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Mechanisms of interference competition in the western tree-hole mosquito, *Aedes sierrensis*

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Abstract. 1. Mechanisms of interference competition affecting *Aedes sierrensis* (Ludlow) were investigated in laboratory microcosms using reconstituted, natural tree-hole detritus as food and substrate.

2. Pupation success, larval development time, and pupal weight were all affected by larval density but not by surface area:volume ratio of the microcosm.

3. Mature fourth instars affected pupation success, pupal weight, and development time of developing cohorts separated from them by a 2 μm pore membrane impermeable to bacteria, indicating that chemical competition is proportional to density of at least older instars.

4. Cannibalism does not occur, regardless of the presence or absence of food or physical complexity.

5. Fourth instars inhibited each other's feeding at densities of 64 larvae/ml or greater. Feeding inhibition due to physical contact (encounter competition) was abated but not eliminated by increasing physical complexity of the microcosm by the addition of leaves.

6. Levels of detritus and larval density both affect weight of day-1 fourth instars. Resistance to encounter competition is proportional to fourth instar weight and weight-specific resistance is correlated with rank weight within a developing cohort.

7. At densities around the population equilibrium in nature, encounter competition should be taking place, especially in tree holes with few leaves or other large litter.

Key words. Competition mechanisms, chemical inhibition, encounter competition, habitat surface/volume ratio, insect development, physical interference, cannibalism.

Introduction

Among mosquitoes, intraspecific competition as a consequence of increased larval density and/or reduced food levels results in longer development time, reduced pupation success, and reduced pupal weight. These consequences of food deprivation and density have been observed repeatedly in nature (Mogi, 1984; Hawley, 1985a; Bradshaw & Holzapfel, 1986a, b), in quasi-natural microcosms (Frank & Curtis, 1977; Livdahl, 1982; Bradshaw &

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Holzapfel, 1989), and in the laboratory (Hawley, 1985b; Hard *et al.*, 1989; Fisher *et al.*, 1990; references therein). In addition to the depletion of per capita food by scramble or resource competition, competitive interference may occur through direct physical contact (Shannon & Putnam, 1934; Dye, 1984), through chemical inhibition by metabolites or growth retardants (Moore & Fisher, 1969; Ikeshoji & Mulla, 1970; Dye, 1984), and/or through cannibalism among otherwise non-predatory larvae (Mogi, 1978; Koenekoop & Livdahl, 1986). Thus, all three modes of interference competition have been clearly demonstrated in mosquitoes.

The present study concerns *Aedes sierrensis* (Ludlow) that completes its immature development only within tree-holes in western North America. Because of photoperiodically controlled embryonic and larval diapauses (Jordan & Bradshaw, 1978; Jordan, 1980), *A.sierrensis* is probably univoltine throughout its range. In tree-holes at Eugene, Oregon, U.S.A., population regulation occurs at the larval stage. At high larval density, pupal weight declines and, consequently, so does expected lifetime fecundity (Hawley, 1985a, b, c). In laboratory microcosms containing reconstituted tree-hole substrate, the effects of density on development of *A.sierrensis* become manifest as retarded development, lowered pupal weight, and reduced pupation success (Fisher *et al.*, 1990). The present paper sets aside the problem of exploitative competition and determines whether density-dependent alteration of the above traits can be attributed to interference competition via physical contact (encounter competition *sensu* Schoener, 1983), chemical competition, and/or cannibalism.

Materials and Methods

All experiments in this study used natural tree-hole sediment as a food source. Substrate from a 120 litre tree-hole in Eugene, Oregon (44°03′N; 123°04′W), was collected and separated into three fractions: leaf litter (all material >1 cm), course substrate (1 cm > all material > 1 mm), and fine material (all remaining soluble/insoluble material). These fractions were allowed to air dry in open pans at 23°C for 3 weeks. Once dry, the empirical weight ratio of leaf:course:fine fractions was determined to be approximately 1:5:1. This ratio was maintained in all experiments involving tree-hole sediment.

All experiments in this study used *Aedes sierrensis* eggs obtained from a mass swarm of mosquitoes. The population was originally collected from tree-holes in Eugene, Oregon, and had been run through five generations in the laboratory. Eggs were chilled at 4°C for at least 3 months prior to hatching. Hatching was stimulated by placing eggs in distilled water containing 1–2% anaerobic hatching stimulus (decomposing commercial guinea-pig food and yeast).

