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FREQUENT MULTIPLE INSEMINATION IN A NATURAL POPULATION OF *DROSOPHILA PSEUDOOBSCURA*

Fecundity of female *Drosophila* is an essential component of their fitness; fecundity in turn depends on the supply of sperm available to fertilize eggs. A female may mate repeatedly, replenishing her supply of sperm. How frequently this occurs in nature is presently unknown; here I report on the frequency of multiple insemination in a natural population of *D. pseudoobscura*.

Dobzhansky and Spassky (1967) showed that multiple insemination of *D. pseudoobscura* females is common in laboratory cultures. They placed females homozygous for the Standard, Arrowhead, and Chiricahua gene arrangements of the third chromosome in bottles or creamers containing males of these same three karyotypes. After 5 days, 65 of 138 females, or 47%, had mated with at least two different males; after another 5 days, 54 out of 97, or 56%, had done so. These estimates are conservative, since repeated matings with males of the same karyotype as the female will go unnoticed. Dobzhansky et al. (1963) attempted to measure the frequency of multiple insemination in nature by a technique employing the "sex-ratio" X-chromosome in *D. pseudoobscura*. They showed that a single father usually provided sperm for eggs laid by a female during a

24-hour period; only two of 98 females in their sample could be proven to have laid eggs inseminated by different males. Dobzhansky and Spassky (1967) found a wide variation in the frequency of sperm from each of the males who had inseminated the same female. The degree of sperm mixture is not known, nor is it known whether females copulate again only when their supply of sperm is low. Thus, eggs laid over a 24-hour interval may well come from a single male even if the female has mated several times.

In the past several years, I have been engaged in a survey of chromosome frequencies in natural populations of *D. pseudoobscura*. Typically, chromosomes of a single larva from the progeny of a female inseminated in nature are examined. When a sample of flies is small, however, it is necessary to examine eight or more larvae in the progeny of a single female and then infer the chromosomes of the female and the male or males with which she mated. If five or more different types of chromosomes are seen, the female clearly laid eggs fertilized by more than one male. Similarly, double inseminations are indicated when four different chromosome polymorphs are present in a culture with at least one homokaryotype. Only in cultures with four or more different types of chromosomes can multiple inseminations be detected. And, the more polymorphic the population, the more readily will multiple inseminations be ascertained.

A collection of *Drosophila* was taken at San Gabriel Canyon, near Riverside, California, early in April 1973 by Professor Dobzhansky. Females were placed singly in culture bottles and allowed to lay for 10 days. For the first time in 30 years, *Drosophila persimilis* was frequent in this locality; only 15 females were *D. pseudoobscura*. I therefore prepared 10 chromosomes from the progeny of each female; I also examined chromosomes in the progeny of crosses between San Gabriel males and virgin females of known karyotype. In all, 72 chromosomes were observed, with gene arrangements in the following frequencies: Standard, 39%; Arrowhead, 18%; Chiricahua, 18%; Treeline, 21%; Pikes Peak, 3%; and San Jacinto, a rare polymorph not seen since the forties, 1%. The population is sufficiently polymorphic that a significant fraction of multiple inseminations should be observed. In fact, six of the 15 cultures, or 40%, were products of multiple insemination. Only seven of the 15 cultures contained the four or more different gene arrangements necessary for detection of repeated matings. The actual number of multiple inseminations was undoubtedly much greater than six, since many would not have been detected. At least one-half, and probably more, of the females in the sample from San Gabriel Canyon carried sperm of more than one male. A table of confidence intervals for sample percentages, based on the binomial distribution, may be used to set a lower bound for the true frequency of multiple insemination in the San Gabriel population. For this sample of 15 and the observed frequency of six, the lower limit at the 95% probability level is 16%; if the sample frequency were adjusted for ascertainment, the lower limit would be even higher. The true frequency of multiple insemination in this natural population of *D. pseudoobscura* is clearly high, enough so that repeated mating must be an important component of fitness. Other natural populations may not differ from San Gabriel in this regard, although only a few could provide material for an experimental test of this hypothesis.

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A REANALYSIS OF VUILLEUMIER'S DATA

Vuilleumier (1970) recently demonstrated that the avifauna of isolated mountaintops in South America have insular patterns of distribution. The number of species present on each "island," as well as the number of endemic taxa, was predicted from multiple regression equations. To predict the number of species on páramo "islands" (N_1), Vuilleumier used a stepwise multiple regression model (program BMDO2R) with seven independent variables. Using his data, we duplicated his results (table 1). Our F to Remove values differ from Vuilleumier's because he used the F to Remove value from the step in which the variable in question was added to the regression equation. We used the values computed in the final step, after inclusion of all seven variables.

Examination of the correlation matrix reveals that a number of the "independent" variables are highly correlated with one another. Vuilleumier's data are not orthogonal. Hoerl and Kennard (1970*a*, 1970*b*) pointed out that use of nonorthogonal data leads to biased estimates for regression coefficients. As each new variable is added to the equation, regression coefficients, their standard errors, and F to Remove values change unpredictably. Signs of regression coefficients may be biologically unreasonable. Such biased coefficients therefore make very unreliable predictors. Evidence of the effect of nonorthogonal variables is readily observed in table 1. The F