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Male Mating Speed as a Component of Fitness in *Drosophila*

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From a survey of published data on the genus Drosophila, *it is clear that male mating speed or male virility is probably the most important component of fitness. Rapid matings tend to be controlled by the male genotype, while the genotype of the female may assume importance for slower matings. Where data exist, male mating speed is subject to directional selection in the direction of rapid speed, as would be expected for an important component of fitness.*

KEY WORDS: *Drosophila*; mating speed; fitness; genetics.

INTRODUCTION

Fitness can be defined as the average number of progeny left by the carriers of a given genotype relative to the number of progeny left by other genotypes. As stated the concept is simple enough, but fitness depends on the environment, the background genotype, and interactions between genotype and environment. Furthermore, while we can look at fitness under laboratory conditions, extrapolation to the wild where there is heterogeneity of environments is another complication. Fitness can be subdivided into a number of components all of which are relevant to the average number of progeny produced. With few exceptions, relationships between fitness factors have not been considered (see Prout 1971*a*, for references). Even fewer of these studies involve behavioral traits.

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However, Wallace (1948) reported on sexual activity and other fitness differences between strains of *Drosophila pseudoobscura* for his "sex ratio flies" such that male sex ratio flies were inferior to other male flies for sexual activity, larval stage survival, longevity, fecundity, and egg hatchability, at 25°C. Merrell (1949) studied the effect on mating of four sex-linked mutants of *D. melanogaster*, singly and in combination in the same fly, using male- and female-choice experiments. Deviations from random mating were mainly due to variations in male mating vigor. Only in the least vigorous males were variations in female receptivity important. Merrell (1953) followed gene frequency changes in populations each containing one of the four sex-linked genes. Initially, the populations had equal numbers of mutant and wild-type males and only heterozygous females, so that the gene frequency of the mutants was 0.5. In all cases, the frequency of the mutants fell quite rapidly over a number of generations, and agrees with predictions taking into account levels of selective mating for these mutants. This shows that selective mating due to differences in male vigor is a component of fitness in these populations.

INVERSIONS (GENE ARRANGEMENTS)

In *D. pseudoobscura* at 25°C, strong heterokaryotype advantage has been observed in population cages, leading to stable balanced polymorphisms (Wright and Dobzhansky, 1946). Some of the numerous fitness factors for which heterokaryotype advantage has been found include innate capacity for increase, population size and productivity, egg to adult viability, and mating frequency compared with the corresponding homokaryotypes (see Parsons, 1973, for references). The associations between these components of fitness in one experiment have been relatively unexplored.

For mating speed in *D. pseudoobscura*, Spiess and Langer (1964*a*) found substantial differences in stocks collected at Mather, California, for homokaryotypes of the Standard (ST), Chiricahua (CH), Tree Line (TL), Pikes Peak (PP), and Arrowhead (AR) inversions. In order of mating speed, AR $\approx$ ST $>$ CH $\approx$ TL $>$ PP, which corresponds to the frequency of the inversions in natural populations at Mather, the observed frequencies being ST = 40.1%, AR = 36.0%, CH = 10.8%, TL = 7.2%, and PP = 4.3%. From this, it can be suggested that mating speed is a major factor in maintaining the observed frequencies of the chromosomes in the population, although because of the numerous other components of fitness known, this interpretation must be qualified. It must also be qualified because homokaryotypes rather than heterokaryotypes are being tested, which means that karyotypes having high fitnesses are ignored.

Spiess *et al.* (1966) studied mating speeds in *D. pseudoobscura* for a number of chromosomal combinations and consistently found that male heterokaryotypes had a higher mating speed than the corresponding homokaryotypes. In females, there was no consistent superiority. Therefore, the heterosis must be due to the greater activity of the males, e.g., their persistence in courtship, or to greater female acceptance of certain male heterokaryotypes because of their higher sexual activity. Kaul and Parsons (1965) found heterokaryotype advantage for the sum of mating speed and duration of copulation for the karyotypes ST/ST, ST/CH, and CH/CH. The important differences were between male rather than between female karyotypes.

