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MULTIPLE MATING, SPERM COMPETITION AND THE FERTILITY COMPONENT OF FITNESS IN *DROSOPHILA PSEUDOOBSCURA*

MONTE E. TURNER*

SYNOPSIS

Those aspects of an organism's biology that influence the number of progeny produced make up the fertility component of its fitness. The fertility of both male and female *Drosophila pseudoobscura* is influenced by multiple matings. In the former, rates of multiple matings and the genotypes of females' other mates interact to affect male fitness. Female fecundity and productivity increases with multiple matings, while longevity declines. Mating rates could be the result of these conflicting selection pressures. Density is a non-genetic factor influencing multiple mating. The mechanisms by which multiple matings increase female fertility is not the same in different species of *Drosophila*. In *D. melanogaster*, subsequent matings appear to replenish diminished sperm stores, while in *D. pseudoobscura*, females may absorb sperm for use as a nutrient. These differences emphasize that there need not be single "model systems" even within a genus.

INTRODUCTION

Because many factors over an organism's life contribute to its fitness, this total fitness can be divided into separate components, each of which relates to a specific life stage (Prout 1965, 1969, 1971a, 1971b). This division into smaller fitness components allows for a better understanding of their individual contributions. Two major components are usually recognized, viability and fertility. The viability component of fitness includes parameters such as egg to adult survival and specific age group survival. The aspects of an organisms biology that influence the number of progeny, such as fecundity or male mating success, are included in the fertility component.

While there has been a historical emphasis on the viability component, laboratory experiments with *Drosophila pseudoobscura* have demonstrated that the fertility component can be as large or larger (Anderson and Watanabe 1974). As an illustration imagine two genotypes A_1A_1 and A_2A_2 which have very different fitnesses. If A_1A_1 individuals have more adult offspring than A_2A_2 individuals, it may be that A_1A_1 females

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lay more eggs (fertility) or more A_1A_1 eggs survive to adulthood (viability). In the experiments described here, fitness has been defined in two ways, either as the number of eggs (fecundity) or as the number of adult progeny (productivity) produced by a particular genotype. Productivity includes both fecundity and egg to adult survival, although in a laboratory setting conditions are usually modified such that egg-adult survivals are not significantly different between the tested genotypes. In these cases, results from fecundity and productivity are not qualitatively different. Note that traits such as male mating success are included in the fertility component as a male genotype that mates more often has more offspring and thus a higher fitness. High levels of multiple mating occur in natural populations of *D. pseudoobscura* (Anderson 1974, Cobbs 1977, Levene et al. 1980) as do significant differences in male mating success among certain third chromosome inversion karyotypes (Anderson et al. 1979). Using such differences, the question arises as to how multiple mating and the resulting opportunity for sperm competition affect the fertility component of fitness in *D. pseudoobscura*. Since males and females are affected differently by multiple mating, first results focusing on males will be presented, then results from a female perspective.

MALE FITNESS AND MULTIPLE MATING

Sperm Competition, the competition between sperm from two or more males for the fertilization of a female's eggs, frequently results in the differential utilization of sperm from different ejaculates (Parker 1970). This can have significant effects on male fitness. Sperm precedence refers to the proportion of progeny from a multiply-mated female that are fathered by each male. The preponderance of offspring from the last male has been termed sperm displacement or sperm predominance. The latter term is preferred since it implies no mechanism (Gromko et al. 1984). From a fertility fitness perspective the highest male fitness would be the genotype that maximizes the number of offspring fathered regardless of the order of mating.

If we assume that multiply-mated females have mated with only two males, the total sperm competition fitness component for males is dependent on three parameters; P' , P_1 , and P_2 . P' is the number of offspring fertilized by a male genotype *before* the female remates. P_1 and P_2 are the proportion of offspring fertilized by a male genotype *after* a female remates; P_1 when he was the first male and P_2 when he was the second, (Gromko et al. 1984, Turner and Anderson 1984). From a fitness perspective the important parameter is the total of all three, which give an average number of offspring fertilized by a particular male genotype. As a complication, P_1 and P_2 would have to be weighted by rates of multiple mating and the male mating success for that genotype. These fitnesses could be density dependent, since changing density changes the rate of multiple mating and, therefore, the contribution of P_1 and P_2 to the total. In general, with little remating P' may be the best predictor of a male's reproductive fitness component while in populations with high remating rates, the sum of P_1 and P_2 may be the best predictor. All three parameters (P' , P_1 , P_2) have not been measured for any genotype (in any species) but for some genotypes in *D. pseudoobscura* at least P_1 and P_2 have been measured. Note that from the perspective of any one female $P_1 + P_2$ must equal 1.0 (assuming she has mated twice) but for a particular male $P_1 + P_2$ need not equal 1.0 since the two values are measured in different females.

