

Effect of larval crowding on adult mating behaviour in *Drosophila melanogaster*

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The effect of larval density on male mating success has been investigated with two strains of *Drosophila melanogaster*, a wild strain and a mutant strain, under low and high larval competition, and four different genotypic frequencies. The results show a strong sexual selection against mutant males when flies have been raised under low larval competition. Under high larval competition, there is a reduction in mating disadvantage of mutant males. In both instances, a frequency-dependent sexual selection exists. These results explain adequately the evolution of experimental populations where egg to adult viability and male mating success are the most important components of fitness.

INTRODUCTION

There are many experimental data in *Drosophila* showing that larval food shortage affects nearly all components of fitness. Most of these studies have focused upon the effect of larval density on egg-adult viability, showing that, generally, larval crowding produces an important decrease on viability (Sang, 1949; Birch, 1955; Bakker, 1961; Bentvelzen, 1963; Lewontin and Matsuo, 1963; Barker, 1973; Barker and Podger, 1970*a, b*). It has also been shown that larval crowding acts to reduce adult body size and female fecundity (Alpatov, 1932; Pearl, 1932). Pownser (1935), Sokoloff (1955) and Ménsua and Moya (1983) pointed out that high density cultures lengthen the developmental period. Robertson and Sang (1944), Sameoto and Miller (1966) and Mueller and Ayala (1981) demonstrated a reduced population productivity in crowded populations.

Most of these studies pointed towards larval crowding, but Spiess and Spiess (1969), Moth (1974), and Eckstrand and Seiger (1975) showed also that adult crowding may affect the mating rate of different *Drosophila* species.

On the other hand, it is a well-known fact that selective values may vary with gene frequencies, favouring genotypes which are less frequent. The phenomenon of rare male type was first observed by Petit (1951) in sexual selection of the sex linked

mutant *Bar* of *D. melanogaster*. Although *Bar* males were always less successful as mates than wild-type ones, their disadvantage diminished as they became rarer in the population. Female mating propensity seems to be independent of their relative frequency. The same results have again been observed by Ribó (1977). It is well known that frequency dependent selection acts also on egg-adult viability (for a revision see Ayala and Campbell, 1974).

Some authors pointed out that sexual selection, as a component of fitness, may be one of the most important factors in the selection of one genotype or karyotype, and, if mating propensity of rare male types is frequency dependent, it could be a mechanism leading to balanced polymorphism without the consequence of segregational load at equilibrium.

The present work is part of a study of components of fitness in experimental populations, in order to explain the mechanisms involved in the evolution of a mutant allele of *D. melanogaster* in competition with its wild type allele. The purposes of this study are twofold: (1) to study the sexual selection component of fitness with flies reared in low larval competition and with flies reared in population cages where the level of larval competition for food is very important, and (2) to seek for frequency dependent sexual selection.

MATERIAL AND METHODS

A wild strain and a mutant strain homozygous for the gene *caramel* of *D. melanogaster* have been used. The mutant gene *caramel* affects the eye colour of flies and it has been localized on the second chromosome at 71.2 units (Ribó, 1968). Both strains were obtained from the progeny of some wild females captured in a natural population located a few kilometres south of Barcelona (Spain).

The flies tested were reared under two conditions: (1) in bottles containing 90 cc of medium in which only one hundred eggs were laid and therefore developed with very little larval competition for food ("low competition"), and (2) in food cups containing 70 cc of medium, introduced in population cages where the wild and mutant strains were maintained separately. The estimated number of flies in these population cages is around 6000. Three food cups were introduced weekly and maintained in the cages during four weeks. During this period those cups are therefore putative laying sites of all the females in the cage. In contrast to the "low competition" condition, this is a situation with a very high level of larval competition ("overcrowding"). Cultures were maintained at $17 \pm 1^\circ\text{C}$.

We have used the technique of direct observation of matings in the situation of "multiple choice". Virgin males and females were separated under light anaesthetisation and stored separately for 3 days. They were introduced into a 1 litre glass jar and matings were observed for one hour; as each copulation occurred, the pair mating was aspirated out to prevent the males from a second mating. Mating observations were carried out at room temperature.

