studied at five sets of male karyotypic frequencies. The mating success of the male homokaryotypes ST/ST and CH/CH, relative to that of the heterokaryotype ST/CH, was frequency dependent. Both ST/ST and CH/CH males displayed a statistically significant mating advantage at low frequency by comparison with their mating success in the midrange of karyotypic frequencies. Both male homokaryotypes also showed a significantly greater mating success at high homokaryotypic frequency than at intermediate frequencies, which is the same as saying that the heterokaryotype not only failed to show a rare male advantage but actually suffered a mating disadvantage at low frequency. We conclude that rare male mating advantage is not always an experimental or methodological artifact but does occur in laboratory populations of D. pseudoobscura. It may occur for some genotypes and not for others, however, and it may be only one of several forms of frequency-dependent mating behavior operating in a population.

NATURAL selection is seldom constant. More often than not, it varies with physical and biological factors in the environment (AYALA and CAMPBELL 1974), and a particularly important class of variation is the dependence of selection on genotypic frequency. One of the best studied examples of this frequency-dependent selection is the rare male mating advantage in Drosophila. Males of a number of genotypes have shown a sizable increase in their mating success when their frequency is low, by comparison with their mating success when they are common. The rare male mating advantage has been reported for several Drosophila species and a variety of other organisms. The extensive literature on this subject has been summarized by PETIT and EHRMAN (1969), EHRMAN and PARSONS (1981), SPIESS (1970, 1982a,b) and BRYANT, KENCE and KIMBALL (1980).

As more examples of rare male mating advantage were published between 1965 and 1980, it began to seem as though this form of frequency-dependent sexual selection might be ubiquitous. Lewontin (1974) pointed out a conceptual problem with a general rare male advantage: since almost every male is rare for quite a few genes, the advantages of rarity at various loci would cancel, leaving a questionable net effect. The prevalence of rare male advantage is probably overstated in the literature, since experiments that fail to show it have undoubtedly suffered the fate of most negative results—they were not published. Several workers have recently addressed this problem by reporting their failures to detect rare male mating advantage (Markow 1978; Markow et al. 1980), and Spiess (1982a) devoted a section of his recent review of Drosophila mating behavior to negative results.

In the past few years the experimental evidence for the effect has been questioned on methodological grounds. Markow (1980) showed that the usual lab procedure for storing and retrieving flies to be used for studies of mating frequency may introduce a serious bias in favor of the rare male type. She found that active, vigorous males near the top of bottles were more effective maters than males from the bottom of the bottles. Since rare male types are used in smaller numbers than the common males, an experimenter may unconsciously choose flies near the top of a bottle, since they are easiest to reach, and thus bias the results toward a rare male mating advantage.

Bryant, Kence and Kimball (1980) pointed out that the process of marking flies in order to tell them apart, usually by clipping off a small piece of wing near the tip, may bias measurements of mating success. The usual method of measuring mating success in Drosophila is to place males and females of two types in a small observation chamber and then to record the matings that occur. Replicate chambers are set up, and in half of them one type of fly is marked, and in the other half the second type is marked. It was widely believed that rotating the marking between types this way averaged out any influence of the marking on mating behavior. Bryant, Kence and Kimball (1980), however, argued on the basis of a model for fly mating behavior that, whenever the sexual vigor of the two types of males fluctuates in replicate chambers, then the rarer type of male will be more successful in mating as the result of a statistical bias. Any effect of marking on the sexual vigor of males will intensify this bias in favor of rare males. Various aspects of this model have been criticized, defended, and discussed recently (Spiess and Dapples 1981; Bryant 1982; Leonard and Ehrman 1983; Knoppien 1984; Anderson 1984), and it is not clear how large an effect on average success is expected as statistical bias. Bryant, Kence and Kimball (1980), however, demonstrated a spurious rare male advantage in matings between geographic strains of the house fly, and they proposed that this type of statistical bias, accentuated by marking effects, could account for many of the reports of rare male mating advantage in the literature.

