

SHORT PAPERS

Competitive mating in *Drosophila melanogaster*

By PAUL M. SHARP

Institute of Animal Genetics, West Mains Road, Edinburgh EH9 3JN, Scotland

(Received 18 March 1982)

SUMMARY

Selective differences among male *Drosophila melanogaster* due to differences in ability to compete for mates may often have been under-estimated in the past because, under the test procedure used, females did not represent a limited resource. In the experiment reported here, no difference was detected between inbred and outbred males 'competing' to mate with an equal number of females. When the receptive female: male ratio was halved a large reduction in male mating ability due to inbreeding became apparent.

INTRODUCTION

A large body of work has been devoted to the estimation of the components of fitness in *Drosophila melanogaster*. Sexual selection, arising from differential success among males competing for mates, is recognized as being of major importance in this species (Prout, 1971; Bundgaard & Christiansen, 1972). Any fitness measurement is likely to be dependent upon the circumstances under which it is estimated, so that real differences in fitness may be overlooked if the competitive conditions are not appropriate. I would suggest that one technique that has often been used to assess male mating abilities (for example recently by Brittnacher, 1981; Clark & Feldman, 1981), in which males 'compete' to mate with an equal number of females, may be unsatisfactory for two reasons.

(1) In any continuous population the number of adult males seeking mates is likely to greatly exceed the number of females receptive at that time. Males are always willing to mate, but the majority of females, once inseminated, resist re-mating for a period of 4–6 days (Manning, 1962; Pyle & Gromko, 1978).

(2) The competitive ability of the weaker group is likely to be overestimated. This arises because copulation in *D. melanogaster* lasts for about 20 min (Fowler, 1973). If, as is usually observed, most of the stronger competitors are successful soon after the start of the test, then while they remain in copula the weaker group of males may court the residual females without significant competition.

In order to verify this second point I have tested inbred and outbred males, expected as a consequence of their genotypes to differ in competitive ability, against a standard mutant strain, under two sets of experimental conditions expected to provide different intensities of competition.

2. MATERIALS AND METHODS

All flies were derived from the Prevosti population cage, which had been initiated from a large collection made in the Canary Islands by Professor A. Prevosti. A large outbred 'scarlet' population was set up by inserting the *st* (scarlet-eyed) gene into the Prevosti background, by a combination of balanced marker chromosome and back-crossing techniques. Ten inbred lines were derived from the Prevosti population by full sib mating, and were tested after one generation (i.e. the males tested had an inbreeding coefficient $F = 0.25$). All flies used in tests were reared under conditions of minimal competition, and all anaesthesia was by CO_2 . All flies were 3–6 days old when tested, and all groups of competing males were matched for age.

The basic test regime involved 25 wild-type (outbred or inbred) males and 25 *st* males competing to mate with 50 *st* females. There were two types of tests:

(1) '50 ♀♀': 50 females were shaken into the test arena with the 50 males at the beginning of the test.

(2) '25 ♀♀ + 25 ♀♀': 25 females were added at the start, and a further 25 females 2 h later.

Approximately 5 h after the start of the tests the females were placed in individual vials, so that the genotype of their mate could be deduced from their progeny.

Under each set of conditions, two sets of 25 ♂♂ from each of five of the inbred lines were each tested twice (on consecutive days). Exactly equivalent experiments were also conducted with outbred 'lines', so that in all some 4000 matings were monitored.

3. ANALYSIS OF RESULTS

The male mating ability or virility of a group of males, relative to a specified standard, may be defined as a male competitive index, CI ♂ (Latter & Robertson, 1962). If Q and P represent the number of females inseminated by wild-type and *st* males respectively, then

$$\text{CI } \sigma = \frac{Q}{P}. \quad \text{Also CI } \sigma = \frac{\bar{q}}{1 - \bar{q}}$$

where q is the proportion of females mated by wild-type males ($q = Q/(Q + P)$). Results of replicate estimates are combined using \bar{q} , as this has preferred statistical properties. The standard error of this index was also derived by Latter & Robertson (although misprinted there):

$$\text{S.E. CI } \sigma = \frac{\sigma}{\sqrt{n(1 - \bar{q})^2}}$$

where σ^2 is the variance of the repeated measurements of q , and n the number of replicates.