In all the tests carried out the females were present in equal numbers and only the ratio of

mutant and wild-type males was varied. Each test involved combining 30 females (15 of each type) with 70 males in order to increase male competition for mates. Females of each type were placed in the glass jar followed by the simultaneous introduction of two male types. Ten replicates for each male combination were tested.

RESULTS

Table 1 summarizes the results of mating experiments with flies which have been raised in low larval density and with flies reared in high larval density. In both cases we have tested four frequencies: 50, 20, 10 and 5 per cent of mutant males relative to wild type males. Chi-squares for "random mating" distribution, where expected values are calculated on the basis that the four kinds of mates should have the same probability, are highly significant, both for flies raised in low competition and for flies raised in crowded conditions, except for extreme frequencies. It is due to a male selection favouring wild type males ($\chi^2_{\delta\delta}$ are most of them significant at 0.01 level) and not to any female selection ($\chi^2_{\varphi\varphi}$ are not significant except one of them).

Indices of Levene have been calculated to measure sexual selection of mutant genotype in males and in females. If the observed number of matings of the four possible types are noted by:

	n_1	n_2
	females	females
	strain 1	strain 2
m_1 males strain 1	x_{11}	x_{12}
m_2 males strain 2	x_{21}	x_{22}

Table 1 Matings observed by multiple choice technique at different genotypic proportions

Genotypes	Proportions	Mating types				χ^2 random mating	$\chi^2_{\varphi\varphi}$	$\chi^2_{\delta\delta}$
		1F×1M	1F×2M	2F×1M	2F×2M			
1 (+/+)	2 (ca/ca)	1:2						
Low competition	50:50	120	24	90	17	121.35**	5.45*	113.79**
	80:20	133	12	112	18	16.86*	0.82	14.20**
	90:10	144	6	135	10	7.71**	0.08	6.86**
	95:5	142	4	136	3	4.09*	0.17	4.26*
Overcrowding	50:50	90	44	95	38	40.19**	0.004	39.73**
	80:20	126	17	93	21	9.97**	3.27	4.37*
	90:10	116	8	97	8	4.06*	1.58	2.31
	95:5	111	7	109	9	1.93	0.00	1.57

* Significant at 0.05 level.

** Significant at 0.01 level.

The Levene's male selection index is defined as:

$$Z_m = \left(\frac{m_2}{m_1} \right) \sqrt{\frac{x_{11} \cdot x_{12}}{x_{21} \cdot x_{22}}}$$

and the female selection index as:

$$Z_f = \left(\frac{n_2}{n_1} \right) \sqrt{\frac{x_{11} \cdot x_{21}}{x_{12} \cdot x_{22}}}$$

Using Taylor first order series expansion, the following variance estimators are derived:

$$\hat{\sigma}^2(Z_m) = \frac{1}{4} Z_m^2 H$$

$$\hat{\sigma}^2(Z_f) = \frac{1}{4} Z_f^2 H$$

where

$$H = \frac{1}{x_{11}} + \frac{1}{x_{12}} + \frac{1}{x_{21}} + \frac{1}{x_{22}}$$

Inferences on these indexes are frequently based on the preceding estimations and on the assumptions of approximate normal distribution of Z indexes and expected value $E(Z) = 1$ under the null hypothesis of random mating (but see criticisms outlined below in the text).

Z_m estimates the geometric mean of the ratio of male mating propensity in strain 1 to strain 2 (with the two kinds of females), and Z_f does the same thing for females. The selection indices vary from infinity to zero; values of the index higher than one show an advantage for strain 1, and those between one and zero a disadvantage. Statistical tests of significance have been carried out using Student's t distribution (see Ehrman and Petit, 1968). Its employment as a measure of sexual selection and significance test based on the asymptotic theory outlined by Levene has been criticized by Goux and Anxolabéhère (1980). We have performed exact significance tests, based on Z_m and Z_f , not based on asymptotic assumptions.