Ehrman and her colleagues have been among the most active workers on rare male mating advantage. Her studies date to the early 1960s, when Th. Dobzhansky, in the course of studies on gene arrangements in D. pseudoobscura populations, noted remarkable frequency changes that seemed to be the
result of a mating advantage of rare males. When a gene arrangement was rare among the adults of a population, its frequency among their larval offspring was often strikingly higher. EHRMAN et al. (1965) undertook behavioral observations on these D. pseudoobscura strains and found that the males did indeed have a mating advantage when rare. It is sometimes overlooked that EHRMAN’S research on rare male mating advantage was initiated with a combination of behavioral observations and population cage analysis. We decided to test for rare male advantage under circumstances like those in this early experiment, to see whether we could duplicate these early results. We used independently derived strains of D. pseudoobscura in large population cages, and we designed our experiment so that the rare males were not the most active ones and so that neither a procedure for marking the flies nor for replicate trials of mating behavior in observation chambers was involved.

**MATERIALS AND METHODS**

Unmated females of one karotype were placed in large population cages (25 × 30 × 40 cm) with males of three karyotypes. Cages were set up with male karyotypes in frequencies ranging from 9 to 90% (see Table 1). Mating was allowed for 1 day, after which the females were isolated in individual vials. The progeny of each female were used to infer the karyotype of the male mating her. Thus, the mating success of each male karyotype was determined at several male frequencies. These data permit a direct test of the hypothesis of rare male mating advantage, based on the frequencies of matings that actually result in offspring.

The number of populations we could study was limited, and we decided to test as many different frequencies as possible rather than to set up replicate populations for a smaller set of frequencies. Previous research has shown that mating success can vary significantly among replicate populations (ANDERSON and McGuire 1978). We reasoned, however, that any pattern of frequency-dependent mating behavior is unlikely to be the result of chance variations of mating success, and that we could obtain the greatest information by beginning our five populations at different frequencies.

Four strains of D. pseudoobscura isolated from a collection at Mather, California, in 1959 were utilized. Each of them was made homozygous for a single gene arrangement on a genetic background from the Mather population. These strains have been used in several population genetic studies (e.g., Pavlovsky and Dobzhansky 1966; ANDERSON et al. 1968; EHRMAN, ANDERSON and BLATTE 1977), and further details of their derivation are given in the first of these references. The gene arrangement of the third chromosome was the Standard (ST) type in two strains (nos. 292 and 300) and Chiricahua (CH) in the other two (nos. 249 and 252). The Amylase locus is on the third chromosome within the inverted region distinguishing ST and CH. ST chromosomes typically carry the Amy₁.⁰⁰ allozyme, whereas CH chromosomes carry Amy₈⁴ (PRAKASH and LEWON-
Since the ST and CH chromosomes differ by multiple inversions, recombination between them is eliminated, and the amylase alleles serve as convenient markers for the gene arrangements.

All of the flies used in our experiment were crosses between strains, so that, for example, the two ST lines were crossed to give ST/ST homokaryotypes. The three karyotypes should all have enjoyed any advantage of between-strain heterozygosity, although ST/CH was heterozygous for crosses between four strains, whereas ST/ST and CH/CH were heterozygous for two strains each.

Males and females for the experiment were etherized on collection and stored for 1.5-4 days under near-optimal conditions before being added, unetherized, to the cages. Special care was taken to avoid the "active male" bias reported by Markow (1980). Counted numbers of males were stored in yeasted bottles or vials, and whenever possible the entire set of males in a container was added as a unit to a population. When only some fraction of the males in a container was used, the bottle or vial was inverted to give the most active males a chance to crawl or fly upward. The males remaining at the bottom were removed by aspiration first, followed by males at progressively higher locations in the bottle or vial. If there were a bias in our procedure for selecting males, then according to Markow's (1980) results, it should have operated to lower the mating success of rare male karyotypes.