The importance of males compared with females in *D. pseudoobscura* was also shown by Kaul and Parsons (1966) in two series of choice experiments, one consisting of one female with three males (female choice), and the other of three females with one male (male choice). The pattern for each karyotype was similar, and the mean time elapsing to the first mating was 0.53 min in the male-choice and 1.40 in the female-choice experiments (Table I). The difference can be interpreted by postulating that interference between males occurs in the experiment, three males thereby delaying mating. In the reverse situation where there is only one male, that male tends to mate more quickly, having no interference from females. Spiess and Ehrman (as reported in Spiess, 1970) confirmed these observations with other karyotypes of *D. pseudoobscura.*

In *D. persimilis*, an excess of males did not delay the time to mating (Spiess, 1970). In this species, females play a greater part in determining mating speed than in *D. pseudoobscura*. Spiess and Langer (1964*b*) studied mating speeds for karyotypes involving the Whitney (WT) and Klamath (KL) inversions and found both sexes of importance for various combinations between WT/WT, WT/KL, and KL/KL karyotypes. WT/WT fe-

Table I. Time (min) Elapsing to First Mating in Male-Choice (1 male, 3 females) and Female-Choice (3 males, 1 female) Experiments in *D. pseudoobscura*[a]

	Karyotype			
	ST/ST	ST/CH	ST/ST	Mean
Male-choice	0.56	0.35	1.00	0.53
Female-choice	1.22	1.08	2.28	1.40

[a] After Kaul and Parsons (1966).

males tended to accept males and KL/KL females tended to refuse them, and WT/WT males courted more actively than KL/KL males. The differences can be explained in terms of the relative intensities of the copulation tendency for males and the acceptance (or avoidance) of females.

In most natural populations of *D. pavani*, heterokaryotypes exist in fairly uniform frequencies. Male mating ability has been assessed by using virgin females of a sibling species, *D. gaucha*, having a standard gene arrangement (Brncic and Koref-Santibañez, 1964). Heterokaryotypic males were superior to the corresponding homokaryotypes, from which it can be argued that superiority of the heterokaryotypic males may be important in the maintenance of balanced polymorphisms in natural populations. Female mating ability was not investigated because females are difficult to culture and test under laboratory conditions.

In *D. robusta*, Prakash (1967, 1968) found that the mating speed of heterokaryotypic males exceeded that of homokaryotypes over a period of 1 hr. In females, there was a tendency for higher mating frequency of heterokaryotypes, which was not as pronounced as for male heterokaryotypes. The situation is somewhat complicated by interaction between second and third chromosome karyotypes (Prakash, 1968).

In all cases discussed, differences between male genotypes are relevant, but, with the exception of *D. persimilis*, only occasionally are differences between female genotypes. To what extent is mating speed an important component of fitness? Some associated fitness traits in *D. pseudoobscura* have already been cited. In *D. robusta*, Prakash (1967) found that in males there is a positive correlation between fast mating, repeat mating, and fertility. Such a correlation suggests that mating speed is an important component of fitness, being indirectly a measure of fertility.

STRAINS OF *D. MELANOGASTER*

Parsons (1965) set up a 5 × 5 diallel cross of five inbred strains for mating speed. An analysis of variance showed that the strain of the male was important, especially for rapid matings occurring in $\leqslant$ 10 min after flies were placed together. For total matings at 40 min, the strain of the male was relatively less important and that of the female approached significance. Although different total numbers of matings occurred at the 10- and 40-min time periods, it seems that initially the vigor of the males leads to rapid matings, but later variations in female receptivity may become important. Therefore, the time after flies of opposite sex are shaken together is an important variable. This agrees with Merrell's (1949) observation that only for the least vigorous males do variations in female receptivity become important. If rapid mating is an important component of fitness, the strain of the male must be a factor of considerable significance.

Fulker (1966) looked at the association of male mating speed and other fitness parameters by testing single males from each of six inbred strains with six virgin females, one from each strain, over a period of 12 hr. Since each male was given the same array of females to mate with, the females can be considered as a standard testing set. Of particular interest (Table II) was a highly significant negative correlation of the time of the first copulation (A) with the observed number of copulations (B), the number of copulations resulting in fertilization (C), and the number of offspring produced (D). Positive correlations were found between B, C, and D taken in pairs, as might be expected. All four measures therefore appear to be aspects of a general characteristic of male mating behavior, since males which mate more quickly on the first occasion also copulate more often, more successfully, and leave more progeny. From a diallel cross analysis, Fulker concluded that there is strong directional selection for rapid mating. This argues for a history of natural selection for rapid mating. Therefore, although females were not specifically tested, the importance of male mating speed as a component of fitness is clear, as for *D. robusta*.

