

## REDUCED REPRODUCTIVE SUCCESS FOR A CONDITIONING MUTANT IN EXPERIMENTAL POPULATIONS OF *DROSOPHILA MELANOGASTER*

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### ABSTRACT

Male *Drosophila melanogaster* that have courted newly-emerged males can modify their subsequent courtship behavior to avoid further courtship with immature males for up to 6 hr (previously reported). Here, it was hypothesized that such an experience-dependent modification would afford a mating advantage to normal males over males that carried a mutation that affects learning and memory. Coisogenic lines were constructed which varied at the dunce gene ( $dnc^+$  and  $dnc^{M14}$  alleles) in order to test this hypothesis. Whether previously experienced with immature males or not,  $dnc^+$  and  $dnc^{M14}$  males were indistinguishable in their response and mating efficiency when individually paired with virgin females. However, courtship performance of  $dnc^+$  and  $dnc^{M14}$  males was different if they were first experienced with immature males and were then individually tested in an artificial population of nine immature males and one virgin female. In this situation,  $dnc^+$  males spent much less time in courtship with immature males and achieved copulation in one-third the time required for  $dnc^{M14}$  males. As a control, the behavior and mating efficiency of courtship-naïve  $dnc^+$  and  $dnc^{M14}$  males in the artificial population was indistinguishable. In competition for a single virgin female, experienced  $dnc^{M14}$  males showed a slight mating advantage over experienced  $dnc^+$  males. But when competition by experienced males for a single virgin female took place in the presence of nine immature males,  $dnc^+$  males were the successful maters in three-fourths of the trials.

**S**EXUALLY mature male *Drosophila melanogaster* not only court and copulate with virgin females, they also exhibit what appears to be fruitless courtship behavior with objects of "ardor" that do not (or rarely) copulate. Males court fertilized females (e.g., BASTOCK and MANNING 1955), and they court newly emerged, sexually immature adults—both females (MANNING 1967) and males (JALLON and HOTTA 1979). Males that have performed such courtship can be conditioned to modify their subsequent behavior. Courtship of fertilized females can result in a depressed response to subsequent virgin females (SIEGEL and HALL 1979; GAILEY, JACKSON and SIEGEL 1984), and courtship of immature males can result in a subsequent avoidance of further courtship with immature males (GAILEY, JACKSON and SIEGEL 1982). Both these

effects are transient (lasting on the order of hours) and appear to be conditioning-like or "learned" responses (reviewed by SIEGEL *et al.* 1984).

We report here a practical test of the hypothesis that the ability to express such conditioned courtship can afford a selective advantage. We have constructed coisogenic strains which are different from each other at a locus involved in learning and memory (*dunce*, DUDAI *et al.* 1976). The courtship and mating potential of males from these strains is very different with respect to populations in which virgin females are rare and immature males are common.

#### MATERIALS AND METHODS

Fly stocks were maintained at 25° on a medium of cornmeal, sucrose, agar and yeast. Details of collection procedures and treatment of flies before testing have been previously described (GAILEY, JACKSON and SIEGEL 1982). In brief, males whose courtship was to be monitored were collected under light ether anesthesia, isolated in food vials, and tested on the fourth day after eclosion. Virgin females were treated in a similar fashion, but were grouped ten per vial. Newly emerged flies were collected by aspiration and then were used in tests before 8 hr after emergence. All virgin females and newly emerged flies were collected from a Canton-S strain. Test males carrying either the *dnc*<sup>+</sup> or *dnc*<sup>M14</sup> allele were generated from stocks for which the derivation is described below.

Mutant *dnc* alleles appear to result in aberrantly brief memory when they are hemizygous or homozygous (reviewed by QUINN and GREENSPAN 1984). Flies expressing mutations at this locus have increased levels of cyclic AMP compared with wild type, due to a defect in Form II of the enzyme cyclic-AMP phosphodiesterase (PdE II, reviewed by DAVIS and KAUVAR 1984). The *dnc*<sup>M14</sup> allele was isolated as a female-sterile mutation (MOHLER 1973) and was later found also to affect shock-odor associative conditioning (BYERS, DAVIS and KIGER 1981). No form II PdE activity is detectable in *dnc*<sup>M14</sup> flies, and it thus is interpreted to be a null allele (DAVIS and KAUVAR 1984). The female-sterile and enzyme-defect phenotypes cannot be separated by recombination (SALZ, DAVIS and KIGER 1982). The *dnc*<sup>M14</sup> stock that was the starting point for this study carries the recessive markers *y* (yellow cuticle), *cv* (crossveinless wings), *v* (vermilion eye color) and *f* (forked bristles), and it is maintained with the *FM7* balancer chromosome.