RESULTS

Results for the five cages used to test for rare male mating advantage are reported in Table 1. The three male karyotypes were added to the cages in Hardy-Weinberg proportions. We recovered 86% of the females put into the cages, and 56% of them produced offspring from matings in the cages. At the
TABLE 2

Analysis of male mating success

<table>
<thead>
<tr>
<th>Karyotype</th>
<th>ST/ST</th>
<th>ST/CH</th>
<th>CH/CH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Input male frequency</td>
<td>x</td>
<td>y</td>
<td>z</td>
</tr>
<tr>
<td>Relative male mating success</td>
<td>$M_\text{e}$</td>
<td>1</td>
<td>$M_\text{e}$</td>
</tr>
<tr>
<td>Expected mating frequency</td>
<td>$\frac{xM_\text{e}}{\bar{M}}$</td>
<td>$\frac{y}{\bar{M}}$</td>
<td>$\frac{zm_\text{e}}{\bar{M}}$</td>
</tr>
<tr>
<td>Observed mating frequency</td>
<td>$\hat{a}$</td>
<td>$\hat{b}$</td>
<td>$\hat{c}$</td>
</tr>
</tbody>
</table>

$\bar{M} = xM_\text{e} + y + zM_\text{e}$ and $N = \text{total number of matings observed}$

$\hat{M}_\text{e} = \hat{a}/(\hat{b} \hat{c})$ and variance $\hat{M}_\text{e} = \hat{M}_\text{e}^2 (1/\hat{a} + 1/\hat{b})/N$

$M_\text{e} = \hat{y}/(\hat{z} \hat{b})$ and variance $M_\text{e} = M_\text{e}^2 (1/\hat{b} + 1/\hat{c})/N$

Covariance $(\hat{M}_\text{e}, M_\text{e}) = \hat{M}_\text{e} M_\text{e}/(N\hat{b})$

The mating success of male karyotypes can be estimated according to the scheme in Table 2. The basic model is like that used to estimate viabilities (STAM 1971), and the same statistical methodology applies. Absolute mating success depends on the total number of matings recorded, which varies with environmental conditions in the cages and with success in collecting mated females and carrying out electrophoresis on their progeny. Measures of absolute mating success cannot be compared between cages unless these environmental and experimental factors are carefully controlled. Such control is difficult to achieve and, for our purposes, unnecessary. From the standpoint of population genetics, the parameters of interest, the ones that govern gene frequency changes, are the relative mating successes of the male karyotypes. Since the heterokaryotype is the only karyotype present in all of the cages, it was chosen as the reference karyotype, and the mating success of ST/ST or CH/CH homokaryotypes was estimated relative to that of ST/CH. $\hat{M}_\text{e}$ and $M_\text{e}$ are maximum likelihood estimators whose variances will asymptotically approach those given in Table 2 as sample size increases. Monte Carlo simulations of estimators like these, by ANDERSON (1969) and STAM (1971), provide evidence that our sample sizes are large enough that the variances calculated by these formulas should be reliable. The estimates $\hat{M}_\text{e}$ and $M_\text{e}$ are the same as PETIT’S coefficient of mating success, which is designed to compare the mating frequency of one Drosophila genotype to another in mating trials (see PETIT and EHRMAN 1969). We have written the variances and covariance of the estimators of mating success in Table 2 in the way we have in order to emphasize three relationships: a direct dependence on the square or product of the estimate itself, an inverse dependence on sample size, and an inverse relationship with the observed proportions of matings by the heterokaryotype and one of the homokaryotypes.
TABLE 3
Estimates of mating success (± standard errors) for the male homokaryotypes ST/ST and CH/CH, relative to that of the heterokaryotype ST/CH, at four homokaryotypic frequencies

<table>
<thead>
<tr>
<th>Cage</th>
<th>% ST</th>
<th>% ST/ST</th>
<th>ST/ST</th>
<th>ST/CH</th>
<th>CH/CH</th>
<th>% CH</th>
<th>% CH/CH</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>5</td>
<td>1</td>
<td>0.73 ± 0.16</td>
<td></td>
<td></td>
<td>95</td>
<td>90</td>
</tr>
<tr>
<td>II</td>
<td>30</td>
<td>9</td>
<td>3.69 ± 0.55</td>
<td></td>
<td></td>
<td>70</td>
<td>49</td>
</tr>
<tr>
<td>III</td>
<td>50</td>
<td>25</td>
<td>1.57 ± 0.20</td>
<td></td>
<td></td>
<td>50</td>
<td>25</td>
</tr>
<tr>
<td>IV</td>
<td>70</td>
<td>49</td>
<td>0.51 ± 0.07</td>
<td></td>
<td></td>
<td>30</td>
<td>9</td>
</tr>
<tr>
<td>V</td>
<td>95</td>
<td>90</td>
<td>2.57 ± 0.93</td>
<td></td>
<td></td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

* and ** indicate that two estimates of mating success for the same genotype at different frequencies differ at 0.05 and 0.01 probability levels.