The mean proportions of females inseminated by each of the tested lines are presented in Table 1. These are averaged over lines and converted into competitive indices in Table 2 and Fig. 1. It may be seen that when there was a 1:1 ratio of females to males at the start of the test, the competitive index of neither the outbred nor the inbred males differs significantly from 1.0 (no apparent selection). The estimates for the two types of males do not differ significantly from each other ($t_8 = 0.98$, $P > 0.20$). Under the revised set of test conditions the outbred males fare much better than either the *st* stock or the inbred males, the reduction due to inbreeding being highly significant ($t_8 = 4.00$, $P < 0.005$).

Table 1. Mean proportion, \bar{q} (and s.d.) of females inseminated by wild-type males, under two different test conditions. Each mean is derived from four tests

(i) 50 ♀♀		(ii) 25 ♀♀ + 25 ♀♀	
Outbred	Inbred	Outbred	Inbred
0.531 (0.021)	0.503 (0.054)	0.516 (0.023)	0.488 (0.043)
0.478 (0.027)	0.524 (0.053)	0.576 (0.099)	0.456 (0.047)
0.445 (0.058)	0.489 (0.045)	0.572 (0.072)	0.409 (0.077)
0.435 (0.075)	0.517 (0.039)	0.588 (0.082)	0.531 (0.018)
0.536 (0.051)	0.495 (0.019)	0.595 (0.056)	0.488 (0.051)

Table 2. Male competitive index, CI_{δ} , and standard error, for outbred and inbred males under different test conditions

50 ♀♀	25 ♀♀ + 25 ♀♀
0.942 (0.079)	Outbred 1.320 (0.075)
1.024 (0.027)	Inbred 0.901 (0.073)

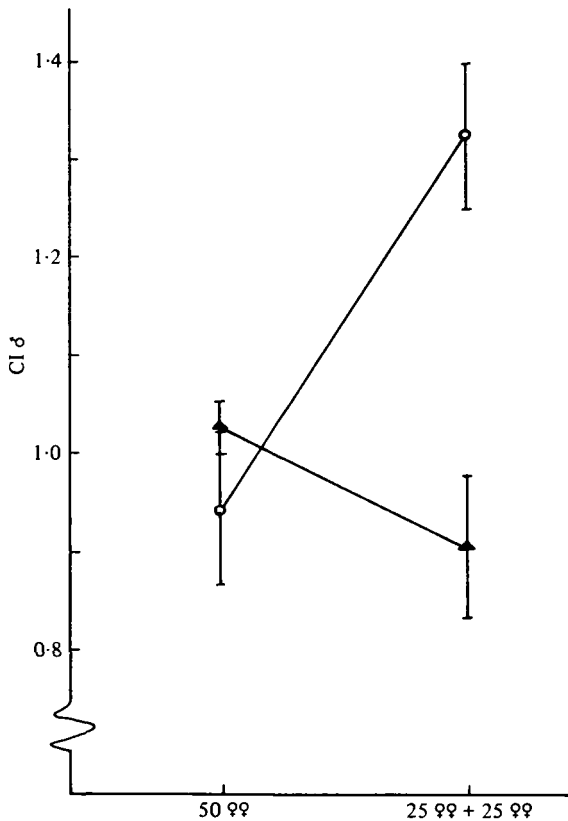


Figure 1. Effect of male:female ratio on male competitive index, CI_{δ} . '50 ♀♀': 1:1 male:receptive female ratio; '25 ♀♀ + 25 ♀♀': 2:1 male:receptive female ratio. ○, Outbred males; ▲, inbred males.