1. *Density*. In experiments demonstrating the effects of physical interference on *A.aegypti*, Dye (1984) varied the volume of water in 5 cm diameter perspex pots while holding food and the number of larvae constant. This procedure varied the surface:volume ratio at the same time as volume. To ascertain the independent effects of density and surface area on the fitness of developing mosquitoes, density per unit volume and per unit surface area were independently manipulated. Three types of experimental containers were employed which varied in their surface area/volume ratio: 15 × 1.5 cm (diameter × depth) petri dish (S/V ratio = 0.58 cm^2/ml), 7 × 7 cm glass jar (S/V ratio = 0.28 cm^2/ml), and 4.5 × 9 cm nalgene bottle (S/V ratio = 0.10 cm^2/ml). 7 g of tree-hole sediment were added to each experimental container. The contents of each container were mixed with 150 ml distilled water and allowed to rehydrate for 1 week at 23°C. The depth of the tree-hole sediment averaged 0.5 cm in the shallow container, 1.8 cm in the intermediate container, and 3.3 cm in the deepest container. In the first experiment, the surface–volume ratio was held constant at 0.58 cm^2/ml and density varied by allowing ten, twenty-two or sixty larvae to develop in identical dishes. In the second experiment, density was held constant at sixty larvae per jar and the surface–volume ratio was varied by using the three types of containers listed above. Three replicates were made of each treatment in both experiments.

All containers were placed in an incubator at 21±0.5°C with an unambiguously long-day light:dark regime of 16:8 h. The dishes were checked every other day for pupae. Each pupa was collected, blotted dry, sexed and weighed

to the nearest 0.01 mg. After 180 days, since the number of larvae remaining in any container was very low and the pupation rate was lower than one pupa per week in all containers, the experiment was terminated.

2. *Chemical competition*. To test for possible long-term chemical competition among *A.sierrensis* larvae, cohorts of larvae were isolated from experimentally manipulated populations with semi-permeable filters, and then fitness correlates of the larvae were measured as a result of manipulating the population density in the attached chamber. Clear plastic dishes (9 × 5 cm) were cut in half and the separate halves connected by 0.2 μm Millipore filters. This pore size was sufficient to prevent contamination via protozoa, bacteria or food, but large enough to permit molecular flow. From the use of labelling dyes, it was estimated that 100% water exchange between the two chambers occurred every 48 h. In one side of these chambers, ten freshly-hatched *Aedes* larvae were placed. In the other side, fully mature fourth instars were placed at various densities (10, 50, 100, 250). Fourth instars that died or pupated were replaced with new larvae to maintain a constant density at all times. Containers with an equal density (ten) of developing cohorts on both sides of the barrier acted as a control.

The experimental chambers were placed in an incubator at 21±0.5°C with a light:dark regime of 16:8 h. Excess food was provided at all times. These conditions were selected to mimic the natural environment, resulting in maximal development rate. Each container was checked every 2 days for pupae. Pupae were collected, blot-dried, sexed and weighed to the nearest 0.01 mg.

3. *Cannibalism*. To examine possible cannibalism of fourth instars on first instars, various densities of newly-hatched larvae were placed in experimental containers with fully mature, actively feeding, fourth instars. Three manipulations were carried out to test independently for the effects of food and physical habitat complexity on cannibalism:

(1) To test for cannibalism in the absence of food or physical complexity, ten (133 larvae/litre) or 250 (3333 larvae/litre) first instars were placed within 2 h of hatch in 75 ml distilled water in 100 × 25 mm culture dishes with zero (control) or ten (experimental) mature fourth instars. After 72 h, all larvae were removed and the number of living, dead and missing larvae were tallied. Ten replicates were run of each treatment.

(2) To test for the effects of physical complexity on cannibalism, the same experimental regime was set up as in (1) but 5 g dry weight of minced oak leaves were added prior to the start of each replicate. Dry leaves of California black oak were collected from a protected area of a rooftop, cut into approximately 1 × 2 cm pieces, hydrated in hot distilled water, rinsed and then boiled for 0.5 h each in two successive rinses of distilled water to kill and remove surface bacteria and fungi.

