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Influence of Ocular Morphology on Mating Speed and Duration of Copulation in *Drosophila Melanogaster*

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Abstract

The possible effects on the sexual behaviour of *D. melanogaster* of mutants in which sensory organs needed for mating are affected were studied. Four ocular mutants were used and two parameters of sexual behaviour were measured: mating speed and duration of copulation. A clear influence of the mutants was observed on mating speed but not on duration of copulation. The influence on mating speed was greater for the mutants with more severe morphological phenotypes.

Introduction

Although sexual behaviour may be one of the most important factors determining fitness in natural populations of *Drosophila*, it is a very complex process, involving the transmission and reception of sound, odour, taste, tactile and visual stimuli (Tompkins 1984). Sexual behaviour can be modified by mutations in sensory organs (e.g. Siegel and Hall 1979; Markow and Manning 1980; Tompkins *et al.* 1980; Ochando 1981; Willmund and Ewing 1982). In this work we analyse the influence on mating speed and duration of copulation of four morphological eye mutants from a natural population of *D. melanogaster*.

Materials and Methods

A natural population of *D. melanogaster* from Asturias, Spain, was used. By inbreeding the F_1 from 106 wild-caught females, four mutant phenotypes were obtained. In these mutants the ocular morphology of the flies was affected. After isolation of the mutants several generations of mass backcrosses between the mutant strains and a mass culture derived from the original population, without inbreeding, were carried out, in order to achieve similar genetic backgrounds in the four mutants.

Two of the mutants were identified by allelism tests as white-apricot (w^a) and glass (*gl*). The other two mutants, *m* and *r*, were not systematically compared with known mutants but showed the following characteristics:

m: eyes of reduced size with an expressivity ranging from no eyes to almost wild-type; ocular pigments and omatidia unaltered;

r: ovoid eyes; omatidial structure altered, glossy surface and a dark red colour (xanturenic acid and aurodrosopterin absent and neodrosopterin reduced, referred to Oregon-R strain level).

A wild-type strain (*N*), without inbreeding, from the same population was also used.

Sexual behaviour was assessed from direct observations of matings among previously unmated pairs, 48 h old and with the same environmental conditions (25°C, 12 h light and 12 h darkness). Pairs were tested without exposure to ether in individual vials. The observation period was 60 min, and always at the same hour of the day (10–11 a.m.).

Two parameters were measured: mating speed (time from when the male and female are introduced into the same vial until copulation began) and duration of copulation. Fifty trials were carried out for each of the 25 possible combinations of genotypes.

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Results

Table 1 presents the mean mating speed and the total number of matings recorded for each of the 25 different genotypic combinations. Two statistical analyses were made with these data. First, a contingency χ^2 test with the number of unmated pairs, which was not significant ($\chi^2 = 2{\cdot}81$, $P > 0{\cdot}05$). Second, an analysis of variance with all pairs to detect possible differences in mating speed. In the calculation of mating speeds a value of 61 min was assigned to unmated pairs (Parsons 1964). The males quickest to mate were w^a and wild phenotypes, and the slowest males were *r* and *gl*. The females quickest to mate were *r* and *gl* and by far the slowest females were *N*.

Table 1. Mean mating speed (in minutes) and total number of matings (in parenthesis) of several mutant phenotypes of *Drosophila melanogaster*

Female	Male					Mean
	N	*gl*	*m*	*r*	w^a	(Totals)
N	26·96	42·46	33·20	47·12	19·94	32·94
	(33)	(22)	(29)	(20)	(43)	(147)
gl	13·32	28·78	15·72	26·10	12·12	19·21
	(44)	(36)	(43)	(37)	(46)	(206)
m	21·28	26·96	12·24	30·18	15·54	21·24
	(39)	(38)	(46)	(33)	(42)	(198)
r	13·54	25·36	18·68	26·76	11·18	19·10
	(46)	(37)	(40)	(40)	(46)	(209)
w^a	14·10	36·86	15·94	32·82	13·94	22·73
	(42)	(29)	(42)	(34)	(43)	(190)
Mean	17·84	32·08	19·16	32·60	13·54	23·04
(Totals)	(204)	(162)	(200)	(164)	(220)	(950)

Table 2. Mean duration of copulation (in minutes) of several mutant phenotypes of *Drosophila melanogaster*

Female	Male					Total
	N	*gl*	*m*	*r*	w^a	mean
N	19·33	20·00	20·10	19·60	20·37	19·88
gl	16·73	19·61	18·23	18·73	19·09	18·48
m	20·38	19·16	20·52	20·91	19·83	20·16
r	19·11	20·08	19·17	20·00	19·02	19·48
w^a	21·26	19·52	20·38	20·44	21·19	20·56
Total mean	19·40	19·67	19·68	19·94	19·90	19·71

The mating speed data were normalized and made homoscedastic by a cube root transformation (Pyle and Gromko 1981). An analysis of variance of the transformed mating time indicated that the differences between genotypes were significant for both sexes ($F_{4,16} = 26{\cdot}32$; $P < 0{\cdot}01$, for males and $F_{4,16} = 8{\cdot}86$; $P < 0{\cdot}01$, for females). Importantly, the analysis also indicated that there were no significant interaction effects ($F_{16,925} = 0{\cdot}45$; $P > 0{\cdot}01$). We further analysed these significant effects by a multiple comparison (Student–Newman–Keuls) test. The results of this test showed that there were significant differences between normal and mutant females. And, in the case of males, it appeared to be three significantly different groups: *r* and *gl* mutants, *m* and *N* genotypes, and w^a.