The determination of P_1 and P_2 requires a means of determining paternity in the offspring of multiply-mated females. In *D. pseudoobscura* two methods of detection have been used, either a recessive morphological marker, orange eyes (Beckenbach 1981; Pruzan-Hotchkiss et al. 1981) or an amylase allozyme marker (Turner and Anderson 1984). A problem with the orange eye marker is it has significantly lower P_1 and

P_2 values (Beckenbach 1981) than wild type (red eye) individuals, while the allozyme marker seems to have no significant effect (Turner and Anderson 1984).

There are no significant differences in P_2 in the naturally occurring genotypes that have been tested. Eight third chromosome gene arrangement karyotypes (Turner and Anderson 1984) and two X-chromosome gene arrangements (Beckenbach 1981) have been used to measure P_2 with the first male genotype constant. In all cases P_2 values ranged from .82 to .90. These results simplify the sperm competition fitness component for *D. pseudoobscura* since for these genotypes the P_2 component can be eliminated, thus any fitness differences must occur through differences in either P' or P_1 .

There are significant differences in P_1 for these *D. pseudoobscura* genotypes. Values of P_1 for eight third chromosome gene arrangement genotypes ranged from .15 to .49 with 6 of 28 pairwise combinations being significant (Turner and Anderson 1984). However, Beckenbach (1981) found no significant P_1 differences between the two X-chromosome gene arrangements. How do these P_1 values relate to observed total fitnesses in laboratory cage populations? The best data are for populations containing the ST (Standard) and CH (Chiricahua) gene arrangements (Dobzhansky and Pavlovsky 1967, Anderson unpubl. data) which have relative fitnesses in the following relationship, ST/CH > ST/ST > CH/CH. The rank order of P_1 values for these genotypes is ST/CH > ST/ST > CH/CH. These parallel results suggest that a portion of the total fitness difference between these *D. pseudoobscura* lines results from differences in the sperm competition abilities of males, and more specifically differences in P_1 .

Male fitness parameters are not constant for any particular genotype, but dependent on the genotype of the other mates of the multiply-inseminated female. For instance, in the measurement of P_1 for third chromosome gene arrangements six crosses had the same genotype second male and P_1 's varied from .12 to .49 (Turner and Anderson 1984). If P_1 had this variation then P_2 for the second male genotype also varied from .88 to .51 depending on the genotype of the first male. Thus, for any genotype the values of P_1 and P_2 are an array of pairwise comparisons with all other genotypes in the population. The possibility that the female genotype influences P_1 and P_2 values has been tested, and there is no statistically significant effect (Turner and Anderson 1984). However, this lack of significance may well be the result of small sample sizes, since there was a great deal of variation observed.

Sperm competition data indicate that a male's fertility component of fitness is a very complex parameter. It is influenced by: rates of multiple mating, male mating success (first and subsequent matings), genotypes of the females other mates, P' , P_1 , P_2 and possibly the female genotype. Many of these parameters are not constants but vary according to other male (and female) genotypes in the population.

MULTIPLE MATING AND FEMALE FITNESS

Although students of sperm competition have focused primarily on males, multiple mating can also influence fitness in females. In *D. melanogaster* both males (Partridge and Farquhar 1981) and females (Kidwell and Malick 1965) show reductions in longevity due to the act of mating. For multiple mating to persist it would seem this decrease in the viability component must be offset by a gain in the reproductive (or some other) component of fitness. Boggs and Gilbert (1979) demonstrated that in three species of butterflies, females absorb part of the male ejaculate and incorporate it into protein. Similarly, *D. mojavensis* females also absorb a portion of the ejaculate, though *D. melanogaster* females do not (Markow and Ankney 1984). Species with this ability may be able to offset the viability disadvantage of multiple mating, since a female with more mates enhances her nutritional state. An increased nutrient uptake allows a female to produce more eggs thus increasing her fitness.