One exigency in experimental design was the behavioral comparison of males carrying a normal *dnc* allele with males carrying a null allele of *dnc*—but whose genetic backgrounds were essentially isogenic. Such stocks were established simultaneously in the series of crosses given in Figure 1. Since the *dnc* gene resides at a locus much closer to *y* than *cv* (region 3D of the X-chromosome; BYERS, DAVIS and KIGER 1981), it is consistent that only one of the 60 recombinant *cv v f* lines established in cross 2 showed female sterility (*i.e.*, expressed the *dnc* mutation), and that when "+" recombinants were selected from that line (cross 4), three of the five lines established were female-sterile. One female-fertile line and one female-sterile line were selected for subsequent behavioral analysis and are designated *dnc*<sup>+</sup> and *dnc*<sup>M14</sup>. Experimental males were generated by crossing either *dnc*<sup>+</sup>/*FM7* or *dnc*<sup>M14</sup>/*FM7* heterozygous females to *FM7* males derived from an independently maintained *FM7* homozygous stock.

All experiments were carried out under normal room light at 25° and 60% relative humidity. For each session of behavioral observations, equal numbers of *dnc*<sup>+</sup> and *dnc*<sup>M14</sup> males were always tested in a particular experimental protocol, and the vials housing the males were encoded so that the genotype of the test male was unknown to the experimenter until after an experiment was completed.

The experimental sequence for most of the behavioral tests was as follows. An individual male was first given 30 min of courtship experience with either a single newly emerged male or a single newly emerged female in the 0.4 cm<sup>3</sup> chamber of a plastic "mating wheel" (HOTTA and BENZER 1976); one control experiment was carried out in which males were merely isolated in chambers for 30 min. All males were then returned to their original food vials for either 1, 3 or 6 hr before their subsequent courtship was observed. A *dnc*<sup>+</sup> or a *dnc*<sup>M14</sup> male was introduced into a fresh

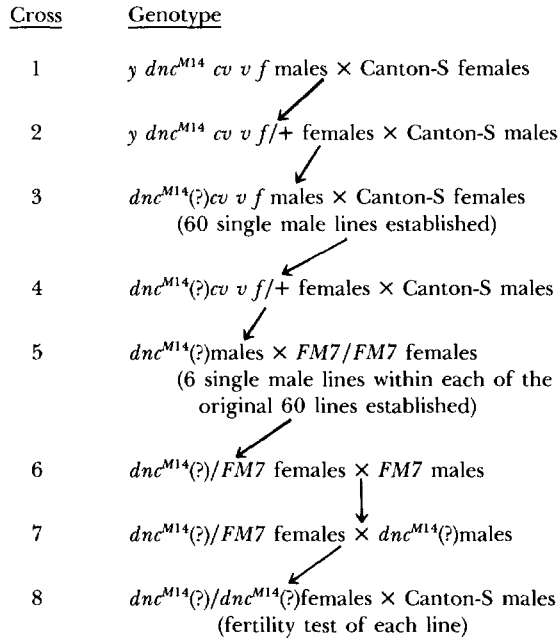


FIGURE 1.—The generation of  $dnc^+$ ,  $dnc^{M14}$  coisogenic lines.

food vial (25 mm in diameter by 95 mm) containing nine newly emerged males and one virgin female, and for a period of 10 min the following events were recorded: (1) the total amount of courtship (see below) displayed with immature males and the virgin female and (2) the number of courtship bouts initiated with these males and the virgin female. If copulation occurred in less than 10 min, then the time at copulation was recorded as the length of the observation period for that particular male (and this value was used in computing the courtship "vigor"; see below). Males that had not copulated at the close of the courtship measuring period were, thereafter, monitored only for copulation; if no copulation was observed in 30 min, the observation was terminated at that point.

