OVIPOSITION SITE SELECTION BY *DROSOPHILA MELANOGASTER* AND *DROSOPHILA SIMULANS*

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Abstract.—The effects of texture and larval residues in the medium on oviposition site selection (OSS) by *Drosophila melanogaster* and *Drosophila simulans* were studied. *Drosophila melanogaster* laid over 95% of its eggs in sieved medium (vs. unsieved medium); *D. simulans* laid all of its eggs in sieved medium. Surgical removal of antennal segments, and of fore-, mid-, or hindtarsi did not affect this result, indicating that sense organs involved in discriminating between sieved and unsieved medium are not confined to only one of the tested structures. In a "multiple choice" experiment, females were allowed to lay eggs in sieved medium of three types: unconditioned (fresh) medium, medium conditioned by *D. melanogaster* larvae (i.e., medium containing larval residues of *D. melanogaster*), and medium conditioned by *D. simulans* larvae. This choice experiment was performed with *D. melanogaster* and with *D. simulans,* using three densities of females (10, 20, and 40 per experimental unit). Both species laid more eggs in unconditioned medium than in either of the conditioned media, and density had no effect. *D. melanogaster* laid more eggs near the edges of food patches than in the center, whereas *D. simulans* showed no preference for edge or center. Under crowded conditions, both species survived at a higher rate in conditioned media (egg-to-adult survival) than in unconditioned medium, leading to the anomalous conclusion that females of these species seem not to maximize the survival of their offspring. This anomaly was partially resolved by the finding that medium already containing larvae gave lower survival rates than unoccupied medium.

An important type of habitat selection in insects is oviposition site selection, or OSS (e.g., Richmond and Gerking, 1979; Takamura and Fuyama, 1980). It is important because oviposition sites in nature vary in quality, affecting fitness of offspring. In the genus *Drosophila,* many factors influence OSS, including texture of the medium (David, 1970; Rockwell and Grossfield, 1978), color of the substrate (Carfagna and Lancieri, 1971; del Solar et al., 1974), gregariousness (del Solar and Palomino, 1966), larval conditioning of the medium (Dawood and Strickberger, 1969; Weisbrot, 1966), larval density (Lewontin, 1955), and competitive interactions between species (Barker, 1971; McKenzie and Parsons, 1972; Soliman, 1971). The adaptive nature of OSS is clear for some of these factors, especially in the case of intra- and interspecific competition. Survival can

be lowered by crowding in monospecific cultures (Lewontin, 1955; Gilpin, 1974) and by interspecific competition (Miller, 1964). OSS may serve as a mechanism to reduce intraspecific competition as well as competition between species (Fogleman, 1979).

The purpose of this study was to investigate OSS by *Drosophila melanogaster* and *Drosophila simulans,* two cosmopolitan, sibling species that live sympatrically in many areas (Parsons, 1973, 1975). We asked two questions: What factors influence OSS by these two species and what effect do they have in reducing competitive interactions? Does OSS by *D. melanogaster* and *D. simulans* enhance the fitness of the offspring? To answer these questions, experiments were performed testing the influence of larval conditioning, density, texture, and sensory organs on OSS by *D. melanogaster* and *D. simulans.*

GENERAL MATERIALS AND METHODS

A genetically heterogeneous wild-type stock of *D. melanogaster* was derived by

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TABLE 1. Mean number of eggs per replicate laid by *D. melanogaster* and *D. simulans* in sieved vs. unsieved medium (10 replicates for *melanogaster*, 8 replicates for *simulans*; 10 females per replicate).

	Sieved		Unsieved	
	Edge	Center	Edge	Center
D. melanogaster				
$\bar{x}$	42.3	10.6	1.0	1.4
SE	7.98	1.79	0.32	0.70
D. simulans				
$\bar{x}$	3.25	12.38	0	0
SE	1.11	3.37	—	—

mass crossing 60–80 flies from each of three laboratory strains obtained from the National Drosophila Stock Center at Bowling Green, Ohio (Oregon-R, Samarkand, and Lausanne-S) and a locally caught isofemale stock. A stock of *D. simulans* was similarly produced, using three geographic stocks obtained from the University of Texas at Austin (H134.18 Kenscoff, Haiti; 3015.8 Nueva, California; 2372.17 Australia). Progenitor stocks had been maintained for years in the laboratory before we obtained them; our stocks had been made about two years before we used them. Medium was made from a standard cornmeal-agar-yeast recipe. Conditioned medium was produced by culturing several hundred larvae in 250 ml culture bottles until the top layer of medium acquired a soupy, relatively viscous appearance (5–8 d), after which the bottles were refrigerated at 3°C for several days to kill the larvae. The conditioned medium was then sieved through a 1.0 mm mesh to remove most larvae. Unconditioned medium was also sieved to control for texture. Food was placed in 2 ml plastic sample cups (diameter = 12 mm, height = 24 mm, Fisher Scientific, Cat. No. 2-544-19), level full. Conditioned medium was spread over unconditioned medium, in a 2 mm layer.

