Letter to the Editor

DOES THE RARE MALE ADVANTAGE RESULT FROM FAULTY EXPERIMENTAL DESIGN?

"Rare male advantage" is a simple designation for a complex behavior exhibited by a number of animals. It was first described by PETIT (1951, 1954, 1958) and by EHRMAN (1966, 1968) in *Drosophila melanogaster* and *D. pseudoobscura*, respectively. It has subsequently been identified in other orders and phyla. When two strains of flies of the same species are present, the relative mating success of each strain of males is inversely related to that strain's relative abundance in the population. Thus, the more abundant variety in the experimental chamber will, on the average, mate less frequently than the rare variety. An extensive review of the prevalence and significance of such behavior is given in EHRMAN and PARSONS (1981).

KENCE and BRYANT have recently suggested that this apparent advantage is not a fundamental phenomenon but the result of a systematic bias in the experimental design (KENCE 1981; BRYANT, KENCE and KIMBALL 1980). Their suggestion is supported by an algebraic model, a computer model and experiments with *Musca domestica*. In this note we shall demonstrate that their model is fundamentally at odds with the actual behavior of the flies in *D. pseudoobscura* mating experiments.

KENCE and BRYANT assume that clipping the wings of the flies leads to a debilitation that affects mating behavior. They further assume that only this debilitation affects the observed mating frequencies. Thus, the apparent advantage of rare males is due to a weakness in experimental design. In their computer model (BRYANT, KENCE and KIMBALL 1980) the effect of this debilitation on the time dependence of mating is explicitly considered. This model has been the subject of a recent exchange of articles (SPIESS and DAPPLES 1981; BRYANT 1982). In our results, however, the females mate rapidly and quantitatively, so there is little information obtainable from such an analysis.

The algebraic model of KENCE (1981) considers the static end result of such debilitation on observed mating success. The model defines x and y to be the population frequencies of males of the rare (R) and common (C) strains, respectively. These are defined in equations 1 and 2, where n_i is the number of males of strain i. It can be seen that $(x + y) = 1$.

$$x = n_R/(n_R + n_C) \tag{1}$$

$$y = n_C/(n_R + n_C) \tag{2}$$

KENCE explicitly assumes that the "mating propensities" of the two strains are equal. (We have previously referred to this propensity as "vigor," but the term could be confusing in the current context. See LEONARD and EHRMAN 1976.) Thus, the expected mating frequencies should be equal to the population frequencies unless there is some special effect being observed.

The effect, according to the KENCE model, is that the debilitation due to wing clipping reduces the probability that the clipped males will mate. This reduction in mating probability is measured by the variable s. Although not explicitly stated in the original paper, it is clear that $0 \leq s \leq 1$. Equations 3 and 4 give the altered mating frequencies x' and y' when the rare male is clipped; m_i indicates the number of matings by males of strain i.

$$x' = m_R/(m_R + m_C) = x(1 - s)/(1 - xs) \tag{3}$$

$$y' = m_C/(m_R + m_C) = y/(1 - xs) \tag{4}$$

Once again it is clear that $(x' + y')$ is unity. KENCE gives similar equations for the case in which the common strain is clipped, but they are not necessary for our present purposes.

One direct consequence of the debilitation model is that no rare male advantage should be observed if only the rare strain is clipped. This can be seen by computing what KENCE has termed the "spurious frequency-dependent fitness" for this case. This is shown in equation 5; W represents the spurious frequency dependence.

$$W = (x'/y')(y/x) = 1 - s \tag{5}$$

Since $0 \leq = s \leq 1$, $W < 1$ except in the trivial case that $s = 0$. KENCE derives the value of W for the case in which the clip is alternated between the rare and common strains. In such cases a meaningful value of s always produces $W > 1$, so that an advantage is expected. In the present case, however, only a disadvantage should be observed.

To test equation 5 (and, by extension, the more elaborate equation of KENCE) we ran four chambers of 50 flies each using the wild-type *D. pseudoobscura* inversion types Arrowhead (AR) and Chiricahua (CH). These strains have been described in previous papers (see LEONARD and EHRMAN 1976). Wing clipping and mating trial procedures have been described by EHRMAN (1965, 1975). In each of two chambers the AR strain was rare and clipped; in the other two chambers CH was rare and clipped. The results of these experiments are presented in Table 1.

Clearly, the rare male advantage does not disappear when the rare males are clipped. The experimental value of W for the 100 matings is 3.40. This leads to an estimate of s of -2.4 which is nonsensical. If the model fails in such a simple case, its applicability to more complex cases is surely problematic.

The rare male advantage is clearly strong enough to override any debilitation due to the act of wing clipping. This result is not surprising in *D. pseudoobscura.*

TABLE 1

Outcome of mating trials with clipped rare males of the Arrowhead and Chiricahua strains of D. pseudoobscura[a]

		Fraction of rare males			
Clipped strain	No. of matings	In population (x)	Mating (x′)	W	χ_1^2
AR	50	0.20	0.60	6.0	50.00[b]
CH	50	0.20	0.32	1.9	4.50[c]
Summed	100	0.20	0.46	3.4	45.25[b]

[a] The simple χ_1^2 statistic was employed to compute the level of significance of the results.
[b] $P \ll 0.01$.
[c] $P < 0.05$.

In a recent paper ANDERSON (1983) analyzed the results of ANDERSON and EHRMAN (1969) to determine the effect of wing clipping on the results of mating. He found a debilitation of about 16%, which would lead (using KENCE's equation for *W* with an alternating clip) to a *W* of 1.008; the observed values were much higher. W. W. ANDERSON and C. J. BROWN (unpublished results) also showed that the rare male effect was observable in population cages in which *neither* strain was marked. The mating success was assessed in this case by electrophoretic analysis of the offspring.

Is the BRYANT-KENCE-KIMBALL model valueless? No. In *D. pseudoobscura*, for which there is a plethora of evidence for the importance of the rare male advantage, it does not accurately predict the mating behavior. However, in *M. domestica*, for which no rare male advantage has previously been observed, BRYANT, KENCE and KIMBALL were able to induce a rare male advantage by clipping the flies and then immediately conducting mating trials. By doing so they made full use of the debilitation factor. Thus, they have reemphasized an important potential experimental pitfall, namely, testing new species without controlling for clipping. We have previously commented on the importance of using healthy strains for which all females mate (LEONARD and EHRMAN 1976) and on the difficulty of interpreting experiments in which the experimental animals are mutilated (AVERHOFF *et al.* 1979). The KENCE-BRYANT-KIMBALL results provide ample evidence for our caveats.

The presence of a rare male advantage when only the rare strain is marked can serve as a stringent test of the presence of the behavior and adequately meet the problems noted.

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