Male mating success and fertility in *Drosophila melanogaster*

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SUMMARY

The male mating ability and male fertility of 40 third chromosome homozygote lines has been measured. There was significant between-line differentiation for both characters, and comparison with a heterozygous stock indicated inbreeding depression and hence dominance variation for them. The characters showed significant positive correlation both with each other and with other fitness components and total fitness, as measured by Mackay (1985). This pattern of large positive correlations between fitness components is not expected to occur in outbred populations.

1. INTRODUCTION

Several studies have generated results implying that in *D. melanogaster* the male reproductive component of fitness may be a very important one. For example Prout (1971) and Bundgaard & Christiansen (1972) found that male 'virility' (a combination of fertility and mating success) was important in explaining the dynamics of artificial polymorphisms. Brittnacher (1981) has demonstrated in-breeding depression for virility while Sharp (1984) showed that the behavioural component of male mating success also shows marked inbreeding depression, suggesting that it, as well as male fertility, may be a fitness component.

It was the aim of the present study to evaluate the relationships between male mating success, male fertility and total fitness for different third chromosome homozygotes, so as to assess the contributions of variation in these two fitness components to total fitness.

2. MATERIALS AND METHODS

The lines used were derived from a stock collected in Death Valley, California, by Dr L. Nunney. The lines were constructed by Mackay (1985), and consisted of two replicates each of 41 lines made homozygous for their third chromosome and outbred for the other three. The total fitness of each line was measured by Mackay

(1985) using the balance technique of Sved & Ayala (1970) and Sved (1971). The method is based on balancing the third chromosome of each line against *TM3*. The heterozygote *TM3/+* is always fitter than both *TM3/TM3* (lethal) and *+/+*, so that the lines equilibrate at a relative frequency of *TM3/+* and *+/+* that depends upon the fitness of the latter (the former is assumed to be constant). Mackay (1985) also measured other fitness components and some quantitative characters.

The male mating success of 40 of these 41 lines was measured (the remaining line suffered a balancer breakdown before these experiments were started). Mating success was measured relative to that of males from an outbred stock made homozygous for the *yellow* mutant. Fifty individual wild-type males from each replicate of each line were used, and were allowed to compete with one *yellow* male for a mating with one *yellow* female. All flies used were 3-day-old virgins. The males were stored in pairs in glass shell vials (25 × 75 mm) containing Droshila food medium and at the start of the test the female was aspirated into the vial. The identity of the first male to mate was noted, and the vial was discarded, and not included in the analysis if mating did not occur within 1 h. Less than 5 % of vials came into this category. *Yellow* males were used because they constituted a standard competitor of fairly low male mating ability (Bastock, 1956), since the wild-type males from the balancer lines were themselves of low mating ability. *Yellow* females from long established stocks are more receptive than wild-type females (Bastock, 1956; Dow, 1976; Heisler, 1984), and were therefore suitable for use in these experiments. A competitive mating test was used because competitive tests are a more sensitive index of male mating ability (Sharp, 1982), and are anyway a more accurate reflection of normal culture conditions, where males are usually present in numbers in excess of receptive females. This measure takes into account only matings with virgin females, whereas *D. melanogaster* females will remate readily (Milkman & Zietler, 1974; Gromko, Sheehan & Richmond, 1980). However, rematings were probably relatively rare in Mackay's (1985) study because the generation time was 14 days, so that events during at most the first 4 days of adult life contributed to the measure of total fitness.

For measurement of male fertility, 20 wild-type males from each replicate of each line were put individually in vials with two virgin *yellow* females. After 4 days, the adults were removed, and the progeny cultured under relaxed competition and counted on day 14. The progeny were therefore hemizygous *yellow* males and heterozygous females. This measure of fertility includes an element of mating success since the male has to mate at least once for his fertility to be expressed, and progeny production will be increased by subsequent matings. The measure also ignores the importance of sperm competition in matings with inseminated females. The justification for ignoring these has been mentioned.

The culture medium was standard Edinburgh cornmeal-agar-molasses medium, and flies were kept at 25 °C.