(3) To test for the effects of food on cannibalism, the same experimental regime was set up as in (1) but 2 g of finely ground tree-hole sediment were added to each dish and allowed to rehydrate for 72 h prior to the start of each replicate.

4. *Encounter competition*. To assess the degree of encounter competition, mosquito larvae were allowed to feed on a dyed food source at varying densities and food consumption measured colourimetrically. A stained substrate was first prepared. Tree-hole detritus was dried in open pans, homogenized in a high-speed blender, and suspended for 1 day in 50 g/l oil red (fast red 3) in acetone. The suspension was filtered, dried, and sifted to a homogeneous size. Weighed amounts of the dyed detritus were reconstituted in 100 ml distilled water in 5 × 9 cm clear plastic dishes. Since the oil-red is insoluble in water, it remained bound to the substrate. The intent was to present a dyed food source that was present in excess and to keep the experiment brief so that (1) mosquito alimentary tracts were not saturated, (2) resources were not significantly depleted, and (3) there was no time for build-up of metabolites or other putative inhibitors. Following exposure to the dyed substrate, each larva was homogenized in a ground glass homogenizer and the dye extracted from ingested food in 2 ml of 2-propanol. The homogenate was decanted into a cuvette and read at OD_{490} in a colourimeter.

To adjust feeding time for saturation of mosquito alimentary tracts, samples of four larvae per dish were allowed to feed for 15–120 min, sampled in 15-min increments. A plot of OD_{490} of extracted larvae approached saturation after about 90 min (Fig. 1A). 90 min was therefore

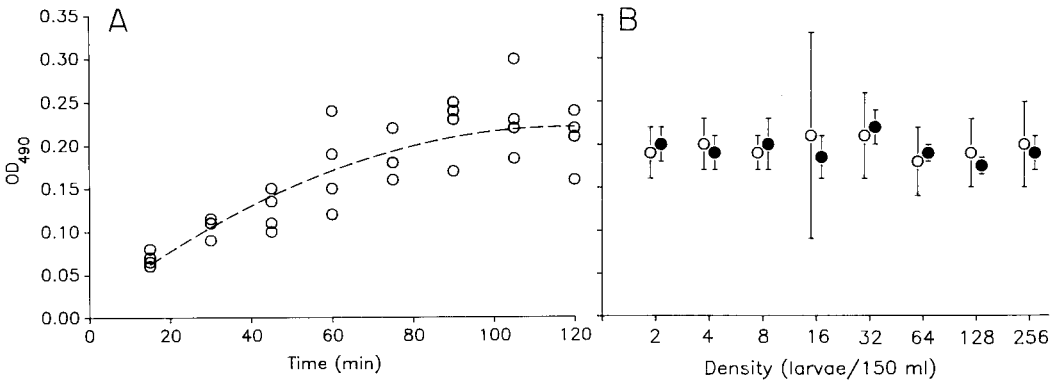

Fig. 1. Food consumption measured as OD_{490} of fourth instars feeding on dyed substrate. (A) Dependence of consumption on feeding time of individual larvae. (B) Food consumption (Mean OD_{490} ±2 SE) of four fourth instars allowed to feed in the same container for 90 min either before (closed circles) or after (open circles) the number of larvae shown on the horizontal axis. Experimental densities were run from low to high.

chosen as the experimental exposure time to maximize the amount of food consumed at low density and minimize the degree of gut saturation. To examine the possibility of resource depletion, 256, 128, 64, 32, 16, 8, 4 or 2 larvae per dish were allowed to feed for 90 min each. Preceding and following the run of each experimental density a control replicate of four larvae of similar size, age, and nutritional background was run (Fig. 1B). There was no difference in OD_{490} between the four larvae introduced before and after an experimental density (ANOVA: $F_{1,61}$ for adjusted, means = 0.06; $P>0.05$); nor was there a correlation between OD_{490} of the four larvae and density of the experimental series ($r = 0.052$; $P>0.05$). It was therefore concluded that resources were not being depleted and that feeding inhibitors were not accumulating during an experimental series of densities. Nonetheless, to ensure that these factors could not contribute to density-dependent effects, experiments were back-biased by always running experimental series from highest to lowest densities. Each experimental series included 256, 128, 64, 32, 16 and 8 day-3 fourth instars. This series was replicated three times in three dishes whose dyed detritus had been independently reconstituted.