In the course of experiments, there were several cases in which the female did not copulate within the 30-min observation period (see RESULTS). To test for mating potential in such a case, the test male and virgin female were immediately isolated from the immature males and were paired in a small mating-wheel chamber. In this more restrictive condition, copulation occurred in every case within 10 min. Therefore, in the calculation of the mean time at copulation, these males were assigned the value 30.0 min.

From the raw data recorded as above, the following parameters of courtship in the test period were quantified for each male: (1) the total Courtship Index (CI, or the percentage of time within an observation period in which a male expressed courtship behavior) with newly emerged males and the CI with the virgin female (see TOMPKINS 1984 for a review of earlier usage of this parameter); (2) the average number of courtship bouts initiated per minute of the observation period with newly emerged males and the virgin female; and (3) the average courtship bout length with a newly emerged male and with the virgin female. Twenty males of each genotype were tested in a particular experimental protocol, and the values of the above-listed courtship parameters are given as mean  $\pm$  SEM.

## RESULTS

*Courtship response to an individual immature male or virgin female:* Preliminary experiments were first carried out to measure the courtship response of the

TABLE 1

*The courtship response of  $dnc^+$  and  $dnc^{M14}$  males to immature males (IM) and virgin females*

Pretest experience/isolation	Test male genotype	CI $\pm$ SEM with IM in pretest interval		CI $\pm$ SEM with test virgin	Time at copulation (min)
		0-10 min	20-30 min		
A. None/1 hr	$dnc^+$			4 $\pm$ 1	8.3 $\pm$ 1.4
	$dnc^{M14}$			3 $\pm$ 1	6.7 $\pm$ 1.0
B. IM/1 hr	$dnc^+$	54 $\pm$ 5	3 $\pm$ 1	8 $\pm$ 2	3.8 $\pm$ 0.7
	$dnc^{M14}$	53 $\pm$ 4	20 $\pm$ 2	7 $\pm$ 1	4.0 $\pm$ 0.5

The experimental sequence was as follows. Individual  $dnc^+$  and  $dnc^{M14}$  males were either isolated or paired with an immature male (IM) in a mating-wheel chamber for 30 min; the amount of courtship displayed toward the immature male was recorded in the first and final 10-min intervals of the 30-min pairing. Then, test males were isolated in food vials for 1 hr, after which each male was transferred to a fresh food vial containing a virgin female; CI with the virgin and the time at copulation were recorded ( $n = 20$  males of each genotype for each protocol).

coisogenic  $dnc^+$  and  $dnc^{M14}$  males to immature males and virgin females. As previously reported, normal males respond to immature males with intense courtship, which then rapidly wanes, and experienced males then avoid further courtship with immature males for up to 6 hr (GAILEY, JACKSON and SIEGEL 1982). Mutant dunce males show a similar initial response to immature males, but do not express as sharp a drop-off in courtship; nor is there a depressive aftereffect on subsequent courtship (GAILEY, JACKSON and SIEGEL 1982).

When either a  $dnc^+$  or a  $dnc^{M14}$  male was directly paired with a virgin female in a fresh food vial, no obvious difference in the quality of courtship performed by males of the two genotypes could be detected. As seen in section A, Table 1, there was no quantitative difference between the two genotypes, either in the average CI with virgin females or the average time to copulation. However, measurement of the average CI of  $dnc^+$  and  $dnc^{M14}$  with immature males revealed a very striking difference. For the first 10-min interval of pairing, both  $dnc^+$  and  $dnc^{M14}$  males spent more than half the time in courtship (section B, Table 1). With time, there developed a very obvious difference in the courtship performance of  $dnc^+$  males with immature males, compared with  $dnc^{M14}$ . In the final 10 min of the 30-min pairing, the courtship by  $dnc^+$  males had become very sporadic; 17 of the 20 males each courted for less than 30 sec, and the average CI for all 20 was only 3  $\pm$  1. Courtship bouts initiated in this interval were fewer in number and much briefer in duration, as measured by the 18-fold decrease in CI for  $dnc^+$  males from the first 10-min interval. On the other hand, the courtship performance by  $dnc^{M14}$  males did not change nearly so dramatically during the 30-min pairing period. All 20 males courted for more than 1 min in the final 10-min interval (13 of the 20 each courted for more than 2 min), and by comparison with  $dnc^+$ , there was only a 2.5-fold decrease in CI. Thus, it is important to note that, although both genotypes showed a significant decrease in CI during their sessions with immature males ( $P <$

0.001, two-tailed *t*-test within each genotype), the CI for *dnc*<sup>+</sup> was significantly lower in the final 10 min of pairing than the CI for *dnc*<sup>M14</sup> ( $P < 0.001$ , two-tailed *t*-test between genotypes).