In addition, as data in table 1 are based on ten replicate experiments, it is acceptably correct to use Levene indices as a measure of sexual selection. These indices, summarized in table 2, show a strong sexual selection against mutant males when flies have been raised in low competition. The intensity of sexual selection diminishes when the proportion of males diminishes. When larvae have been raised in crowded conditions the disadvantage of mutant males is less important than in the preceding situation. Also, when mutant males are at a very low frequency (5 per cent) they do not show a selective disadvantage relative to wild type males ($Z_m = 0.72$, $P > 0.05$). In females, indices of sexual selection only show a disadvantage for mutant females when male proportion is 50:50 and reared in low competition.

Z_m indices suggest frequency-dependent sexual selection, specially in the experimental situation with overcrowding. Frequency-dependence has been tested by the linear regression of the logarithm of the ratios at which the two types of males were present in the population. This method was proposed as a test for frequency-dependence in sexual selection by Ayala (1972) and employed subsequently by a number of authors (Anxolabéhère, 1980; Alvarez and Fontdevila, 1981; Petit and Nouaud, 1984). The equation of regression for the case of no larval crowding, is $Y = -0.65 + 0.62X$. The regression coefficient ($b = 0.62 \pm 0.11$) is significantly different from unity ($t_b = 6.405$, $P < 0.05$). Likewise, with larval overcrowding, the equation of regression line is $Y = -0.39 + 0.63X$. The regression coefficient differs also significantly from unity ($t_b = 5.899$, $P < 0.05$). As both coefficients of regression are less than unity, a frequency dependent sexual selection exists in both instances. Fig. 1, in addition to showing graphically the existence of frequency-dependent sexual selection, suggests that this selection is not the same

Table 2 Coefficients of sexual selection

	Proportions	Z_m	t	Exact test	Z_f	t	Exact test
Low competition	50:50	5.37 ± 0.39	18.23	***	1.50 ± 0.21	4.12	***
	80:20	2.07 ± 0.28	5.93	***	0.91 ± 0.19	-0.82	
	90:10	2.00 ± 0.36	4.18	***	0.80 ± 0.24	-1.44	
	95:5	2.11 ± 0.55	3.21	**	1.33 ± 0.45	1.27	
Overcrowding	50:50	2.26 ± 0.20	11.59	***	1.04 ± 0.14	0.49	
	80:20	1.43 ± 0.21	3.62	**	1.04 ± 0.18	0.38	
	90:10	1.47 ± 0.30	2.13	*	1.10 ± 0.27	0.64	
	95:5	0.72 ± 0.22	2.12		0.87 ± 0.24	-0.94	

* Significant at 0.05 level.