The above experiment allowed measurement of feeding behaviour only in a relatively homogeneous environment. In natural habitats, *Aedes* larvae experience a significantly more complex environment. To vary physical complexity, weighed amounts of dry oak leaves cut in 1 cm^2 squares were added to the dishes. The experimental level of leaf litter was set at 1 or 2 g (dry weight) per dish while the above series served as zero litter controls. Experimental containers were assembled as above with the first unsupplemented, the second containing 1 g of leaf litter, and the third with 2 g leaf litter. Larvae were allowed to compete for the dyed substrate. Again, three independent series of densities were determined for each level of leaf litter.

5. *Developmental history*. Moore & Whitacre (1972) found that larvae were less sensitive to chemical inhibition when reared at high, rather than low, density. To examine the question of whether past environment (density, food level) has an effect on competitive ability later in life, four different developmental conditions were generated by varying food level and larval density:

Density	Food level (g)	Description
10	5	Low density/high food
10	2	Low density/low food
40	5	High density/high food
40	2	High density/low food

Food was provided in the form of finely ground, homogenized tree-hole sediment without leaf-litter. All larvae were reared in a 21±0.5°C incubator with a L:D regime of 16:8 h

to provide an unambiguous long day.

Larvae were reared until the first day of fourth instar development. Four equal weight (± 0.25 mg) day-1 fourth instars from each treatment were competed against fifty-six fully mature fourth instars from the low density/high food control container (strong competitor). Size acted as a marker to distinguish the two competing cohorts. In each case, the rate of food consumption was measured via colourimetric methods as described above.

Results

Density constraints

Fitness of *A.sierrensis* larvae reared on natural tree-hole sediment at various densities was measured as pupation success for the population as a whole and as pupal weight and $\log_{10}$ (development time) of both males and females (Fig. 2). Larval density had a large impact on all three parameters. Increasing densities resulted in decreased pupation success and in decreased