4. DISCUSSION

Multiple-choice competitive mating experiments are commonly a part of investigations of fitness in *Drosophila*. Care must be taken, however, in ensuring that the experimental conditions actually do induce inter-male competition. The results presented here suggest that when a group of males are supplied with an equivalent number of females little or no competition will occur. Under a set of conditions designed to intensify competition a previously undetected effect of reduced male mating ability, due to inbreeding, became apparent. Subsequent work has confirmed the estimate of CI ♂ for outbred flies under the revised procedure, and has also shown that continued inbreeding further reduces this component of fitness (Sharp, unpublished).

The importance of male mating ability as a component of fitness has previously been stressed (e.g. Parsons, 1974). Under certain experimental conditions it appears to be the major factor influencing gene frequency changes (Prout, 1971; Bundgaard & Christiansen, 1972). Although selective differences have been detected by these and other authors (Latter & Robertson, 1962; Åslund & Rasmuson, 1976; Clark & Feldman, 1981; Brittnacher, 1981) using the 1:1 male:female ratio, these differences may well have been underestimated by this technique. As a consequence the role of male mating ability in natural selection in *D. melanogaster* may yet have been understated.

An alternative revision of the testing procedure would simply be to use only one-half the number of females. However, since in this test scheme the unit of measurement is a single insemination, the ensuing reduction in the fineness of the scale of measurement would be undesirable. It is probable that under our revised test conditions most, if not all, of the first batch of females have been mated before the second batch are added, and it is proposed that competition for the second group of females is quite independent of the first half of the test. To reflect truly the extent of competition in the wild would probably require the use of an even lower receptive female:male ratio, although ecological evidence on this point is lacking. That selection for mates does occur in the wild among male *D. pseudoobscura* has been demonstrated (Anderson *et al.* 1979).

I wish to thank Dr Linda Partridge for critical reading of the manuscript. This work was supported by a Science Research Council Postgraduate Studentship, under the supervision of Professor Alan Robertson.

REFERENCES

- ANDERSON, W. W., LEVINE, L., OLVERA, O., POWELL, J. R., DE LA ROSA, M. E., SALCEDA, V. M., GASO, M. I. & GUZMAN, J. (1979). Evidence for selection by male mating success in natural populations of *Drosophila pseudoobscura*. *Proceedings of the National Academy of Sciences, U.S.A.* **76**, 1519–1523.
- ÅSLUND, S.-E. & RASMUSON, M. (1976). Mating behaviour as a fitness component in maintaining allozyme polymorphisms in *D. melanogaster*. *Hereditas* **82**, 175–178.
- BRITTNACHER, J. G. (1981). Genetic variation and genetic load due to the male reproductive component of fitness in *Drosophila*. *Genetics* **97**, 719–730.
- BUNDGAARD, J. & CHRISTIANSEN, F. B. (1972). Dynamics of polymorphisms. 1. Selection components in an experimental population of *Drosophila melanogaster*. *Genetics* **71**, 439–460.
- CLARK, A. G. & FELDMAN, M. (1981). The estimation of epistasis in components of fitness in experimental populations of *Drosophila melanogaster*. II. Assessment of meiotic drive, viability, fecundity and sexual selection. *Heredity* **46**, 347–377.
- FOWLER, G. L. (1973). Some aspects of the reproductive biology of *Drosophila*: sperm transfer, sperm storage, and sperm utilization. *Advances in Genetics* **17**, 293–360.

- LATTER, B. D. H. & ROBERTSON, A. (1962). The effects of inbreeding and artificial selection on reproductive fitness. *Genetical Research* **3**, 110–139.
- MANNING, A. (1962). A sperm factor affecting the receptivity of *Drosophila melanogaster* females. *Nature* **194**, 252–253.
- PARSONS, P. A. (1974). Male mating speed as a component of fitness in *Drosophila*. *Behavior Genetics* **4**, 395–404.
- PROUT, T. (1971). The relation between fitness components and population prediction in *Drosophila*. I. The estimation of fitness components. *Genetics* **68**, 127–149.
- PYLE, D. W. & GROMKO, M. H. (1978). Repeated mating by female *Drosophila melanogaster*: the adaptive importance. *Experientia* **34**, 449–450.