** Significant at 0.01 level.

*** Significant at 0.001 level.

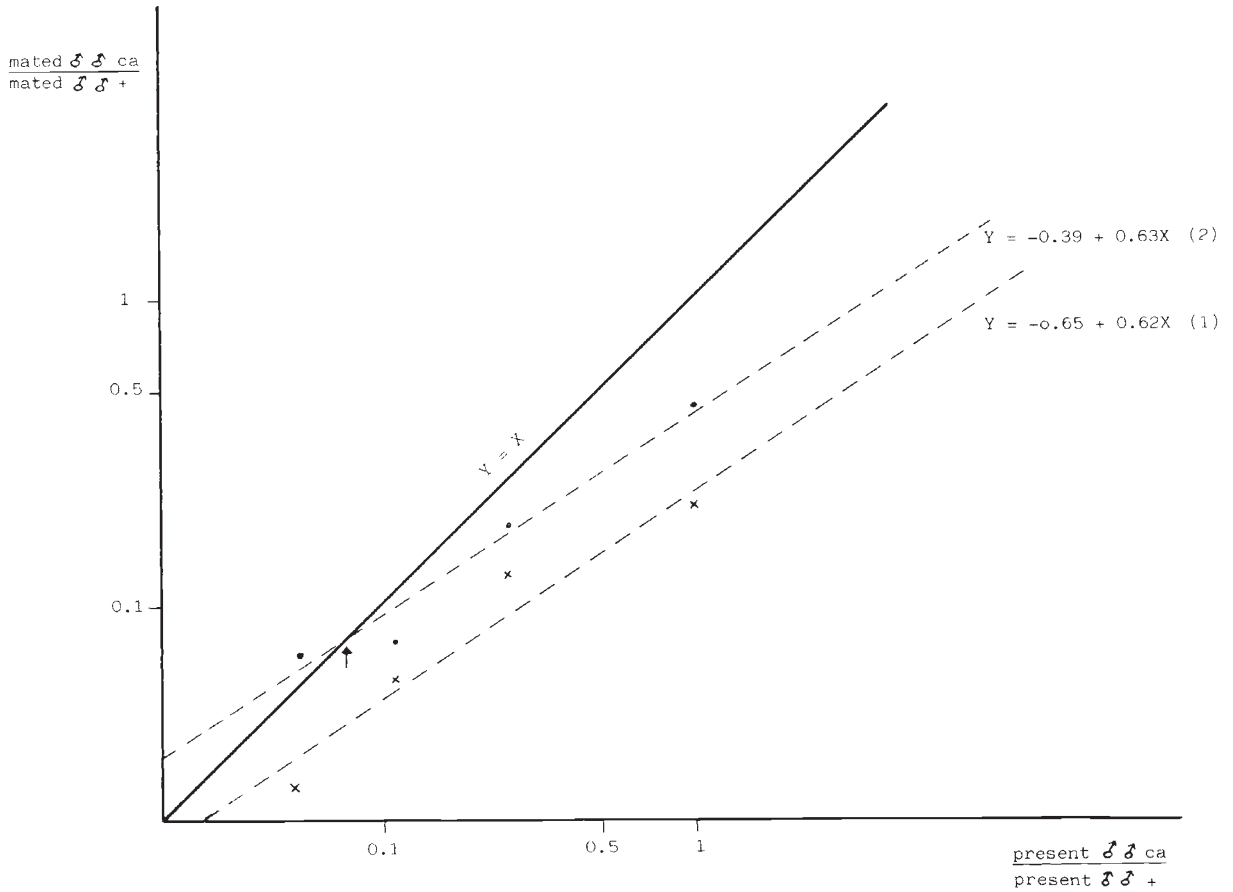


Figure 1 Linear regression of the logarithm of the ratios of males having mated on the logarithm of the ratios at which the males were present, in low competition (1) and crowded conditions (2). The ratio at which the two types of males have identical mating success is given by $Y = X$.

for males raised under low larval conditions as for males raised under crowded conditions, being both straight parallel lines. A comparison of the two equations of regression indicates that they differ significantly ($F = 9.7, P < 0.05$ for $F_{2,6}$). Furthermore, only the regression line $Y = -0.39 + 0.63X$ intersects the line $Y = X$ at a point which represents the frequency at which the two types of males would have identical mating success. This would be the equilibrium frequency of mutant males in the population if no selective forces other than sexual selection operated in these experimental populations.

DISCUSSION

Several experimental works show that in *Drosophila* populations, the mating success,

specially in males, differs from one genotype to another. There is a great bulk of literature on this subject, cited by Petit and Eherman (1969), Ehrman and Parsons (1981), Spiess (1970, 1982, a, b), and Bryant *et al.* (1980). Furthermore, several authors have pointed out that in *Drosophila*, male mating success is the most important component of fitness, both in laboratory populations (Merrell and Underhill, 1956; Prout, 1971a, b; Bundgaard and Christiansen, 1972; Anderson and Watanabe, 1974) and in natural populations (Anderson *et al.*, 1979).