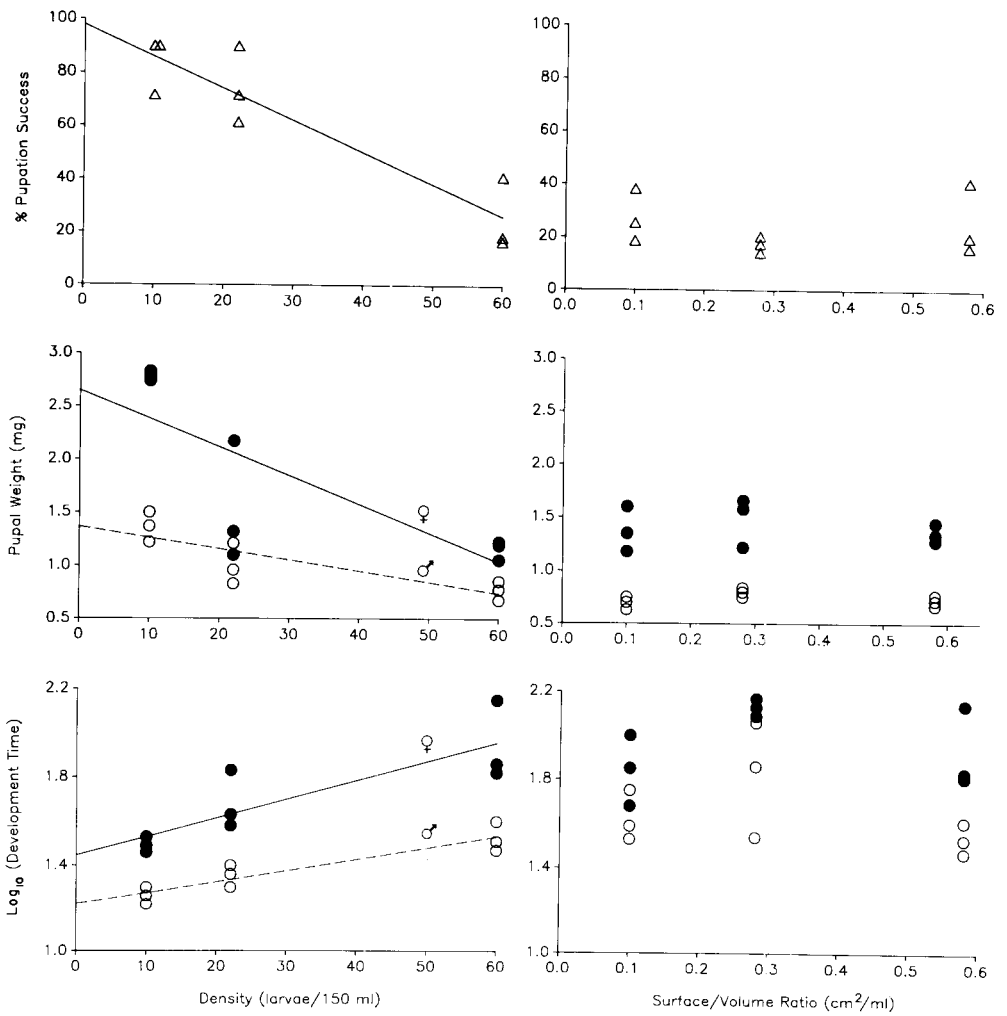

Fig. 2. Left, effect of larval density and right, effect of surface/volume ratio on pupation success, pupal weight and development time. Each point represents the mean of one replicate. Regression lines are shown for significant correlations only. •, Females; ○, males.

male and female pupal weight while development times of both sexes increased with increasing larval density. By contrast, varying the surface area while holding volume constant had no significant effect on pupation success, on male or female pupal weight, or on development time.

Chemical competition

When cohorts of ten larvae developed from day of hatch to pupation in a chamber separated from fourth instars of varying density by a millipore filter, pupation success and pupal weight of both males and females (Fig. 3) declined with increasing density of neighbouring fourth instars. Development time of females, but not males, increased with increasing density of neighbouring fourth instars. These results show that factors affecting density-dependent constraints to development are transportable through membrane pores sufficient to exclude bacteria and protozoa.

Cannibalism

In the absence of food or habitat complexity (Fig. 4A), neither the presence/absence of fourth instars ($F_{1,36}$ = 0.60; P>0.05), the density of first instars ($F_{1,36}$ = 0.38; P>0.05), nor their interaction ($F_{1,36}$ = 0.04; P>0.05) significantly affected the survivorship of first instars. With leaves added to provide habitat complexity but not nutrition (Fig. 4B), neither the presence/absence of fourth instars ($F_{1,36}$ = 0.01; P>0.05), the density of first instars ($F_{1,36}$ = 1.44; P >0.05), nor their interaction ($F_{1,36}$ = 0.03; P>0.05) significantly affected the survivorship of first instars. With ground substrate added to provide nutrition with minimum physical complexity (Fig. 4C), first instars survived better at lower than higher density ($F_{1,36}$ = 20.65; P<0.001) but neither the presence/absence of fourth instars ($F_{1,36}$ = 0.06; P>0.05) nor the interaction of first and fourth instars ($F_{1,36}$ = 0.54; P>0.05) significantly affected the survivorship of first instars. No fourth instars pupated during any of the experiments. There was therefore no evidence that survivorship of first instars during the first 72 h after hatching was significantly affected by the presence or absence of fourth instars regardless of nutrition level or habitat complexity.