The estimates of relative male mating success are presented in Table 3 with their standard errors (the square roots of the variances). The difference between two estimates of mating success for the same karyotype at different frequencies, e.g., $\hat{M}_i(1) - \hat{M}_i(2)$, was tested by

$$Z = \frac{\hat{M}_i(1) - \hat{M}_i(2)}{(\text{Var } \hat{M}_i(1) + \text{Var } \hat{M}_i(2))^{1/2}}.$$  

Under the null hypothesis that $\hat{M}_i(1) = \hat{M}_i(2)$, $Z$ will be normally distributed with unit variance.

Comparisons between the estimates of relative male mating success for ST/ST from one cage and CH/CH from another follow the same procedure. Comparisons between the relative mating success of ST/ST and CH/CH in the same cage must, however, incorporate the covariance between $\hat{M}_i$ and $\hat{M}_e$ so that

$$Z = \frac{\hat{M}_i(i) - \hat{M}_e(i)}{(\text{Var } \hat{M}_i(i) + \text{Var } \hat{M}_e(i) - 2 \text{ covar } (\hat{M}_i(i), \hat{M}_e(i)))^{1/2}}.$$  

The results of comparisons between the estimates of male mating success are indicated by asterisks in Table 3.

The frequencies of the ST gene arrangement in the long-term experimental populations begun with the strains used in the mating test are graphed in Figure 1. For comparison, ST frequencies in two similar cases studied in 1975 are also shown. The populations in 1975 were begun with five strains containing ST and five containing CH gene arrangements from Mather; the strains we utilized to test for rare male mating ability are a subset of these lines. Samples of between 100 and 150 salivary chromosomes were studied toward the end of the long-term cage experiment. No contaminant gene arrangements were found, and the frequencies of ST and CH observed cytologically were very close to those assayed by electrophoresis of adults reared from the same samples.
Fig. 1.—Frequencies of the ST gene arrangement in experimental populations of *D. pseudoobscura* containing ST and CH chromosomal lines used to test for rare male mating advantage. The populations in 1982 were begun with a subset of the same strains used to establish the populations of 1975. One generation is taken to be a month.

**DISCUSSION**

The main features of the results are apparent from a comparison of the input male frequencies and those in mating males, shown in Table 1, and from comparisons of the estimates of relative mating success shown in Table 3. The estimates and their variances permit us to test the statistical significance of differences in male mating success at various karyotypic frequencies. We did not test the patterns of matings observed in our experiment against expectations based on random mating, but, rather, we tested the mating success observed at one frequency against that observed at another. It would be unrealistic to test against the expectations based on random mating, since some karyotypes are "good maters" with relatively high mating success at all frequencies, including those in the intermediate range of karyotypic frequencies in which any frequency-dependence of mating may be weak or absent. And, of course, some karyotypes will be "poor maters" with relatively low mating suc-
cess at all frequencies. Frequency dependence can best be assayed by comparing the values of mating success measured at several karyotypic frequencies.

Our null hypothesis was that mating success of the karyotypes was the same in the five populations initiated at different karyotypic frequencies. The comparisons among estimates of mating success in Table 3 lead us to reject it. The relative mating success of both homokaryotypes was frequency dependent, increasing significantly at the lowest homokaryotypic frequency and also at the highest.

The estimates of male mating success make it clear that the relative mating success of both homokaryotypes increased significantly as the homokaryotypic frequency decreased from the midrange of frequencies to the low frequency of 9%, that is, as each homokaryotype became a rare male type. At CH frequencies of 50 and 70%, corresponding to CH/CH frequencies of 25 and 49%, CH/CH males had significantly lower mating success than did either ST/CH or ST/ST males. The relative mating success of CH/CH males did not differ significantly at these two frequencies. At the CH frequency of 30%, CH/CH male frequency was 9% and it was the rare male. The CH/CH mating success at this frequency was more than threefold larger than its value at CH frequencies of 50 and 70%; this change in mating success was statistically highly significant. The mating success of CH/CH males did not differ significantly from that of the heterokaryotype when CH/CH was the rare male, so that the mating advantage of CH/CH males at the lowest frequency was just enough to make its mating success equal to that of the heterokaryotype.

