

Short Communication

FEMALE COMPETITION IN MATE CHOICE DECREASES FITNESS IN FLIES
(*Drosophila pseudoobscura*) FROM COLOMBIA

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Ever since Falconer (1960) discussed how additive genetic variance for fitness rapidly decreases both theoretical and empirical interpretations have shown that there is a low parent-offspring correlation for fitness (Maynard-Smith, 1978). Williams (1975) discussed with his characteristic intellectual power that under equilibrium genetic variation affecting fitness should not be heritable. Williams' Sisyphian genotype terminology (instead of Dobzhansky's (1964a) genetic elite) signifies that low heritability of reproductive success or viability would be instrumental in dropping the most fit genotypes down into the range of mediocrity in the next generation. Thus, a female does not produce fitter offspring by mating with an above average male (Maynard-Smith, 1978) or by mating several times (Bateman, 1948). More recently other reports (Partridge, 1980) have found that when females choose their mate, their offspring are more successfully competitive. Our results (Table I) partially agree with those of Partridge.

Females from the progeny of a mass culture with three original isofemale lines (10, 11 and 41 freshly brought from nature) were placed to oviposit and to grow progeny. From an abundant progeny, three randomly picked groups (A, B, and C) were established in vials. Group A consisted of ten virgin females, randomly chosen from the original mass culture mentioned above, crossed to a single male, also randomly chosen out of isofemale line 10 from Oicatá, Colombia. Group B consisted of a virgin female, randomly chosen from the same original mass culture, and a single male, also randomly chosen from males of the isofemale line 10 made into a mass culture. In group C, groups of 10 pregnant females from the mass culture were allowed to oviposit in vials. Three different comparisons were made. The offspring of group A compared with the offspring of group C was A, C. The comparison was made by taking first instar larvae from eggs laid by females from group A (no choice, ten females) and first instar larvae from eggs laid by females from group C (choice, 10 females) and competing each set of larvae against an equal number of larvae bearing the recessive mutation vermilion (eye color) from a *D. pseudoobscura* stock made exclusively for this experiment.

In group B, the offspring of a single adult virgin

female taken from the mass culture from Oicatá and mated singly to a male, also taken at random from the isofemale stock 10, were compared with offspring of inseminated females collected from the mass culture (this is B, C). As with A, C, comparison B, C, was made by taking first instar larvae from eggs laid by females from group B (no choice, one female) and first instar larvae from eggs laid by females from group C and competing each set of larvae against an equal number of larvae bearing the recessive mutation vermilion.

The offspring of group A, compared with the offspring of group B was A, B. The comparison was made by taking first instar larvae laid by females from group A (no choice, 10 females) and first instar larvae from eggs laid by females from group B (no choice, one female) and competing each set of larvae against an equal number of larvae bearing the recessive mutation vermilion from a *D. pseudoobscura* stock.

Each group (A, B and C) consisted of 10 replicates. Two experiments were performed, one with 400 larvae one with 300 larvae. In the 400-larva experiment each set of 200 larvae from each group A, B and C were placed with 200 larvae of the recessive mutant vermilion. For the 300-larva experiment, each set of 150 larvae from each group A, B and C were placed with 150 larvae of the recessive mutant vermilion.

Larvae were allowed to compete in plastic vials, which contained the same food medium (banana-agar-propionic acid medium) as that used in the mass culture from Oicatá. The number of wild type and vermilion flies emerging from each vial was recorded. We endeavored to have the larvae compete under conditions similar to those encountered by larvae in the original mass culture from Oicatá. As far as we know food, temperature, CO₂ anesthetics and the genotype of the three competitors were equivalent. Experiments were repeated ten times and the results (Table I) led to five conclusions.

1. There were no statistically significant differences in the 400-larva experiment among the groups (A, B, C). This can be attributed to accidental death due to density instead of death of the weakest genotypes.
2. The percentage of wild-type flies emerging from group B was significantly higher in the 300-larva experiment.
3. The analysis of variance of the 300-larva experiment indicates that each group was statistically different (upper right hand of Table I), $F = 75.22^{***}$.
4. When no choice vs. choice (B vs. C) was analyzed ($F =$

Table I

Increase in offspring fitness of *Drosophila pseudoobscura* females from Oicatá, Colombia, which had chosen (choice) or not chosen (no choice) their males. On the left, competitive success of 400 larvae, on the right competitive success of 300 larvae. (See text for details). C = Choice of 10 females; A = no choice 10 females x 1 male; B = no choice 1 female x 1 male. Mean survivors after competition with vermilion in vials with 300 larvae: A = 38.7; B = 96.5; C = 65.9. Mean survivors after competition with vermilion in vials with 400 larvae: A = 70.1; B = 70.7; C = 70.6.