3. RESULTS

Male mating success was expressed as the replicate mean of the proportion of the 50 matings that were with *+/+* males. The relationship between male mating success and total fitness is illustrated in Fig. 1. The variance between lines for male

mating success was highly significant ($F = 8\cdot6$; $P < 0.0001$), as was the correlation between male mating success and total fitness ($r = 0\cdot432 \pm 0\cdot016$ s.e.). In all cases the standard error of the correlation coefficients has been calculated empirically from the coefficients for the two replicates, to take into account the effects of genetic drift after their separation. The plot of male fertility against total fitness is shown in Fig. 2. The between-line variance was highly significant ($F = 14\cdot20$;
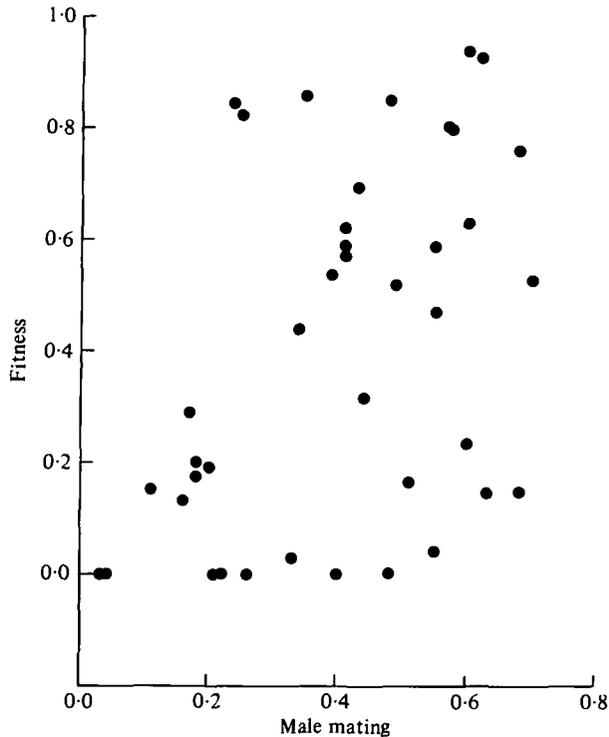
Figs. 1–3. Fitness profiles of male reproductive characters. Each point represents the mean for the male character of a third chromosome homozygous line, averaged over both replicates, plotted against the fitness estimated by Mackay (1985) for that line. Fig. 1. Relationship between male mating ability and fitness.

$P < 0\cdot0001$) and the correlation with fitness was high ($r = 0\cdot690 \pm 0\cdot093$ s.e.). Part of the correlation is accounted for by a cluster of 6 points very close to the origin. The male reproductive component of fitness (virility) is made up of a combination of mating success and fertility. The product of these two is plotted against total fitness in Fig. 3. The correlation was high and significant ($r = 0\cdot635 \pm 0\cdot145$).

The correlations between male mating ability, male fertility and the other fitness components and quantitative characters measured by Mackay (1985) are shown in Table 1. All except that with sternopleural bristles are significant, although that for abdominal bristles is low.

Both male mating ability and male fertility showed inbreeding depression. The mean values for these two characters for the third chromosome homozygotes and
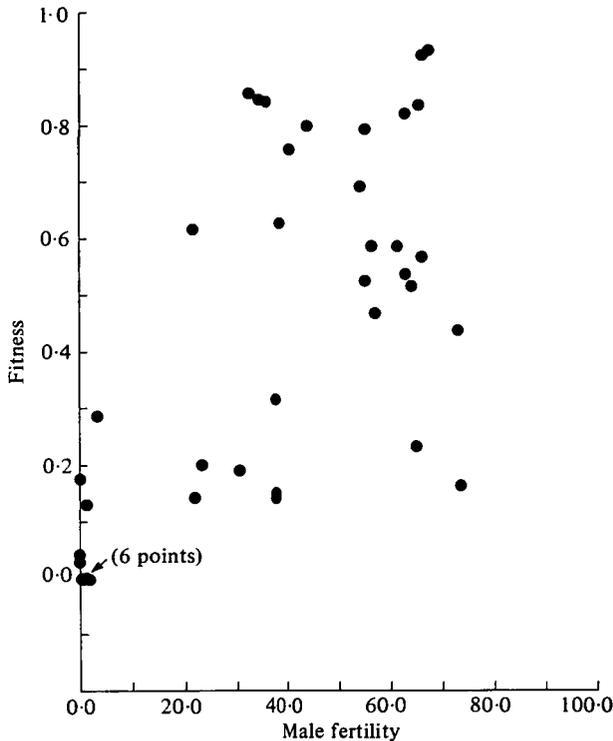
Fig. 2. Relationship between male fertility and fitness. The cluster of points at the origin represents six completely sterile lines.

for a heterozygous stock constructed from the lines (Mackay, 1985) is shown in Table 2. The results indicate that dominance is involved in the differentiation among lines for these two characters.

4. DISCUSSION

Male mating success and fertility have not previously been shown to be positively correlated in *D. melanogaster*, either phenotypically or genetically, and it would be interesting to investigate this correlation further in outbred flies. A phenotypic correlation between male mating success and fertility has been demonstrated in *D. subobscura* (Steele, 1984). Male mating success has been shown to be phenotypically correlated with size (Ewing, 1961, 1964; Ewing, 1978; Partridge & Farquhar, 1983) and the present results suggest that the genetic correlation across these partially inbred lines is also positive, as is that for fertility. The phenotypic correlation between male size and fertility has not yet been investigated; for females the genetic and phenotypic correlation has been shown to be positive (Robertson, 1957).