The location of eggs was recorded when they were counted: eggs laid within about 1 mm of the cup wall were said to be on the edge, whereas the other eggs were said

to be in the center. The edge comprised about 25% of the total area, and the center, 75%. This arbitrary division was chosen because more than half the eggs in preliminary tests using *D. melanogaster* were laid in the outside quarter of vials and food cups.

In experiments and rearing, flies were kept at 23°C ($\pm$1°C) under natural lighting conditions. Flies were lightly etherized and sexed 40–48 hr before experimentation.

EXPERIMENTS AND RESULTS

Experiment 1. Oviposition in Sieved vs. Unsieved Medium

The sieving of conditioned medium for removal of larvae causes the medium to acquire a rough texture. Since previous studies (David, 1970; McCoy, 1962; Rockwell and Grossfield, 1978) have indicated that texture plays a significant role in oviposition site selection, a study was conducted to assess the difference between sieved and unsieved medium.

Materials and Methods. —Each of twenty nonvirgin, 4–6 d old females of *D. melanogaster* was placed into a preparation dish which contained twelve food cups, six with sieved, unconditioned medium and six with unsieved medium. The food cups were randomly distributed in a circle (position determined using a table of random numbers). The flies were allowed to oviposit for 16 hr, and the eggs were counted in each cup. The experiment was replicated ten times. The same experiment was performed using *D. simulans,* in eight replicates. A three-way G-test for each species was used to analyze the data (Sokal and Rohlf, 1981).

Results. —Both *D. melanogaster* and *D. simulans* females laid significantly more eggs in the sieved medium ($G =$ 569.10 for *melanogaster*, $G = 173.29$ for *simulans, d.f.* $= 1, P < 0.001$; Table 1). In addition, *D. melanogaster* preferred to lay eggs on the edge of the food cups ($G = 646.10, d.f. = 1, P < 0.001$), while *D. simulans* showed no preference for either edge or center.

TABLE 2. Total number of eggs laid on sieved vs. unsieved medium for *D. melanogaster* with various sections of antennae removed bilaterally (five replicates).

	Sieved			Unsieved		
	Edge	Center	Total	Edge	Center	Total
Control	83	52	135	0	1	1
Aristaeless	102	70	172	2	0	2
Segment 3 removed	158	115	273	0	0	0
Antennaeless	124	111	235	0	1	1
Total	469	350	819	2	2	4

TABLE 3. Number of eggs laid on sieved vs. unsieved medium for *D. melanogaster* with fore-, mid-, and hindtarsi removed (5 replicates).

	Sieved			Unsieved		
	Edge	Center	Total	Edge	Center	Total
Control	833	392	1,225	6	68	74
Foretarsi	751	554	1,305	3	36	39
Midtarsi	550	416	966	0	16	16
Hindtarsi	391	534	925	0	14	14
Total	2,525	1,896	4,421	9	134	143

The highly significant replicate effect ($G = 215.26$, $d.f. = 9$, $P < 0.001$) and medium by replicate interaction ($G = 35.32$, $d.f. = 9$, $P < 0.001$) for *D. melanogaster* resulted largely from one replicate with only one egg in each type of medium. The significant medium by location interaction ($G = 15.94$, $d.f. = 1$, $P < 0.001$) for *D. melanogaster* suggests that the tendency to lay eggs on the edge in this experiment occurred in sieved medium but not in unsieved medium. There were, however, too few eggs (24/553) laid on unsieved medium to draw firm conclusions about these interactions.

Experiment 2. The Role of the Antennae and Tarsi on Oviposition Site Selection by D. melanogaster

To determine which sensory organs are (or are not) involved in discriminating between sieved and unsieved medium, various parts of the antennae and tarsi were surgically removed.