Note that, in order to permit direct comparison with experimental results presented later (Table 2), the determinations of CI with immature males were carried out in the 0.4 cm<sup>3</sup> mating-wheel chambers. Under these restrictive conditions, the CIs were considerably greater than when the males were next paired with virgin females in food vials; still, no difference in courtship with virgin females was revealed between the two genotypes (section B, Table 1). Whether or not there was previous courtship experience, *dnc*<sup>M14</sup> males were just as efficient as *dnc*<sup>+</sup> males in locating, courting and copulating with virgin females.

*Courtship response in an artificial population of nine immature males and one virgin female:* If experienced *dnc*<sup>+</sup> males "remembered" to avoid courtship with immature males (*cf.* GAILEY, JACKSON and SIEGEL 1982), we predicted that their courtship behavior in an artificial population of nine immature males and one virgin female would be measurably different from their *dnc*<sup>M14</sup> counterparts. To test this hypothesis, males were either isolated or were paired with an immature fly in a mating-wheel chamber for 30 min; then they were returned to their original food vials for 1 hr. Next, the courtship behavior of each male was observed in a food vial that not only contained a single virgin female (as above) but also nine immature males (see MATERIALS AND METHODS for details).

The behavior of courtship-naive *dnc*<sup>+</sup> and *dnc*<sup>M14</sup> males in the artificial population proved to be indistinguishable (section A, Table 2); there was no apparent difference in the CIs with immature males *vs.* the CI with virgin females, nor was there a difference in the average times to initiation of copulation (note that three *dnc*<sup>+</sup> males did not achieve copulation within 30 min of observation, but then *did* copulate in 10 min or less when paired in mating-wheel chambers with the females taken from the artificial populations). Interestingly, for both genotypes the ratio of average courtship bout initiation rates with immature males and the virgin female is about 9:1.

The effect of the mutant *dnc*<sup>M14</sup> allele was revealed in tests involving males that were given a courtship experience with an immature male, followed by measurements of courtship performance in the artificial population. The courtship performed by experienced *dnc*<sup>M14</sup> males appeared to be little changed (compare the results for *dnc*<sup>M14</sup> in sections A and C of Table 2). The bout initiation ratio was 10:1, there was little change in courtship bout lengths, and there was a four-fold increase in the copulation start times, compared with experienced *dnc*<sup>M14</sup> males which were simply paired with virgin females (compare section B, Table 1 with section C, Table 2). Immature-male-experienced *dnc*<sup>+</sup> males, however, modified their courtship in two ways (comparing sections A and C, Table 2). First, there was a three-fold reduction in the CI with immature males (such that the CIs with immature males and the virgin female became identical). This reflects both a reduction in the bout initiation ratio from 9:1 to 5:1 and a reduction by more than one-half in the average courtship

TABLE 2  
*The courtship response of dnc<sup>+</sup> and dnc<sup>M14</sup> males in small populations of nine newly emerged males and one virgin female*