Beckenbach (1981) has shown that *D. pseudoobscura* females will remate within 24 hours after a first mating. In a separate study over 50% of singly-mated females remated when exposed to another male three days after their first mating, (Turner and Anderson 1984). Measurements of fecundity (Beckenbach 1978) or productivity (Turner and Anderson 1983) show that singly-mated females have depleted little of their stored sperm after 1 to 3 days and that remating to replenish stored sperm should not be necessary. How then does multiple mating affect the fertility component of fitness in *D. pseudoobscura* females? Three studies have found that multiply-mated females have a higher fertility component of fitness than females mated once (Beckenbach 1978, Pruzan-Hotchkiss et al. 1981, and Turner and Anderson 1983). The extent of their advantage is dependent on the environment, with a large increase (over 200%) in "poor" environments and a smaller one (about 20%) in "good" environments (Turner and Anderson 1983). These productivity results are consistent with the hypothesis that *D. pseudoobscura* females can and do absorb nutrients from the ejaculate. This is apparent as increased productivity in the poor environment.

Although multiple mating increases the fertility component of fitness, it lowers the viability component in *D. pseudoobscura*. There must be a cost to either the mating itself or the increased egg production because multiply-mated females have significantly lower daily survivals. However, as the fertility advantage outweighs this viability disadvantage, multiply-mated females have a higher overall fitness (Turner and Anderson 1983). Recent results (Hoffman and Harshman 1985) indicate that more than multiple mating may account for this increase. In a study with *D. melanogaster*, females exposed to males after mating but not allowed to remate, had a significant increase (about 35%) in both fecundity and productivity. Their experiments were done under "poor" conditions which was hoped to accentuate any effects. *Drosophila pseudoobscura* was not tested, but it is possible that a portion of the increased fitnesses observed results from a male-produced factor whose effect is to stimulate oviposition in females without mating.

RATES OF MULTIPLE MATING

The first evidence that a *D. pseudoobscura* female in nature would mate with more than one male was a single doubly inseminated female discovered by Koller in 1939. Since then, a number of *D. pseudoobscura* populations have been examined and their frequencies of multiple mating estimated (Dobzhansky et al. 1963, Anderson 1974, Cobbs 1977, Levene et al. 1980). With the exception of an 8% estimate by Dobzhansky et al. (1963), which because of its protocol may have greatly underestimated multiple matings (cf. Levene et al. 1980, for discussion), these estimates range from about 40% (Cobbs 1977) to over 90% (Levene et al. 1980). Although each study used different methods of estimation, the overall conclusion is that natural populations of *D. pseudoobscura* do vary in their frequencies of multiple mating.

With the demonstration that multiply-mated females have significantly more offspring than single-mated females and that the amount of this advantage is dependent on the environment, the potential exists for rates of multiple mating in natural populations to be adaptive, i.e. the result of selection. For example, poor environments might have high rates of multiply-mated females. While in good environments, where a lesser fertility advantage might not offset decreased viability, a lower rate of multiple mating would be expected. A necessary pre-requisite for this is that at some time there was genetic variation influencing whether a female remates. In one laboratory study (Dobzhansky and Pavlovsky 1967) females homozygous for different third chromosome gene arrangements remated at significantly different frequencies. However, this is an isolated result and more investigation is needed.

Selection as a result of fitness differences is not the only factor that could affect rates of multiple-mating. One possible non-genetic influence is density. In *D. pseudoobscura* and *D. persimilis* (a close relative of *D. pseudoobscura*) increasing density increases the frequency of first matings (Spiess and Spiess 1969, Ekstrand and Seiger 1975), and has been hypothesized to have similar effects on multiple matings (Richmond 1976, Levene et al. 1980). However, increasing density decreases the frequency of both first (Jacobs 1960) and second matings in *D. melanogaster* (Gromko and Gerhart 1984). Densities vary widely between different populations and between different seasons in the same population (Dobzhansky and Wright 1947). Most important though, in comparing frequencies of multiple mating with experimental results of productivity, is good and poor environments probably have very different densities (Johnston and Heed 1975). With such differences a knowledge of the effects of density on the frequency of multiple mating is essential to any predictions about rates of multiple mating.