Materials and Methods. — The antenna experiment included the following treatments: 1) intact control, 2) aristae removed bilaterally, 3) segment 3 removed bilaterally, and 4) both antennae removed. The tarsus experiment included the following treatments: 1) intact controls, 2) foretarsi removed, 3) midtarsi removed, and 4) hindtarsi removed. All flies were etherized lightly and allowed to recover for 48 hr. Surgery was carried out as by Ringo (1977).

Results. — All groups in the antenna experiment exhibited a nearly complete preference for sieved medium ($G = 1,084.80$, $d.f. = 1$, $P < 0.001$; Table 2). All the treatments also showed a preference for the edges ($G = 329.76$, $d.f. = 1$, $P < 0.001$).

The flies in the tarsus experiment (Table 3) also exhibited a highly significant preference ($G = 5,055.20$, $d.f. = 1$, $P < 0.001$) for sieved medium and for the edges of the food cups ($G = 1,638.60$, $d.f. = 1$, $P < 0.001$). A significant treatment by location interaction ($G = 117.30$, $d.f. = 3$, $P < 0.001$) present in this analysis is largely accounted for by the tendency of females with the hindtarsi removed to oviposit more eggs in the center of food cups than on the edge (Table 3). The results indicate that other sense organs not located in these structures are involved in discriminating between sieved and unsieved medium.

Experiment 3. Oviposition in Conditioned and Unconditioned Media in a Multiple Choice Experiment

In nature, *Drosophila* females encounter food that has been conditioned by larvae from previous oviposition. Does this larval conditioning affect oviposition site selection? To answer this question, multiple choice experiments were performed, one using *D. melanogaster* and one using *D. simulans*.

Materials and Methods. — Three sieved media were used: 1) unconditioned medium (UM), 2) *D. melanogaster* conditioned medium (MCM), and 3) *D. sim-*

ulans conditioned medium (SCM). Densities of 10, 20, and 40 four to six day old nonvirgin females were used for each species. The experimental design was the same as that of experiments 1 and 2, except that four food cups of each type of medium were used. Fifteen replicates for each species at each density were performed. For each species, an analysis of variance was performed on the mean number of eggs per female per cm², transformed by $\log(X + 1)$ to equalize variances. These analyses should be viewed with caution, since the number of eggs laid on the edge may not be independent of the number laid in the center, and the numbers of eggs in the three media may not be independent. However, the potential problem of independence was reduced by the opportunity each female had to lay more than one egg, at different locations, and by the use of several females per experimental unit.

Results. —Table 4 gives the total number of eggs laid in the edge and center areas by both species for each type of medium and density. *D. melanogaster* laid more eggs on unconditioned medium than on conditioned medium but showed no preference for one conditioned medium over the other ($F = 25.60$, $d.f. = 2,252$, $P < 0.0001$). This species also laid more eggs in the edge areas than in the center ($F = 236.31$, $d.f. = 1,252$, $P < 0.0001$). There was an interaction between medium and position ($F = 14.08$, $d.f. = 2,252$, $P < 0.0001$): significantly more eggs were laid on the edges of unconditioned medium than on the edges of conditioned medium, whereas the numbers of eggs in the center did not vary significantly among media. *D. simulans*, like *D. melanogaster*, showed a preference for unconditioned medium and lack of preference for either conditioned medium over the other ($F = 20.44$, $d.f. = 2,252$, $P < 0.0001$). There was also a significant interaction between medium and position ($F = 5.06$, $d.f. = 2,252$, $P = 0.007$): on UM, significantly more eggs were laid on the center than the edge ($P < 0.05$, Tukey's test), whereas there

TABLE 4. Number of eggs in the edge and center areas for *D. melanogaster* and *D. simulans* in UM, MCM, and SCM at densities of 10, 20, and 40 females (15 replicates).

Species	Density	UM				MCM				SCM			
		Edge	Center	Total	%*	Edge	Center	Total	%*	Edge	Center	Total	%*
D. melanogaster	10	160	75	235	(46.2)	79	60	139	(27.3)	80	55	135	(26.5)
	20	311	175	486	(48.7)	131	136	267	(26.8)	150	95	245	(24.5)
	40	522	236	758	(43.9)	338	227	565	(32.7)	253	151	404	(23.4)
	Total	993e	486	1,479u	(45.7)	548e	423	971	(30.0)	483e	301	784	(24.3)
D. simulans	10	35	139	174	(52.6)	19	70	89	(26.9)	25	43	68	(20.5)
	20	76	376	452	(56.4)	70	136	206	(25.7)	44	99	143	(17.8)
	40	215	873	1,088	(60.9)	123	235	358	(20.1)	122	218	340	(19.0)
	Total	326	1,388	1,714u	(58.7)	212	441	653	(22.4)	191	360	551	(18.9)

e Proportionally more eggs laid on edge of food cup by *D. melanogaster*, $P < 0.01$.
u Greater number of eggs laid in UM, $P < 0.01$.
* Percentage of eggs on each type of medium.