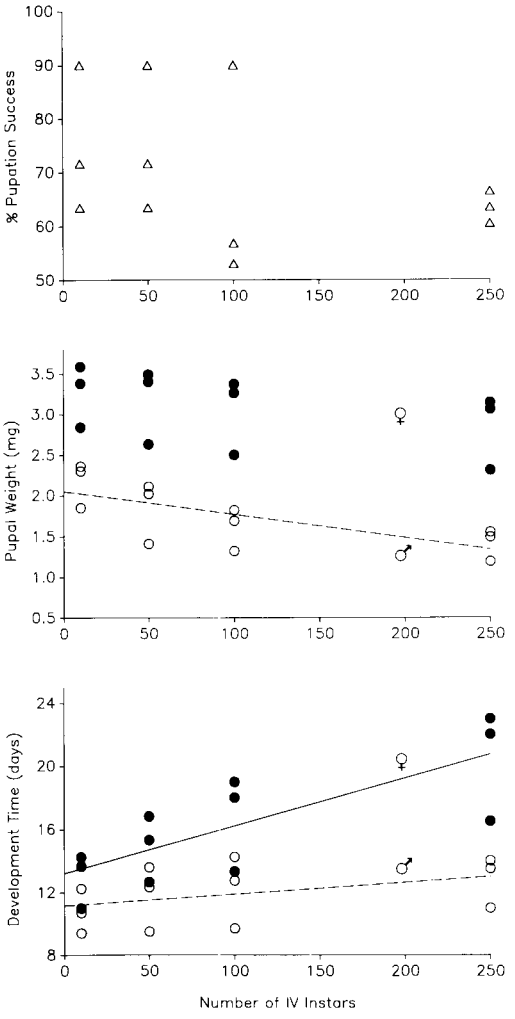

Fig. 3. Chemical competition among larval *Aedes sierrensis*. Pupation success, pupal weights and development times were determined for a cohort of ten developing larvae separated from varying densities of competing fourth instars by a 0.2 μm pore membrane. Symbols as in Fig. 2.

Encounter competition

When larvae competed for colour-labelled food, the amount of food consumed declined with increasing density (Fig. 5). Two-way ANOVA revealed significant effects of density ($F_{5,72}$ = 89.3; P<0.001), leaves ($F_{2,72}$ = 10.3; P<0.01) and their interaction ($F_{10,72}$ = 2.7; P<0.05). The addition of leaves had a greater effect at high than low densities. Likewise, a difference in food consumption between the

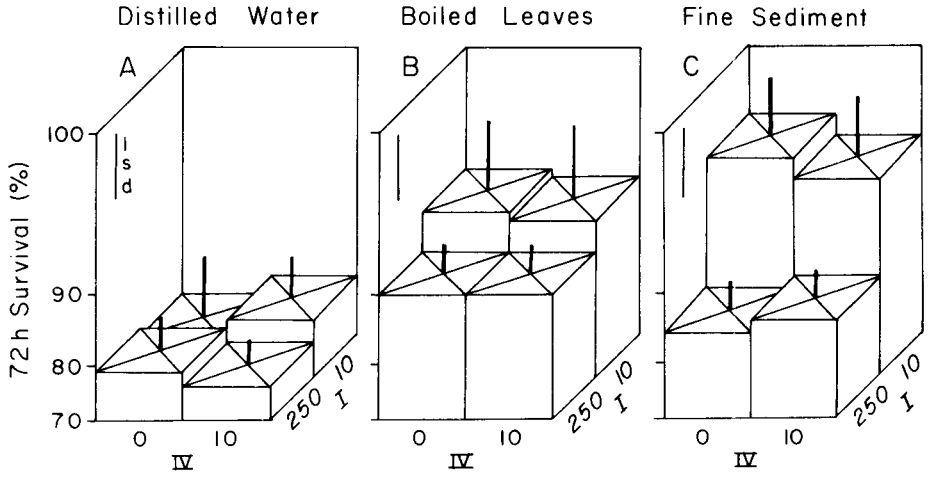

Fig. 4. Incidence of cannibalism in *Aedes sierrensis*. Mean per cent survivorship of ten or 250 first instars after 72 h is given for control (no fourth instars added) and experimental (ten fourth instars added) containers with 75 ml distilled water only (A), with boiled oak leaves added (B), or with fine sediment added (C). Each histogram represents the mean of ten replicates with 2 SE projecting from the top. Least significant differences (lsd) are shown on the upper left of each plot.

amount of leaf litter added became apparent only at the highest two densities.