Pretest experience/isolation	Test male genotype	CI ± SEM		Bouts initiated per min		Bout length (sec)			Time at copulation (min)
		IM	V	IM	V	IM	V	V	
A. None/1 hr	<i>dnc<sup>+</sup></i>	41 ± 3	7 ± 1	4.6 ± 0.4	0.5 ± 0.1	6.5 ± 0.8	9.2 ± 1.0	9.2 ± 1.0	12.0 ± 1.9
	<i>dnc<sup>M14</sup></i>	48 ± 3	8 ± 1	3.7 ± 0.3	0.4 ± 0.1	9.2 ± 1.4	9.6 ± 1.3	9.6 ± 1.3	12.2 ± 1.2
B. Immature female/1 hr	<i>dnc<sup>+</sup></i>	35 ± 4	9 ± 1	5.2 ± 0.5	0.7 ± 0.1	6.0 ± 0.7	9.8 ± 1.1	9.8 ± 1.1	10.7 ± 1.5
	<i>dnc<sup>M14</sup></i>	46 ± 4	7 ± 1	4.9 ± 0.4	0.5 ± 0.1	7.9 ± 1.2	8.8 ± 1.2	8.8 ± 1.2	11.3 ± 1.1
C. Immature male/1 hr	<i>dnc<sup>+</sup></i>	15 ± 2	15 ± 2	5.1 ± 0.6	1.0 ± 0.2	2.4 ± 0.5	10.7 ± 1.4	10.7 ± 1.4	5.0 ± 1.4
	<i>dnc<sup>M14</sup></i>	42 ± 4	7 ± 1	5.0 ± 0.4	0.5 ± 0.1	6.7 ± 1.5	7.5 ± 0.9	7.5 ± 0.9	15.9 ± 2.0
D. Immature male/3 hr	<i>dnc<sup>+</sup></i>	12 ± 2	14 ± 2	4.8 ± 0.5	0.8 ± 0.2	2.2 ± 0.5	9.6 ± 1.3	9.6 ± 1.3	6.4 ± 1.2
E. Immature male/6 hr	<i>dnc<sup>+</sup></i>	29 ± 3	10 ± 2	5.0 ± 0.4	0.6 ± 0.1	4.9 ± 0.6	9.1 ± 1.1	9.1 ± 1.1	13.0 ± 1.6

The experimental sequence was as follows. Males were first either isolated or paired with an immature fly for 30 min and were then returned to their original food vials for 1, 3 or 6 hr. Each male was then placed in a small population of nine immature males and one virgin female, and courtship behavior with the immature males (IM) vs. the virgin female (V) was recorded and quantified (see MATERIALS AND METHODS for details). *n* = 20 males of each genotype for each protocol.

bout length with immature males. Second, there was a decrease by more than one-half in the average time to the beginning of copulation.

Does the foregoing difference between  $dnc^+$  and  $dnc^{M14}$  males become apparent following *any* pretest courtship experience? If so, then the interstrain difference should be observed among males allowed to court immature females—rather than immature males—before tests in the standard artificial population. This possibility is excluded by results given in Table 2 (section B); the performance of  $dnc^+$  and  $dnc^{M14}$  males could not be distinguished after pairings with such females.

Wild-type males which have courted immature males were reported to return to high levels of courtship in the presence of immature males, but not until several hours after their "training session" with the initial young males (GAILEY, JACKSON and SIEGEL 1982). In agreement, courtship values for  $dnc^+$  in the artificial population begin to return to naive levels within 6 hr (sections D and E of Table 2).

*Mating success in competition for a single virgin female:* An extension of the experiments just described was based on the prediction that immature-male-experienced  $dnc^+$  males would, in a competitive situation with experienced  $dnc^{M14}$  in the artificial population, spend significantly less time courting immature males; as a result, the  $dnc^+$  males are predicted to copulate sooner with the target female. In this experiment, it became necessary to mark the males so that they could be genotypically identified. This was accomplished by placing a pinpoint-sized dot of acrylic paint on the dorsal thorax when the males were initially collected and isolated. Two colors were employed, and for each experimental protocol, equal numbers of each color/genotype combination were tested. Color-marked  $dnc^+$  and  $dnc^{M14}$  males were first placed singly into vials containing 10 immature males (but in this experiment, empty of food) for a 30-min period, after which each male was returned to his original food vial for a period of 1 hr. Then, one male of each genotype was simultaneously introduced into a fresh vial, this time containing nine immature males and one virgin female. Each test was scored only for copulation, and the genotype of the copulating male was recorded. The results obtained with the two color combinations were not different and therefore were pooled. In 44 of 60 cases (or 73%), experienced  $dnc^+$  males were the copulators. This result is compared to data from a control experiment. When experienced males were allowed to compete for a single virgin female in a vial—in the absence of immature males— $dnc^{M14}$  males actually showed a slight mating advantage; in 24 of 60 tests (40%) the normal males mated.