Table 1 shows the effect of different densities on rates of multiple mating in *D. pseudoobscura*. Females that had mated three days previously were confined in vials with *Drosophila media* and another genotype male for 48 hours in several different densities. Their progeny were examined using an electrophoretic assay (see Turner and Anderson 1984) to determine whether they had mated with the second male. Density had a highly significant effect on the frequency of multiple mating ($\chi^2 = 24.91$, 3df, $p < .001$). In general there is an optimal density (20 pairs) and changing from this optimum (either higher or lower) decreases the frequency of multiple matings. The frequencies measured compare closely with rates from natural populations, 40% to 90% for natural populations versus 55% to 91% for the current data (Table 1). How these laboratory densities compare to densities in natural populations is not known. The comparison of rates of multiple mating between temporal samples of the same population would be meaningless without correcting for possible density differences. These results demonstrate the high levels of multiple mating in some natural populations need not be the result of selection to increase multiple matings but could be a byproduct of the density of that particular population.

At lower densities *D. pseudoobscura* and *D. melanogaster* females have opposite responses. It could be argued that in each species their response to density is the result of fitness differences for different density responses. Alternatively, these responses could be a byproduct of another aspect of the reproductive behavior. A number of additional experiments need to be done examining rates of multiple mating before either of these alternatives can be any more than speculation.

TABLE 1. NUMBERS OF MULTIPLY-MATED FEMALES, FREQUENCY OF MULTIPLE MATING AND THE NUMBER OF FEMALES TESTED FOR DIFFERENT DENSITIES OF MALES AND FEMALES.

Density (males:females)	Multiply Mated	Total Tested	Frequency
5:5	11	15	.73
10:10	28	36	.78
20:20	63	69	.91
30:30	43	78	.55
$\chi^2 = 24.91$ $df=3$ $p<.001$			