The present results confirm the earlier suppositions that the male reproductive component of fitness contributes to total fitness, since the correlation between them was positive. The components were measured using *yellow* females, whereas in
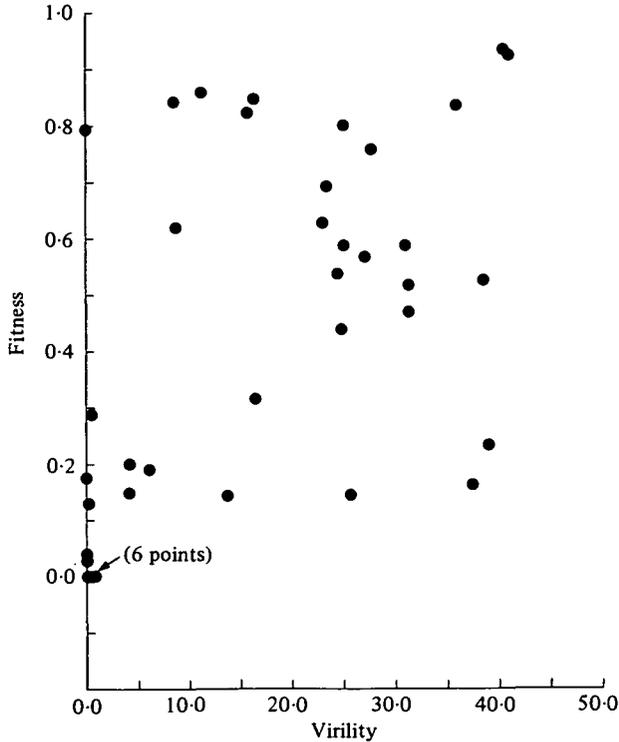
Fig. 3. Relationship between virility (male mating ability × male fertility) and fitness. The cluster of points at the origin represents six completely sterile lines.

Table 1. *Genotypic correlations (± s.e.) between male mating ability, male fertility, and the quantitative characters measured by Mackay (1985). Standard errors are empirical, estimated from variation between replicates*

	Male mating ability	Male fertility
Sternopleural bristle number	0·004 (0·081)	−0·180 (0·029)
Abdominal bristle number	0·179 (0·061)	0·155 (0·001)
Female productivity	0·518 (0·020)	0.688 (0·001)
Male weight	0·450 (0·022)	0.724 (0·049)
Viability	0·573 (0·034)	0·779 (0·031)
Total fertility	0·403 (0·075)	0.688 (0·042)
Male fertility	0·441 (0·057)	—

Table 2. *Inbreeding depressions, expressed as decrease in mean per 10 % increase in* F, *as a per cent of non-inbred mean. The average inbreeding coefficient of each third chromosome lines was estimated to be approximately* F = 0·65 *by Mackay (1985)*

	Mean of all homozygous lines $(\overline{X}_I)$	Mean of total heterozygous lines $(\overline{X}_H)$	Depression $\dfrac{0·1\,(\overline{X}_H-\overline{X}_I)\times 100}{F\overline{X}_H}$
Male mating ability	0·398	0·630	5·67
Male fertility	36·5	71·9	7·57

Mackay's (1985) experiment, the females were $TM3/+$ or $+/+$, so the correlations with total fitness could well be an underestimate. Both experiments largely ignored the contribution of matings with inseminated females, and these are likely to be important in the more natural situation of overlapping generations and higher adult longevity.

The inbreeding depression found in the present study confirms the findings of Brittnacher (1981) and Sharp (1984), and shows that both male mating success and fertility are affected. It is probably inappropriate to attempt a synthesis of the figures obtained because the measures used in the three studies are not directly comparable; Brittnacher's measurement probably gives a high emphasis to fertility and less to the behavioural aspect of virility, while Sharp's was probably mainly a behavioural measure with a slight fertility component.

The major source of variation in fitness between these lines was dominance, with different deleterious recessives becoming homozygous in different lines. Under these circumstances, correlations between different fitness components are in general high and positive (Rose, 1984; Mackay, 1985; Wright, 1977; Rose & Charlesworth, 1981), and the present results confirm this basic pattern. Their correlations in outbred populations may well not conform to this picture since total fitness is expected to show very low or zero heritability, so that overall genetic correlations between different fitness components will in general be low and not necessarily positive (Simmons, Preston & Engels, 1980).

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