However, what is the influence of variations in male mating speed on the performance of populations? Merrell's (1949) study is suggestive. Prout (1971*a,b*) estimated certain components of fitness simultaneously in *D. melanogaster* using the fourth chromosome recessive mutants eyeless (ey^2) and shaven (sv^n) as markers. Since the chromosome is very short, recombination is not a source of complication. The components of fitness estimated were larval viability in each sex, and from adults two components were obtained, one representing female fecundity and the other representing male mating ability or virility. The adult components were found to be the more important, such that $ey^2\ ey^2$ and ey^2/sv^n females were superior to $sv^n\ sv^n$, and the heterozygous males were superior to both homozygotes. In males, the depressed values of the two homozygotes

Table II. Correlations Between Time to First Copulation (A), Observed Number of Copulations (B), Number of Copulations Resulting in Fertilization (C), and the Number of Offspring Produced (D) in *D. melanogaster*[a]

AB	−0.87 ($P < 0.001$)	BC	0.96 ($P < 0.001$)
AC	−0.78 ($P < 0.01$)	BD	0.90 ($P < 0.001$)
AD	−0.69 ($P < 0.02$)	CD	0.95 ($P < 0.001$)

[a] After Fulker (1966).

Table III. Components of Fitness Estimates in *D. melanogaster*[a]

Genotype	Larval viability		Female fecundity	Male virility according to the three female genotypes below		
	Females	Males		ey^2ey^2	ey^2/sv^n	sv^nsv^n
ey^2ey^2	0.865	0.839	1.037	0.363	0.243	0.135
ey^2/sv^n	1	1	1	1	1	1
sv^nsv^n	0.934	0.777	0.458	0.039	0.122	−0.018

[a] After Prout (1971*b*).

varied with the female genotype to which the males were mated, indicating mating interactions (Table III). The high heterozygote advantage for male virility is clear, stressing the importance of male mating behavior as a component of fitness. Prout emphasized the need to define a small number of components of fitness encompassing the entire life cycle which can be evaluated experimentally. He tested his fitness estimates by attempting to predict the performance of experimental populations segregating for these two mutants. The results were in reasonable agreement with prediction, showing that the fitness estimates can account for most of the performance of the experimental populations.

Bundgaard and Christiansen (1972) looked at a division of total selection, applying to the life cycle of an organism, as split into various components each relating to a certain stage in the life cycle: (1) zygotic selection due to differential survival of genotypes from the zygotic stage to fertilization, (2) sexual selection, (3) fecundity selection, and (4) gametic selection, which is where there is prezygotic selection. They assessed these components for a system analogous to Prout's, using fourth chromosome mutants. Although there was some zygotic selection, the major component of importance was sexual selection as measured by differential male mating success, a result in qualitative agreement with Prout (1971*a*,*b*).

SELECTION EXPERIMENTS

If male mating speed is a component of fitness subject to directional selection, it would be expected that artificial directional selection would be less effective for fast than for slow mating speed, because of the previous history of natural selection to which the population had been exposed. Manning (1961) selected for mating speed in *D. melanogaster* without separating out the specific effect of males and found a greater effect toward slowness than rapidity. He argued, as has been done here, that rapid mating is a factor contributing to biological fitness. In agreement, Manning (1963) presented data on selection in one sex only in *D. melanogaster* over 20 generations and found that lines in which males were selected for fast mating showed no response, while males selected for slow mating responded.