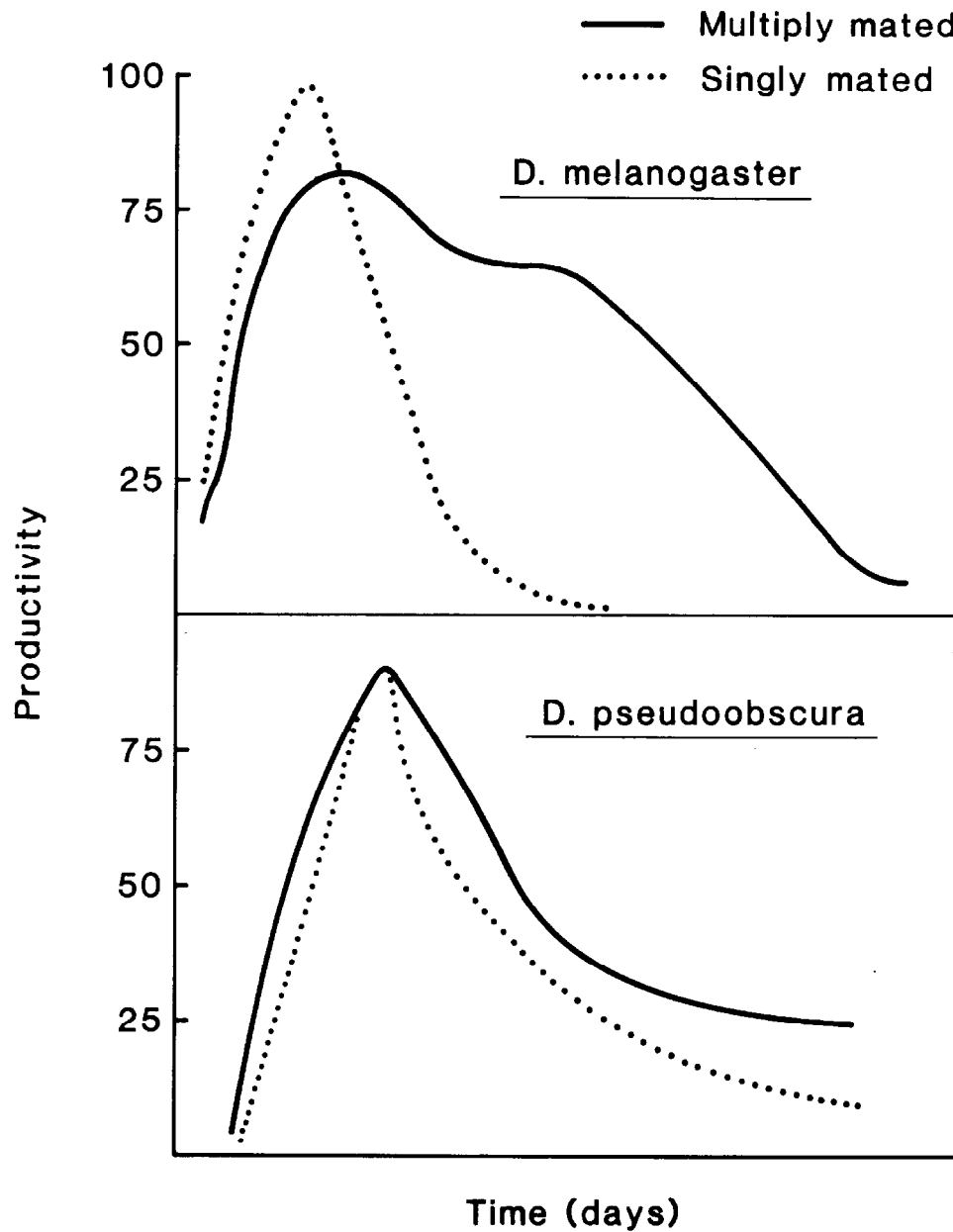


Fig. 1. Generalized daily productivity of *D. melanogaster* (after Pyle and Gromko 1978) and *D. pseudoobscura* (after Turner and Anderson 1983) that have mated singly or multiply.

COMPARISONS TO *D. MELANOGASTER*

Both *D. pseudoobscura* and *D. melanogaster* females experience a fitness advantage with multiple mating, but the nature of their responses are quite different. Figure 1 presents generalized productivity curves for *D. melanogaster* (after Pyle and Gromko 1978) and *D. pseudoobscura* (after Turner and Anderson 1983). The multiply mated *D. melanogaster* female's productivity remains high while the singly mated female's productivity decreases quickly. These curves are of the form expected if multiple mating

were replenishing the sperm load depleted by fertilization. In *D. pseudoobscura* the productivity curves for singly and multiply-mated females have the same shape, but the multiply-mated productivities are consistently higher. This suggests that remating stimulates productivity rather than just replenishing sperm used. Thus the mechanisms through which multiple mated females increase productivity seem different in the two species.

In poor environments, the productivity curves for singly and multiply mated *D. pseudoobscura* females change dramatically (Turner and Anderson 1983). The two curves now have the same shape as the *D. melanogaster* result, but productivities are severely depressed (about 20% of normal). In this poor environment sperm replenishment seems to be occurring. Perhaps replenishment occurs in the poor environment because the females absorbed sperm, while in good environments absorption is reduced. *D. melanogaster* females in poor environments remate at significantly lower rates than females in good environments (Gromko and Gerhart 1984, David et al. 1971). Apparently, sperm replenishment is not needed because the decreased fecundity in poor environments requires fewer sperm for fertilizations. This is observed as a lower rate of multiple mating.

The conclusions from these comparisons are important to general considerations of sperm competition and the fertility component of fitness. The results of sperm competition and multiple mating are species specific, predictions for *D. pseudoobscura* from the *D. melanogaster* data would be wrong and vice versa. In *Drosophila* at least, there is apparently no model system and extensions to other species (both Drosophilids and others) from the results of either *D. melanogaster* or *D. pseudoobscura* should be as testable hypotheses and not as general conclusions. Each species of interest needs to be considered individually in its response to multiple mating and sperm competition.

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