Recently, some authors have questioned the existence of the phenomenon of rare male mating advantage in *Drosophila* (Bryant *et al.*, 1980; Markow, 1980; Partridge and Gardner, 1983), pointing out that it could be due to an experimental bias. For example, Markow noticed that males near the top of bottles were more active and vigorous

than males from the bottom of bottles and that these could have been unconsciously chosen by the experimenter. On the other hand, Bryant *et al.* (1980) found that the process of marking flies in order to recognize them in direct observation of matings may bias the results of mating success. Partridge and Gardner (1983) were unable to obtain the same results as Spiess and Kruckeberg (1980) and they attribute the differences of the results to a weakness in the type of experimental design used by these authors. Nevertheless, Anderson and Brown (1984) conclude that rare male mating advantage is not always an experimental or methodological artifact but does occur in laboratory populations of *D. pseudoobscura*. The results obtained in our experiments once more demonstrate the existence of the phenomenon of the rare male type in *D. melanogaster* since the choosing of individuals for mating experiments is done at random, when the flies are not marked because they can be easily distinguished by their phenotype. We show, on the other hand, an important effect on mating propensity of adults related to the level of larval crowding. When larvae have been developed in low competition, differences of mating propensity between mutant males and wild

type ones are very important, but when cultures are very crowded, mutant males have, relatively, more success in obtaining mates than before. Rivalry undergone during larval phase does not modify frequency-dependent sexual selection, as the parallelism of the two regression lines demonstrates. It can be asserted that frequency-dependent sexual selection is independent of selection by density.

Spiess and Spiess (1969), when studying some factors that influence mating propensity in *D. persimilis*, found that the high density among larvae produces significantly less matings while the low density significantly increases mating propensity, both in KL and MD karyotypes. Clark and Feldman (1981), looking for the effects of larval density on components of fertility fitness with two mutant lines of *D. melanogaster* (*pol* and *ey*²) found important changes in mating success: in both cases, the relative mating success of *ey*² increased at high density, while the mating success of *pol* relative to the hybrids increased in females and decreased in males.

In a previous study (Ribó, 1976), natural selection of the mutant *caramel* in competition with its wild type allele has been followed in three experi-

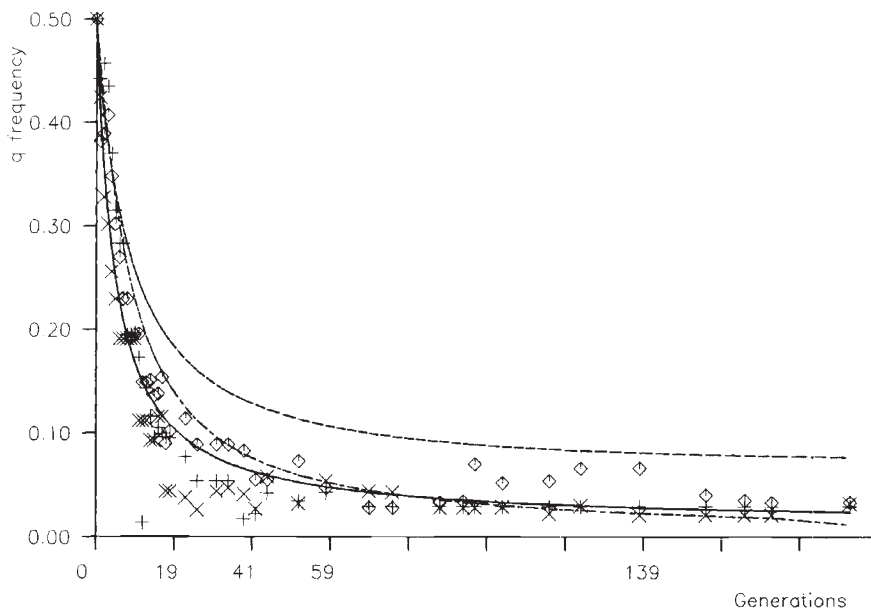


Figure 2 Evolution of gene *caramel* frequencies in the three experimental populations and the three theoretical models. \times , C_1 population; +, C_2 population; \diamond , C_3 population; ---, sexual selection frequency-dependent model (1); - · - ·, larval viability and developmental time model (2); —, combined model (1 and 2).