Developmental history

Size (ln weight) of recently moulted fourth instars was strongly affected by developmental history (Fig. 6) and food consumption was closely correlated with size ($r = 0.935$; $P < 0.001$). ANCOVA revealed heterogeneity of regression coefficients among developmental

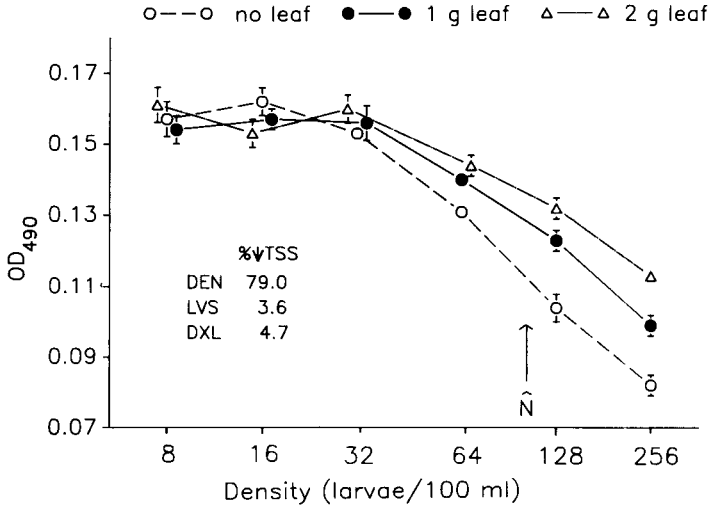

Fig. 5. Encounter competition in larval *Aedes sierrensis*. Fourth instars were allowed to compete for a coloured food source at varying densities for 90 min without leaf litter or with 1 or 2 g leaf litter. Food consumption was measured as OD_{490} of propanol-extracted larvae. Each data point represents the mean ±2 SE of five independent replicates. $\hat{N}$ indicates the equilibrium density of 1200 larvae/litre. % ↓ TSS provides the percentage reduction in total sum of squares in OD_{490} that is attributable to density (DEN), the addition of 0, 1 or 2 g of leaves (LVS) and density–leaves interactions (DXL).

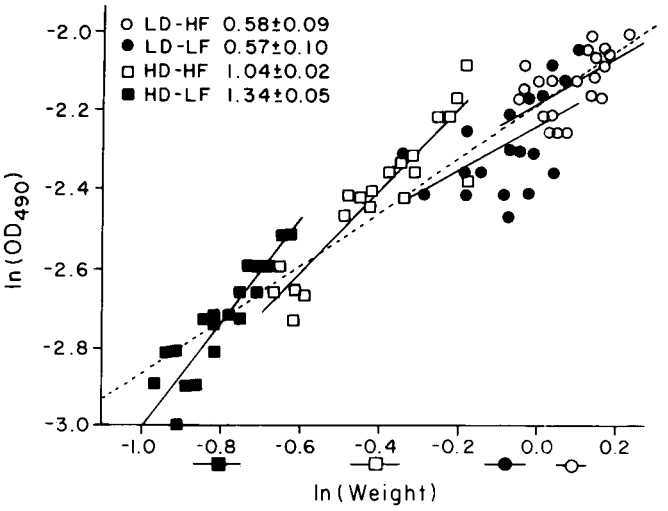

Fig. 6. The effect of developmental history on encounter competition in *Aedes sierrensis* larvae. Food level and larval density were manipulated to generate four populations with distinct developmental histories: high density/low food (■), high density/high food (□), low density/low food (●), and low density/high food (○). Newly emerged fourth instars from each treatment population were matched against mature fourth instars from the low density/high food population as in Fig. 5. Food consumption (OD_{490}) is plotted as a function of larval wet weight in mg. The dashed line plots the common regression. The legend provides the slopes ±2 SE for each regression. The symbols and lines below the *x*-axis plot weight (mean ±2 SE) of day-1 fourth instars for each treatment.

histories ($F_{3,75}$ = 12.79; $P<0.001$). The slope relating food consumption to larval weight declined by treatment, in order, from high density/low food, to high density/high food, to low density regardless of food level. This progressively declining slope meant that where weights overlapped between adjacent treatments, food consumption was greater among the larvae having developed under conditions of high density/low food (■) than under conditions of high density/high food (□) and, sequentially, under conditions of high density/high food (□) than under conditions of low density/low food (●). There were no overlapping weights between larvae having developed under conditions of high density/high food (□) and low density/high food (○).

Discussion

Larval density affects fitness of *A. sierrensis* both in nature (Hawley, 1985a, b, c) and in the laboratory (Fig. 2). In the laboratory, on reconstituted tree-hole sediment, the effects of larval density are manifest on a per volume basis and relative surface area has no significant effect.