The mating success of ST/ST males increased more than threefold as ST/ST frequency decreased from 49 to 25%, and then it increased another two-fold as ST/ST male frequency decreased from 25 to 9%. These changes were statistically highly significant.

It is particularly important to note that both homokaryotypes showed a highly significant increase in mating success as homokaryotype frequency decreased from the intermediate karyotype frequency to the low frequency. The mating advantage was not associated solely with vigor of one male type. Some studies of mating behavior have shown one-sided advantage, in which only one male type shows a higher mating success when rare. BRYANT, KENCE and KIMBALL (1980) attribute this one-sided advantage to a higher mating vigor of one male type. When this vigorous type is rare, its males will compete for mates predominantly with the weaker, common male type, and it is no surprise that the vigorous males show a rare mating advantage. As the vigorous males become more frequent, they will compete for mates more often with other vigorous males, and the mating advantage they enjoyed when rare will diminish. As the weaker male type becomes rarer, it will compete more frequently for mates with the vigorous male, and as a consequence it should show no rare mating advantage. In fact, it might be expected to show a rare mating disadvantage sometimes. PETERSON and MERRELL (1983) have reported just this situation with white-eyed males of D. melanogaster. Wild-type males showed a significant rare male mating advantage, but the white-eyed males showed a rare male disadvantage.
In cages I and V the homokaryotypes were at high frequency (90%) and the only other karyotype present was the heterokaryotype, which was rare at 10%. In cage I, CH frequency was 90%, and the mating success of CH/CH was statistically significantly higher than at CH frequency of 70%, for which CH/CH and ST/CH were about equally frequent. Another way of viewing these results is to say that the mating success of ST/CH relative to that of CH/CH males was significantly lower when ST/CH frequency was 10% and CH/CH was 90% than when ST/CH frequencies were either 42 or 50%.

Likewise, in cage V the frequency of ST was 95% and the mating success of ST/ST males was significantly higher than at the next lower frequency of ST (70%). Again, we may view these results in terms of the ST/CH karyotype: the heterokaryotype showed a significantly lower mating success, this time relative to that of the vigorous ST/ST males, than in cages III and IV, in which ST/CH frequencies were much higher.

The homokaryotypes, then, show a greater mating advantage at high frequency as well as at low frequency. This same pattern of frequency dependence was found by Petitt (1954, 1958) for white-eyed males of *D. melanogaster* in her early studies of sexual selection, which were the first to report a rare male mating advantage. Petitt's (1954, 1958) analyses of these results have been criticized by Merrell (1983), although Petitt (1984) argues that the rare male effect is indeed real. The first two papers reporting a rare male mating advantage in *D. pseudoobscura* (Ehrman et al. 1965; Ehrman 1966) also describe several cases of this sort.

The goal of our experiment was to determine whether the rare male mating advantage really exists, as it was first defined: as a kind of frequency-dependent selection resulting from the increased mating success of rare male types. Our test was at the population level, and we did not design our experiment to provide information on the specific mechanisms that bring about a rare male advantage. The matter of just what causes the rare male advantage is not resolved, and, indeed, it is likely that there is no single mechanism responsible for it. Some of the rare male effect may be the result of differences in the preferences of females for the male types which are present (O'Donald 1977). If a constant proportion of females prefers one type of male, a frequency-dependent selection favoring the rare males will result. We include such frequency-dependent effects in the rare male advantage, even though the female preferences that cause them are constant. What really matters in terms of the rare male effect is that a frequency-dependent mating success be produced, in this case by a fixed behavior of the females. Other behavioral mechanisms have been implicated in rare male mating advantage since the late 1960s and must account for a significant part of the effect. Ehrman (see Ehrman and Parsons 1981 for a summary) has shown that olfactory cues are used by *D. pseudoobscura* females to recognize male types, although auditory and tactile cues may also be involved to some extent. Mate recognition may involve different sets of cues in different species (Averhoff et al. 1979). Spiess (1968, 1982b; but see also O'Donald 1983; Partridge and Gardner 1983) proposed that the sequence of courtship by males plays an important role in the rare male ef-
fert—that females become conditioned against mating with the male types that first court them during their unreceptive period after eclosion. Since these males would usually be the more frequent type, the rare male type would gain a mating advantage when the females became sexually receptive. Probably a combination of specific mechanisms is responsible for the rare male mating advantage, and the set of mechanisms operating in one species may differ from that in another species.