TABLE 5. Mean number of *D. melanogaster* and *D. simulans* imagoes ±1 SE in 0.2 ml of UM, MCM, and SCM at densities of 5, 50, and 100 eggs (10 replicates). Data were analyzed after angular transformation. Unweighted means per replicate are given for each medium. Within each species, mean percentages for all three media with a common letter (a or b) are not significantly different ($P < 0.05$). For *D. simulans,* conditioned medium was associated with significantly higher survival than was unconditioned medium at two higher densities.

Species	Density	UM	MCM	SCM
D. melanogaster	5	4.0 ± 0.40 (80.0%)	4.5 ± 0.21 (90.0%)	4.5 ± 0.16 (90.0%)
	50	6.4 ± 0.65 (12.8%)	10.5 ± 0.94 (21.0%)	8.6 ± 0.75 (17.2%)
	100	1.6 ± 0.40 (1.6%)	6.2 ± 0.94 (6.2%)	5.4 ± 0.71 (5.4%)
	$\bar{x}$	4.0 (31.5%)[b]	7.1 (39.1%)[a]	6.2 (37.5%)[a]
D. simulans	5	4.6 ± 0.16 (92.0%)	3.9 ± 0.43 (78.0%)	3.9 ± 0.30 (78.0%)
	50	8.0 ± 0.68 (16.0%)	13.8 ± 1.03 (27.6%)	11.1 ± 0.50 (22.2%)
	100	4.7 ± 0.96 (4.7%)	8.1 ± 1.10 (8.1%)	7.8 ± 0.74 (7.8%)
	$\bar{x}$	5.8 (37.6%)[a]	8.6 (37.9%)[a]	7.6 (36.0%)[a]

was no significant difference in position in the conditioned media.

Experiment 4. Survival Rates for D. melanogaster and D. simulans on Unconditioned vs. Conditioned Medium

The multiple choice experiment demonstrated that both species preferred UM over MCM and SCM. To see if a relationship existed between the site of oviposition and subsequent viability of the larvae, we performed a survival experiment for *D. melanogaster* and *D. simulans* in UM, MCM, and SCM.

Materials and Methods. —For each species, a 3 × 3 factorial experiment was performed using three media (UM, MCM, and SCM) and three densities of eggs (5, 50, and 100 eggs per replicate). Ten replicates of each treatment were performed. We used a 1 ml syringe to place 0.2 ml of medium on a piece of moist tissue; eggs were also placed on the tissue. The imagoes were counted on a daily basis (8–20 d after oviposition) until virtually all had eclosed. A two-way ANOVA (medium by density) was used to analyze the egg-to-adult survival of each species. Data were analyzed after angular transformation.

Results. —Increasing the density of eggs significantly decreased the survival rate for both species ($F = 292.14$ for *melanogaster*, $F = 203.73$ for *simulans, d.f. =*

2, 80, $P < 0.001$; Table 5). *Drosophila melanogaster* eggs showed a significantly higher survival rate ($F = 3.65$, *d.f.* = 2, 80, $P < 0.05$) on conditioned medium while *D. simulans* eggs showed no significant difference in survival rate for the media tested. The significant density by medium interaction for *D. simulans* suggests that the conditioned medium yields a higher survival rate with increasing density. A posteriori comparisons among means (Student-Newman-Keuls) for *D. simulans* shows no difference in survival rate at the lowest density (5 eggs/vial) but a significantly higher ($P < 0.05$) survival rate in conditioned media at the other densities. We had no reason to suspect that the very low survival rate of *D. melanogaster* on unconditioned medium at the highest density (1.6%) was caused by experimental error.