	Source	400 larvae				300 larvae			
		SS	d.f.	MS	F	SS	d.f.	MS	F
Experiment A, B, C	Between	2.07	2	1.03	5.5×10^{-3}	16723.47	2	8361.74	75.22***
	Within	5049.46	27	187.01		3001.50	27	111.17	
No choice vs. choice (A vs. C)	Between	1.25	1	1.25	7.25×10^{-3}	3700.20	1	3700.20	34.23***
	Within	3101.25	18	172.29		1946	18	108.11	
No choice vs. choice (B vs. C)	Between	0.05	1	0.05	2.2×10^{-4}	3057.80	1	3057.80	37.92***
	Within	4076.50	18	226.47		1451.40	18	80.63	
No choice vs. no choice (A vs. B)	Between	1.80	1	1.80	1.1×10^{-2}	16704.20	1	16704.20	115.44***
	Within	2911.00	18	161.72		2604.60	18	144.70	

F(0.05) 1/18 = 4.41 * F(0.01) = **

F(0.05) 2/27 = 3.35 F(0.001) = ***

37.60***), B (1 female and 1 male) had a significantly higher ($\chi = 96.5$) mean number of wild type flies than C (10 females with choice) ($\chi = 65.9$).

5. When no choice vs. choice (A vs. C) was analyzed ($F = 34.23***$), A (10 females and 1 male) had a significantly smaller ($\chi = 38.7$) mean number of wild type flies than C ($\chi = 65.9$).

The results show that matings between a group of randomly chosen flies containing 10 females and 1 male (A = 10 females x 1 male) produced offspring less "equipped" to compete with mutant larvae, probably between 1st-3rd instar, than matings where choice was possible (C). However, our results also show that matings between randomly chosen pairs of flies, one female and one male at a time (B = 1 female x 1 male), produced offspring better "equipped" to compete with mutant larvae than matings where choice was possible (C). Our results should not be interpreted as overall fitness of the larvae involved. There are many other components of fitness (egg-larva, larva-pupa, pupa-adult survival or time of development in each period of the egg-adult spread) that could be negatively correlated with the one measured here.

The lower survival rate of larvae and adult in offspring of the group A shows that females competed for the randomly chosen male. One is tempted to speculate that female competition constitutes a physiological load, a "stress" as it were, responsible for the suppression of genes that are better equipped to compete with mutant larvae.

Our results demonstrate that mate choice, C, increased competitive success of offspring when compared to A, but not when compared to B. These results could emerge from several genetic mechanisms. One interpretation is offered by Maynard-Smith (1978), who believed that female discrimination between different conspecific

males is due to additive genetic variance of fitness. The genetic mechanism could be that new favorable mutations contribute to additive fitness variance, which consequently makes female choice (C) an adaptive characteristic. Thus, even when females only receive genes from males, their own additive heritability of fitness makes choice worthwhile. This hypothesis contradicts the assumption of non-heritability of genetic variation affecting fitness at genetic equilibrium (Falconer, 1960). However, mate choice appears to be a very complicated phenomenon. To be alone with a male "pays off" in the resulting offspring (B), while competition with other females somehow had a negative effect on survival and larval competition (A). Our results do not confirm those of Partridge (1980), in which mate choice improved offspring fitness in *Drosophila melanogaster*. Our results were conditional: if 10 females and one randomly chosen male mate, their offspring would have lower survival than matings involving female choice. This result is opposite to that observed for offspring of single randomly chosen pairs, which were the most competitively successful.

Our results can be reproduced as long as fitter flies are actively chosen as mates. However, since our best survival rates resulted from single randomly chosen pairs (B) there is an additional interpretation consistent with the previous assumption; all or most females in a population at genetic equilibrium are endowed with the fittest "genetic equipment" to produce the "best" offspring only as long as the whole equipment can be put to work. "Stressing" conditions such as those resulting from female competition (A) could produce a factor that suppresses or dislodges the fittest genetic equipment. The assumption and the inevitable interpretation just discussed suggest that flies are made to prefer the same kind of mates. Since

we have never found heterogamy (Hoenigsberg *et al.*, 1959a,b, 1966; Hoenigsberg and Koref-Santibañez, 1960a,b), we cannot conclude with Partridge (1980) that genetically dissimilar flies should show different patterns of mate choice.

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