The issues of methodological and statistical bias raised by Markow (1980) and Bryant, Kence and Kimball (1980) are justifiable concerns, and these authors have done population genetics a service by focusing attention on the manner in which tests of rare male mating advantage have been carried out. We chose an independent subset of the same genetic variants used in early studies of the phenomenon, and we designed a test for rare male mating advantage that was free of the methodological and statistical weaknesses of behavioral observations in mating chambers. There was a significant rare mating advantage for the D. pseudoobscura homokaryotypes in our populations but not for the heterokaryotypes. We conclude that the rare male advantage does occur in laboratory populations of D. pseudoobscura, apart from any statistical or experimental biases of previous studies.

Why the heterokaryotype should fail to show a rare male mating advantage under conditions in which the two homokaryotypes did show such an effect is not apparent, although as mentioned before, others have found similar patterns of matings with D. pseudoobscura and D. melanogaster. Perhaps we should not be surprised that a process so complex as mating does not strictly obey a simple set of rules, such as "rare males have a mating advantage." Rather, we should expect exceptions based on the strengths of the many possible behavioral interactions among genotypes.

The ST and CH strains used in these experiments are part of a larger set of strains whose mating behavior was studied in observation chambers by Ehrman, Anderson and Blatte (1977). Only the ST/ST and CH/CH homokaryotypes were studied in the mating chambers, so the results are unfortunately not comparable to our populations with all three male karyotypes present. In the mating chambers, ST/ST males showed a large and significant rare male mating advantage relative to CH/CH males, but the CH/CH males did not show a rare male advantage relative to ST/ST males.

Several studies (Anderson and Watanabe 1974; Anderson and McGuire 1978) have shown that male mating success is a major component of fitness for D. pseudoobscura karyotypes in experimental populations like those employed in this experiment, and Anderson et al. (1979) have provided evidence that it is a major component of fitness in natural populations as well.

As may be seen in Figure 1, the frequencies of ST in cages begun at low and high frequencies do not converge to a single equilibrium point but rather remain in a broad band of frequencies between 50 and 80%. This behavior is typical of ST and CH gene arrangements from Mather but differs from that for the same gene arrangements from Pinon Flats. ST and CH from Pinon Flats converge to an equilibrium frequency of about 70%, and it is this selec-
tion curve that is displayed so widely in textbooks as an example of genetic polymorphism under selection. The course of selection on the gene arrangements used in our 1982 test for the rare male advantage is quite similar to that on a larger set of strains in 1975 (Fig. 1).

Although CH/CH males were generally less successful maters than ST/ST males, their mating success was highest at the ST frequency of 70%, which falls within the range of frequencies eventually reached in the experimental populations. At this frequency, the rare CH/CH males enjoyed a mating advantage large enough to overcome their usual mating inferiority in relation to ST/ST males, and in fact at this frequency their mating success was statistically significantly higher than that of ST/ST males. The selection we have estimated for male mating success would contribute to an overall balancing selection over a wide range of frequencies but would not by itself keep ST from going to fixation at very high frequencies. Other components of fitness such as viability, fecundity developmental rate and competitive ability must come into play in determining the overall selection that acts to maintain the chromosomal polymorphism in experimental populations.

This paper was written during a sabbatical visit to the Genetics Department, University of California, Davis. We wish to thank Francisco Ayala and other members of the Department for their encouragement and hospitality. We are grateful to Francisco Ayala, Edwin Bryant, Lee Ehrman, Jack Leonard, Therese Markow, Claudine Petit, Eliot Spiess, and Michael Turilli for critically reviewing the manuscript. This work was supported by the National Science Foundation under grant DEB-7918493.

LITERATURE CITED


Corresponding editor: M. NEI