mental populations (populations C_1 , C_2 and C_3 in fig. 2). These populations have been initiated with 50 per cent of the mutant gene in heterozygous combination. After 200 generations, the frequency of the mutant gene *caramel* was about 0.03 in the three populations. The major conclusions of that study were that viability egg to adult, development time, and sexual selection were the most important components of fitness in its evolutionary process. The only one to be frequency-dependent was sexual selection. Therefore, in these populations net fitness was not constant. In order to see the relative importance of these components in the changes observed in gene frequencies in the experimental populations, we have calculated the expected changes on the *caramel* allele frequency under (1) frequency dependent sexual selection alone, (Model 1); (2) viability and developmental time from egg to adult fitnesses, (Model 2); and (3) the three components of fitness combined together (Model 3). For these calculations we have utilized the values found experimentally (Ribó, 1976). The rationale of these models is outlined in the Appendix.

In fig. 2 the frequencies observed during the evolution of the three experimental populations (C_1 , C_2 and C_3) are plotted and we have also represented the three theoretical curves. Model 1 takes into account only frequency-dependent sexual selection. The coefficient of selection at the beginning is very strong ($s = 0.68$) because the level of larval crowding is not yet very high, but it decreases as the mutant gene frequency becomes less frequent and larval crowding increases. This model does not satisfactorily explain the evolutionary process. The poorness of this fit may be due to the role of viability and developmental time. Model 2 takes into account the viability and developmental time from egg to adult with a constant coefficient of selection of $s = 0.32$ ($w_{22} = 0.72$ and $w_{22} = 0.94$ for larval viability and developmental time, respectively). In this combined model the fit is better than with the model of sexual selection alone, but the theoretical curve indicates that selection is more powerful in the first generations. In this model, too, the final frequency of mutant allele is slightly lower than the observed one (0.01 versus 0.03). Finally, Model 3, which combines the Models 2 and 1, agrees perfectly with the experimental results obtained. Other components of selection in addition to larval viability, developmental time and male mating success, may operate in experimental populations—for example fecundity and fertility—but the combined model presented here indicates that these three com-

ponents account for the greater part of total selection at the *caramel* locus.

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APPENDIX

The expected frequencies according to the hypothesis discussed in this paper have been obtained from the equations resulting from the following, straightforward, reasoning:

Let q be the frequency of the *caramel* allele. Let $S_M(q)$ be the selection coefficient against *caramel* males. It is assumed to be in some cases frequency-dependent. For example, if sexual selection (frequency-dependent), developmental time and viability were considered (Model 3), it would be:

$$S_M(q) = 1 - (0.318q^{-0.44}) \times 0.94 \times 0.72 \quad (\text{A.1})$$

where $0.318q^{-0.44}$ is the fitness for sexual selection component, fitted according to Ayala (1972), 0.94 is the fitness for developmental time and 0.72 is the fitness for viability (from Ribó, 1976). Finally, let S_F be the (non depending on q) selection coefficient against *caramel* females. In any case, the fitness for sexual selection is assumed to be one.

When a fitness component is not considered, the corresponding factor on the right side of (A.1) is assumed to be one. More precisely, Model 1 assumes a selection coefficient, frequency-dependent, against *caramel* males of

$$S_M = 1 - (0.318q^{-0.44})$$

as no selection for developmental time and no selection for viability are considered; Model 2 assumes a (frequency-independent) selection coefficient of

$$S_M = 1 - 0.94 \times 0.72 = 0.32$$

as only selection for developmental time and for viability are considered.

Then, the mean fitnesses for males and females are:

$$\begin{aligned}\bar{W}_M &= (1-q)^2 + 2q(1-q) + q^2(1-S_M(q)) \\ &= 1 - q^2 S_M(q) \\ \bar{W}_F &= 1 - q^2 S_F\end{aligned}\quad (\text{A.2})$$

and the frequencies in the next generation:

$$\begin{aligned}q'_M &= \frac{q - q^2 S_M(q)}{1 - q^2 S_M(q)} \\ q'_F &= \frac{q - q^2 S_F}{1 - q^2 S_F}\end{aligned}\quad (\text{A.3})$$

and

$$q' = \frac{1}{2}(q'_M + q'_F). \quad (\text{A.4})$$