#### DISCUSSION

*The dunce mutation affects experience-dependent courtship performance in a small population:* Wild-type males that have courted immature males have the ability to limit their subsequent courtship encounters with immature males for about 6 hr; unlike wild type, dunce males continue to court immature males at a comparatively high level, irrespective of their previous courtship experience (GAILEY, JACKSON and SIEGEL 1982). We have confirmed and extended these

results here to show that, because of this courtship difference, dunce males can in certain circumstances be at a distinct mating disadvantage to wild type. By monitoring the courtship of *dnc*<sup>+</sup> and *dnc*<sup>M14</sup> males in an artificial population comprised of nine immature males and one virgin female, we have found the following:

1. The performance by individual courtship-naive *dnc*<sup>+</sup> and *dnc*<sup>M14</sup> males in the artificial population is indistinguishable: the time spent courting immature males and the time at which the virgin is copulated is the same for both genotypes.

2. The performance in the artificial population by individual *dnc*<sup>+</sup> and *dnc*<sup>M14</sup> males that have first courted immature males is different: *dnc*<sup>+</sup> males initiate fewer bouts with immature males, and the bouts are of shorter duration. Most important is the finding that *dnc*<sup>+</sup> males copulate sooner with the virgin female.

3. This altered courtship pattern with immature males and the subsequent increase efficiency at copulation is a specific consequence of prior courtship experience with immature males. By comparison, *dnc*<sup>+</sup> and *dnc*<sup>M14</sup> males that have first courted immature females subsequently perform in the artificial population at a level that is not unlike that of their courtship-naive siblings. The array of cuticular hydrocarbons that can be extracted from newly emerged females and males is similar (although not necessarily identical); mature females and males, however, are chemically different, and this has important behavioral consequences (JALLON 1984). In spite of their chromatographic/spectrographic similarity, our experiments show that young flies of the opposite sex can impact the behavior of courting males in a very different way.

4. In a competitive situation in which males of the two genotypes have previously courted immature males, *dnc*<sup>+</sup> males are more efficient at being the first to achieve copulation with the virgin *only* if immature males are present. In the absence of immature males, experienced *dnc*<sup>M14</sup> males mate with about equal propensity, if not at a slight advantage.

In a mixed population of immature males and a single virgin female, one might wonder how the courting male is eventually able to pick out the female from among the other sex-stimulating flies present. Since "aphrodisiac" pheromones seem to be largely responsible for the high level of courtship that young males stimulate (reviewed by TOMPKINS 1984 and JALLON 1984), our population of ten stimulating flies might seem to present a male-female "odor cloud" that triggers the male response (which could be correlated with the fact that courtship with any fly in the population is initiated with equal probability, Table 2). Some recent results suggest that this is not the case. First, courting males may be able to distinguish males and females by *visual* cues (see TOMPKINS 1984 for relevant results and discussion). Second, it appears that the sex-stimulating pheromones of immature males may be perceived by courting males, not as airborne cues, but as contact stimuli (GAILEY, LACAILLADE and HALL 1986); those associated with females, however, are volatile enough to influence male behavior from a distance of a few millimeters (GAILEY, LACAILLADE and HALL 1986), confirming TOMPKINS, HALL and HALL (1980). There-



fore, a group of immature males probably does not form a "plume" of odor that masks a male's ability to discern the female.

*Experience-dependent courtship behavior—a selective advantage?* Reports of conditioned behavioral responses in flies are numerous (reviewed by QUINN and GREENSPAN 1984; SIEGEL *et al.* 1984), but the possible selective advantage for such behavioral plasticity has been mostly speculative (however, see HEWITT, FULKER and HEWITT 1983; KYRIACOU and HALL 1984). The results presented here are a practical demonstration of a potential selective advantage afforded to males that are genetically equipped to express conditioned courtship. ZAWISTOWSKI and RICHMOND (1986) present similar results based on tests of normal males having undergone prior experience with young males.

Thus, it appears that "learning" to avoid extended and fruitless courtship bouts with immature males can add to the probability of locating and copulating with virgin females, which appear to be relatively rare in natural populations (*e.g.*, SPIETH 1968). Interpreting as a selective advantage the avoidance of courtship with virgin females that occurs after a male has courted a fertilized female (SIEGEL and HALL 1979) does not seem so clear-cut (see SIEGEL *et al.* 1984). A fuller understanding of this type of experience-dependent courtship may come with further investigation, the broad outline of which, at least, is suggested by the work presented here (*cf.* ZAWISTOWSKI and RICHMOND 1986).

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