Experiment 5. Egg Survival for D. melanogaster and D. simulans with and without Larvae Present

Both species survived best in conditioned media, yet both species showed an ovipositional preference for unconditioned medium. What factors are responsible for this discrepancy? We hypothesized that the presence of larvae plays a significant role in accounting for the differences that exist between oviposition site selection and egg viability in *D. melanogaster* and *D. simulans.*

TABLE 6. Egg-to-adult survival: mean number out of 50 eggs surviving to adult stage ± 1 SE for *D. melanogaster* and *D. simulans* in 0.4 ml of medium; five types were used (10 replicates). Data were analyzed after angular transformation. Within each species, percentages with different letters (a, b, c) are significantly different ($P < 0.05$).

Medium[1]	*D. melanogaster*		*D. simulans*	
	$\bar{x} \pm$ SE	%	$\bar{x} \pm$ SE	%
UM	29.9 ± 1.38	(59.8)[b]	33.3 ± 1.18	(66.7)[b]
MCM	37.0 ± 2.52	(74.0)[a]	43.9 ± 0.79	(87.8)[a]
SCM	29.4 ± 1.56	(58.8)[b]	36.2 ± 1.30	(72.4)[b]
MCML[2]	7.2 ± 0.77	(14.4)[c]	6.6 ± 0.93	(13.2)[c]
SCML[2]	4.9 ± 0.78	(9.8)[c]	6.1 ± 0.74	(12.2)[c]

[1] UM = unconditioned medium, MCM = medium conditioned by *melanogaster* larvae, SCM = medium conditioned by *simulans* larvae, MCML = medium conditioned by *melanogaster* larvae + 25 *melanogaster* larvae, SCML = medium conditioned by *simulans* larvae + 25 *simulans* larvae.
[2] Survival estimated for transplanted eggs from appropriate break areas in pattern of daily emergence.

Materials and Methods. — Fifty eggs of *D. melanogaster* and *D. simulans* were added separately to the following treatments: 1) sieved UM, 2) MCM, 3) SCM, 4) SCM+25 *simulans* larvae, and 5) MCM+25 *melanogaster* larvae. Twenty-five was an arbitrarily chosen number and is a relatively high density. To increase the overall survival rate for all treatments, 0.4 ml of medium was used instead of 0.2 ml. A one-way ANOVA was performed for egg survival in these five treatments. Data were analyzed after angular transformation. Ten replicates of each treatment for both species were performed.

Results. — Egg-to-adult survival was significantly affected by treatment ($F = 56.01$ for *D. melanogaster*, $F = 196.60$ for *D. simulans*; d.f. $= 4, 45, P < 0.001$; Table 6). The percentage surviving, ranked from highest to lowest was the same for both species; MCM > UM = SCM > MCM + larvae = SCM + larvae ($P < 0.05$). Thus, medium containing larvae gave lower survival rates than unoccupied medium. The doubling of food volume in this experiment, compared with experiment 4, more than doubled the survival rate in both species. This reflected larval competition, as observed in experiment 4.

DISCUSSION

The results of this study show that texture is a major determinant of oviposition site selection in these species. Both *D. melanogaster* and *D. simulans* exhibited a highly significant preference for sieved medium. The sieved medium used in these experiments has a soft texture, perhaps more comparable to fermenting fruit. Studies by David (1970), McCoy (1962), and Rockwell and Grossfield (1978) have also demonstrated a significantly higher number of eggs in substrates that have been scarified or grooved. Takamura and Fuyama (1980) have shown that variation exists for the tendency to oviposit on the surface or to insert eggs into media.

Sensory organs of insects may significantly affect oviposition site selection (Davis, 1976; Takamura and Fuyama, 1980). We demonstrated that neither pairs of tarsi nor antennae are solely responsible for discrimination between sieved and unsieved medium. Perhaps sensilla in the ovipositor alone are used in this OSS, or perhaps the selection of sieved medium by females results from the integration of stimuli received from the antennae, tarsi, and ovipositor. A less likely explanation is that visual cues are used. We speculate that removal of hind-tarsi impaired the ability of the female to stand or walk near the edge of the food cups, resulting in more eggs being laid in the center of the cups.