Density-dependent effects on development are communicable through Millipore membranes that exclude particles as small as bacteria (Fig. 3). These results are consistent with the concept that chemical interference is a significant component of intraspecific competition in *A. sierrensis*. The present study, like earlier studies on *A. aegypti* (Moore & Fisher, 1969; Moore & Whitacre, 1972; Kuno & Moore, 1975; Dye, 1984), does not exclude the possibility that chemical interference is effected through a viral agent.

Physical interference could be manifest through direct inhibition of foraging activities (Dye, 1984) and/or through predation of larger larvae on smaller larvae (Mogi, 1978; Koenekoop & Livdahl, 1986). The present study (Fig. 4) found no evidence for the latter mode of physical interference regardless of available nutrition or habitat complexity. By contrast, physical contact or encounter competition serves as a potent inhibitor of food ingestion (Fig. 5) and may contribute to the prolongation of development as well as decline in pupal

weight seen at increased density (Fig. 2). Barriers to physical contact such as leaf detritus abate but do not eliminate encounter competition (Fig. 5) so that encounter competition is probably taking place at high densities in nature as well as in laboratory microcosms.

Susceptibility to encounter competition is dependent upon the rearing conditions of a cohort. High densities and/or low food result not only in reduced weight at pupation (Figs 2–3) but also in reduced weight at moult to the fourth instar (Fig. 6, x-axis). Thus, the threshold weight for moulting from the third to the fourth instar is not a constant. Consequently, stage duration cannot be assumed to depend upon increasing body weight by a fixed amount (Gilpin & McClellend, 1979; Dye, 1982). Rather, the duration of a stage and the threshold weight to trigger a moult may be interdependent and, as in amphibia, depend upon the interplay of growth and development rates (Wilbur & Collins, 1973; Smith-Gill & Berven, 1979).

Within a cohort of given developmental history, there is varying weight-specific variation of individuals. Especially with a developmental history of high density (Fig. 6, □, ■) heavier larvae within the cohort consume greater food per unit weight than do lighter larvae. Thus, larvae that have been relatively more successful as competitors during the development of their own, overcrowded cohorts are also relatively more able to resist encounter competition from older, larger larvae.

The relative competitive superiority of larger larvae within cohorts reared at high density could have genetic and/or environmental components. Based on comparisons with *Aedes aegypti* (Steinwascher, 1984) or with amphibia (Kaplan, 1980; Berven & Chadra, 1988), the larger individuals may be those that hatched from larger eggs or those that, through purely spatial variation in the microcosm, obtained more resources at first (Wilbur, 1972) and simply possess a multiplicative size advantage through the mechanism of exponential growth. Alternatively or additionally, competitive superiority may reflect genetic variation for competitive ability within the population. In the latter case, the question would remain as to whether increased competitive ability at high density carried with it a compensatory (pleiotropic) cost at low density (Mueller, 1988; Mueller & Sweet, 1986) or could exist without apparent adaptive tradeoffs (Bradshaw & Holzapfel, 1989).

In nature, the population-wide equilibrium density occurs at about 1200 larvae/l (Hawley, 1985a, b, c). If this population-wide density applies to individual tree holes and if density on natural substrate in the laboratory can be extrapolated to natural tree holes, two conclusions can be made. First, the negative slopes of the lines in the vicinity of the equilibrium density (Fig. 5, $\hat{N}$) imply that encounter competition should be a significant source of competition in natural tree holes. Second, the dependence of food consumption on detritus level at this density implies that interference competition should be more intense in holes with small openings that lack leaf litter or other large detritus.

The results of the present study show that chemical and encounter competition but not cannibalism can be important sources of interference competition in *A.sierrensis*. The results of the present study do not reveal how competition varies among actual tree holes, how interference and exploitation competition are related, or how encounter competition interacts with chemical competition. This interaction may be simply additive but could be multiplicative so that the presence of chemical inhibitors greatly facilitates encounter competition or vice versa. The results of the present study also do not necessarily bear on interspecific interactions since competitive ability may evolve independently of density tolerance (Bradshaw & Holzapfel, 1989).

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