Mean values of the duration of copulation, for all combinations of genotypes, are shown in Table 2. These values are within the intervals considered normal for *D. melanogaster*,

15–25 min (MacBean and Parsons 1967), clustering between 16·7 and 21·3 min. The average values for different genotypes are more similar among males than females. However, an analysis of variance did not show significant main effects of genotype for either sex ($F_{4,16} = 4{\cdot}4$ for females, and $F_{4,16} = 0{\cdot}28$ for males, $P > 0{\cdot}01$), nor any interaction between them ($F_{16,925} = 0{\cdot}86$, $P > 0{\cdot}01$).

Discussion

Four mutants in which ocular morphology was affected and isolated from a natural population were found to differ in mating speed but not on duration of copulation. The homogeneity of the results for duration of copulation is consistent with previous studies showing that the duration of copulation varies very little within species (Spiess 1968). On the other hand, genotypic differences in mating speed were apparent in the present study both among males and among females. However, the Student–Newman–Keuls test does not show significant differences among mutant females, the order of the different genotypes according to their mating speed was: $w^a > N > m > gl > r$ for males and $r > gl > m > w^a > N$ for females.

Two salient features of these orders deserve comment. First, these orders among males and females are almost the reverse of each other. Second, there seems to be a relationship between the severity of the mutant phenotype and its effects on sexual activity: w^a presents only pigment alteration; *m*, only reduced eye size; and *gl* and *r* present pigment composition, number, and structure of facets altered.

In relation to this point it is not surprising that males with the most severe mutant phenotypes mate least well. However, it is not immediately obvious why females with more severe phenotypes should mate more readily. It could well be that the greater number of matings made by females of more severe phenotypes is due to their lower sexual receptivity threshold (Mainardi and Mainardi 1966; Spiess and Schwer 1978) and that these are more easily overcome by the males. However, the behavioural effect is weaker in females than in males.

The results thus support the argument of Fuller and Thompson (1960) that mating is the outcome of two opposite tendencies, the copulation tendency of males and the avoidance tendency of females.

In terms of physiological mechanisms, it seems likely that the altered mating behaviour of the four ocular mutants analysed are at least partly the result of visual impairment. However, it is also likely that the mutants may have pleiotropic effects on the central nervous system. These effects could alter the general activity of individuals (Burnet and Connolly 1973) and, consequently, their sexual activity and thus their tendency to courtship (Hall *et al.* 1980) and copulation.

Finally we draw attention to the fact that the four mutants we have analysed all existed as polymorphisms in the source natural population. In fact, all of them appeared in further captures always in low frequencies. Only ocular phenotypes were investigated but mutations in many other characters could have direct or pleiotropic effects on mating behaviour (see Ehrman and Parsons 1981 and Tompkins 1984 for references). It is suggested, therefore, that substantial genetic variance may exist in natural populations of *D. melanogaster* which affect reproductive fitness.

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References

Burnet, B., and Connolly, K. (1973). The visual component in the courtship of *Drosophila melanogaster*. *Experientia* **29**, 488–9.

Ehrman, L., and Parsons, P. A. (1981). 'Behavior, Genetics and Evolution.' (McGraw-Hill Book Co.: New York.)

Fuller, J. L., and Thompson, W. R. (1960). 'Behavioral Genetics.' 1st Edn. (John Wiley: New York.)

Hall, J. C., Siegel, R. W., Tompkins, L., and Kyriacou, C. P. (1980). Neurogenetics of courtship in *Drosophila*. Stadler Symp., Univ. of Missouri, Columbia. Vol. 12, pp. 43–82.

MacBean, I. T., and Parsons, P. A. (1967). Directional selection for duration of copulation in *Drosophila melanogaster*. *Genetics* **56**, 233–9.

Mainardi, D., and Mainardi, M. (1966). Sexual selection in *Drosophila melanogaster*. The interaction between preferential courtship of males and differential receptivity of females. *Atti Soc. Ital. Sci. Nat.* Vol. CV. Fasc. III.

Markow, T. A., and Manning, M. (1980). Mating success of photoreceptor mutants of *Drosophila melanogaster*. *Behav. Neural Biol.* **29**, 276–80.

Ochando, M. D. (1981). Mating behaviour and analysis of eye pigmentation of several mutants of *Drosophila melanogaster*. *Genetica* **55**, 117–21.

Parsons, P. A. (1964). A diallel cross for mating speeds in *Drosophila melanogaster*. *Genetica* **35**, 141–51.

Pyle, D. W., and Gromko, M. H. (1981). Genetic basis for repeated mating in *Drosophila melanogaster*. *Am. Nat.* **117**, **2**, 133–46.

Siegel, R. W., and Hall, J. C. (1979). Conditioned responses in courtship behaviour of normal and mutant *Drosophila*. *Proc. Natl Acad. Sci. U.S.A.* **76**, 3430–4.

Spiess, E. B. (1968). Courtship and mating time in *Drosophila pseudoobscura*. *Anim. Behav.* **16**, 470–9.

Spiess, E. B., and Schwer, W. A. (1978). Minority mating advantage of certain eye colour mutants of *Drosophila melanogaster*. I. Multiple choice and single female tests. *Behav. Genet.* **8**, 2.

Tompkins, L. (1984). Genetic analysis of sex appeal in *Drosophila*. *Behav. Genet.* **14**(5), 411–40.

Tompkins, L., Hall, J. C., and Hall, L. (1980). Courtship-stimulating volatile compounds from normal and mutant *Drosophila*. *J. Insect Physiol.* **26**, 689–97.

Willmund, R., and Ewing, A. (1982). Visual signals in the courtship of *Drosophila melanogaster*. *Anim. Behav.* **30**, 209–15.

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