It would seem that the chemical factors making conditioned medium less attractive than unconditioned medium are different from male pheromones which affect OSS by *D. melanogaster* and *D.*

simulans (Mainardi, 1969; Ayala and Ayala, 1969), since the volatile pheromone characterizing mature males (cis-vaccernyl acetate) is perceived at a distance (Jallon, 1984; Tompkins, 1984). Hoffmann and Harshman (1985) found that a male short-range or contact pheromone, as well as male-transmitted microorganisms, stimulated oviposition in *D. melanogaster.*

In spite of the close similarity in ecological requirements between *D. melanogaster* and *D. simulans,* some differences in oviposition behavior were observed that may reduce competition between these two sibling species when they are sympatric (Soliman, 1971). *D. melanogaster* exhibited a significant preference for the edge of the food patches in the present study, whereas *D. simulans* showed no preference for edge or center. Moore (1952) reported that both species initially preferred the edge of the cups but that *D. simulans* deposited eggs in the center more readily than *D. melanogaster.* Soliman (1971) points out that a preference for edge or center may be strain specific. He demonstrated that populations of *D. melanogaster* and *D. simulans* from Alexandria exhibited no edge or center preferences on food cups but that in Florida populations (data from Moore, 1952), *D. melanogaster* preferred the edge and *D. simulans* the center of food cups. Barker (1971) found that a *vermilion* strain *D. simulans* preferred to oviposit in central areas of food resources; again, the results may be strain specific. The ecological significance of this aspect of OSS has yet to be discovered, however; in view of the high rates of larval movement within a patch (Sewell et al., 1975; Sokolowski and Hansell, 1983), larval fitness would not seem to be affected.

Del Solar and Palomino (1966) found that *D. melanogaster* females laid most eggs in food occupied by larvae, whereas in the present study unconditioned medium was utilized more frequently than medium conditioned by larvae. However, there was a major difference in ex-perimental design between the two studies; del Solar and Palomino used medium to which larvae were added two hours before the oviposition test, while we used medium that had been occupied by first, second, and third instar larvae for 5–8 d and had therefore become somewhat soupy. In addition, del Solar and Palomino did not remove the larvae before the oviposition test, whereas in the present study most larvae were removed by sieving the media, and any unremoved larvae were killed by chilling.

In the present study, both species survived better on conditioned medium, except for *D. simulans* at the lowest density. Conditioned media undoubtedly contain live yeasts (we did not add yeast to the cultures, but the flies carry their own), so that initially, at least, larvae growing on conditioned media encountered more live yeast than larvae growing on unconditioned medium. In addition, dead larvae may have liberated nutrients. These factors apparently outweighed the reduction in nutrients by previous occupants and metabolic waste products. Facilitation of preadult survival in both species was greater with medium conditioned by *D. melanogaster* larvae (MCM) than with any other medium. Various other studies have demonstrated that biotic residues secreted by larvae have either an inhibitory or facilitating effect on the viability of subsequent genotypes present in the medium (Budnick and Brncic, 1974, 1975; Dawood and Strickberger, 1969; Weisbrot, 1966). For example, Weisbrot (1966) demonstrated that the biotic wastes of *D. pseudoobscura* increased the viability of wild-type *D. melanogaster* whereas Budnik and Brncic (1975) showed that the viability of *D. willistoni* is significantly reduced by the metabolic wastes of *D. pavani* larvae.

The fact that *D. melanogaster* and *D. simulans* had the highest preadult viability in MCM is discordant with the tendencies of both species to oviposit in unconditioned medium. Aiken and Gibo (1979) have demonstrated that females of *D. melanogaster* and *D. simulans* can

determine whether a food source has been used by larvae even when no larvae are readily observable. Sang (1949) and Lewontin (1955) using *D. melanogaster* and Lewontin and Matsuo (1963) using *D. busckii* found that larval viability was highest at intermediate larval densities. Since it is advantageous for *D. melanogaster* to have enough eggs in a food source to ensure conditioning by the larvae, females should lay eggs in medium already occupied by larvae (del Solar, 1968).

This may not be the case, however, when the medium has a high larval density and thus is well-conditioned. Numerous studies using *D. melanogaster* and *D. simulans* (Barker, 1973; Barker and Podger, 1970; Chaing and Hodson, 1950; Miller, 1964; Moth and Barker, 1976; Tantawy and Soliman, 1967) have demonstrated that high larval densities reduce adult emergence. This reduction in survival could be caused by cannibalism as well as competition. For both *D. melanogaster* and *D. simulans* in the present study, the detrimental effects of high larval densities outweighed the beneficial effects of larval facilitation by larval conditioning (possibly biotic wastes). This hardly surprising result points to the need for studies to assess the trade-off between larval facilitation and competition.

ACKNOWLEDGMENTS

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