In *D. pseudoobscura*, Kessler (1969) obtained a response to selection for fast and slow mating speeds with a slower response in the fast line. However, the responses were not great, as indicated by his realized heritabilities—a result in agreement with the proposition that male mating speed is an important component of fitness. Crosses between fast and slow lines indicated dominance of genes for fast mating speed. It could be argued that little dominance would be expected in the F_1 generation because Kessler's base population was an intercross between three wild-type strains from Guatemala, British Columbia, and California. This is based on the premise that in one population the genetic architecture leading to dominance might differ from that in another, so that in crosses between populations this might be disrupted; that is, the coadaption in a particular population would be broken down. On the other hand, Kessler's tests were carried out after a number of generations of directional selection for rapid and slow mating, during which time genes previously selected in nature could have been brought together again.

However, a recent unpublished thesis by Spuhler (1973) adds significantly to our evidence. She used for each of AR, PP, CH, and TL strains of *D. pseudoobscura* collected by Dobzhansky at Mather in 1959 and scrambled them together, which would, hopefully, provide a more coadapted population than that used by Kessler. For two fast and two slow selection lines, realized heritabilities over 19 generations, while being slightly positive, were insignificant. This indicates that *within* the Mather population, there was virtually no additive genetic variation and that this had presumably been exhausted by previous natural selection. The contrast with Kessler's experiment is of course that he did obtain a response to selection (even though small) based on crosses between populations from *differing* localities.

DISCUSSION

In all of the species of *Drosophila* mentioned, *D. pseudoobscura, D. persimilis, D. gaucha, D. robusta*, and *D. melanogaster*, male mating speed or male virility is usually an important component of fitness. Although rather tentative, it appears that

1. Male mating speed is subject to directional selection in nature for rapid speed.

2. Within a species, rapid matings tend to be controlled by the male genotype, while the genotype of the female may assume importance for slower matings, an exception being *D. persimilis* in which rapid mating is also under important female control.
3. Mating speed is associated with fertility and the number of progeny.
4. Where studied in relation to components of fitness encompassing the whole life cycle, mating speed is the most important component.

Some studies have been carried out on frequency-dependent matings where rare genotypes tend to be favored at the expense of the common (Petit, 1958; Petit and Ehrman, 1969; Ehrman, 1969) in species such as *D. melanogaster, D. pseudoobscura, D. persimilis, D. tropicalis, D. willistoni,* and *D. equinoxalis* (see Parsons, 1973, for references). Frequency dependence mainly depends on male genotypes, although small female effects have been described. Some work has been done on extrapolating this to populations. In *D. pseudoobscura,* Ehrman (1970*a*) studied a population consisting of 2000 flies that had been released into a room and found frequency dependence. An added complication is that frequency dependence is age and experience dependent (Pruzan and Ehrman, 1974); however, from the natural population point of view it is the early matings which must be most effective. With increasing age, it can be assumed that predators, environmental extremes, and other factors will take their toll more than in the idealized laboratory environment. In a polymorphic population, the advantage of the rare male would be expected to lead to an increase in its frequency, which in turn would be associated with a diminished mating advantage, as shown by Ehrman (1970*a,b*) in *D. pseudoobscura* and Prout (1971*b*) and Bundgaard and Christiansen (1972) in *D. melanogaster.* The result could be a finely tuned balanced polymorphism.

The elucidation of the role of male mating speed must take into account the complete life cycle, since a genotype may affect many components of fitness. This may help us to determine whether it is possible to predict results from one component of fitness to another. Fulker's (1966) and Prakash's (1967) experiments allow a degree of optimism, but Prout (1971*a*) is less optimistic. Some uniformity is, however, seen in Table III, where strong heterozygote advantage occurs for male virility, weak heterozygote advantage for larval viability, and none for female fecundity. In the last case, the heterozygote is equivalent to one homozygote and fitter than the other. Taken together, the overall superiority of the heterozygote is clear. Equally, in *D. pseudoobscura,* heterokaryotype advantage occurs for many fitness traits in many different experiments. It seems that there could be an argument for high fitness as assessed by one component of fitness being associated with another, although the association need not be complete.

Since natural selection for fitness is directional so as to maximize fitness in a given environment (Fisher, 1930), it is reasonable to suppose that there may be correlated responses between components of fitness, so that a high fitness for one component is likely to be associated with high fitnesses for others. On this argument, a genotype for rapid mating would be expected to be of high fitness for other components. The answer lies in more experiments looking at components of fitness simultaneously in several species.

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