

SHORT COMMUNICATION

Cannibalism among *Aedes triseriatus* larvae

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Interactions within populations of *Aedes triseriatus* (Say), a treehole mosquito, are confounded by a phenomenon known as 'erratic or instalment hatching', in which only a fraction of the eggs of the same age hatches in response to a given stimulus (Breeland & Pickard, 1967; Wilson & Horsfall, 1970; Gillett, 1955a, b, 1972; Gillett *et al.*, 1977). Such temporal staggering makes interactions likely between hatching cohorts of different developmental stages.

Livdahl (1982) inspected the intraspecific interactions between two larval cohorts with a field container experiment performed in natural treehole fluid. He showed that the earlier larvae impose a strong adverse effect on a later cohort, which was hatched and added 7 days after the establishment of the experiment. This adverse effect was not reciprocated by the late cohort. On the contrary, the addition of a second cohort buffered the first cohort's female development time against increasing density and relative shortages of food. In addition, at the intermediate density and low food level (forty larvae per 250 ml diluted fluid) the survivorship to adulthood of the earlier larvae was enhanced by the addition of the new cohort. He suggested that facultative cannibalism might provide a simple mechanism for these higher order interactions.

This paper provides evidence that cannibalism is possible in *Aedes triseriatus*. Our work-

ing definition of cannibalism is the combined acts of killing and ingesting conspecifics. Such elimination may occur intentionally or accidentally with the same population consequence. The disappearance of newborn larvae in the presence of older larvae must be attributed to cannibalism provided that no such disappearance occurs in the absence of the older larvae, the time period is too short to permit larval decomposition, and all other conditions are identical.

Ten days prior to the experiment, larvae were hatched from eggs produced by field-collected females, and were grown at low densities with an ample food supply (Formulab Chow 5008® and brewer's yeast) in 9 cm Petri dishes containing 30 ml of water. At the time of the experiment these larvae were in their fourth instar.

The first instar larvae were hatched by the 'hatching tube' stimulus technique of Novak & Shroyer (1978), which was applied twice prior to the experiment to provide two groups, 0–1.5 and 24–25.5 h after hatching. First instar larvae were placed into 35 ml vials at densities of 2, 4, 8, 16, 32 and 64 individuals per vial, each of which was filled with deionized water either containing or not containing the additional food source of brewer's yeast (200 mg/l). Four fourth instar larvae were added immediately to each vial to initiate the experiment. Each combination of treatment levels (first instar density, food and first instar age) was replicated three times. In addition, a set of two control vials were established at each density,

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with and without food, with no fourth instars added.

The first and fourth instar larvae were kept together in an incubator with continuous illumination at 20°C. After a 24 h period the fourth instar larvae were removed and the remaining first instars were counted.

The analysis examines the fraction of first instar larvae eaten in response to the three experimental factors, after an angular transformation to reduce the dependence of cell variances on cell means.

The occurrence of cannibalism. Under all experimental conditions, first instar larvae disappeared, except in the control group, in which no mortality was found, demonstrating that their disappearance is related to the presence of the fourth instar larvae. Hence, saprophagy by fourth instar larvae cannot account for the missing first instar larvae.

Facultative cannibalism provides the simplest explanation of the disappearance of the first instars under certain conditions (Fig. 1). When first instars are very young and food for fourth instars is absent, nearly 50% of the newborn larvae can be eaten by this density of fourth instar larvae.

First instar density. Contrary to our expectations, the rate of cannibalism is not significantly affected by the density of the young larvae

TABLE 1. Analysis of variance for the effects of developmental age, food availability, first instar density, and interactions among these factors on the cannibalism rate of fourth instar *Aedes triseriatus* larvae. Interdependence between pairs of treatments is tested by interaction terms A×F, A×D, and F×D. Alteration of any pairwise interdependence by treatment levels of the third variable is tested by the interaction term A×F×D. SS=Sum of squares, MS=Mean square, F=Treatment MS/Error MS, test statistic, df=degrees of freedom, P=probability of exceeding F by chance. The dependent variable is the number of first instars eaten divided by the initial number of first instars. The angular transformation was applied to reduce the dependence of the variance on the mean in proportionate data.

Source of variation	SS	MS	df	F	P
Main effects					
Age (A)	1.184	1.184	1	19.46	<0.001
Food (F)	1.310	1.310	1	21.52	<0.0001
Density (D)	0.288	0.058	5	0.95	ns
Interactions					
A×F	0.428	0.428	1	7.04	<0.05
A×D	0.256	0.051	5	0.84	ns
F×D	0.382	0.076	5	1.26	ns
A×F×D	0.269	0.053	5	0.88	ns
Error	2.921	0.061	48		

(Table 1). Within the density range of 2–64 larvae per 35 ml, which exceeds the range found in the field, no saturation of cannibalism rates by high density of victims is detectable

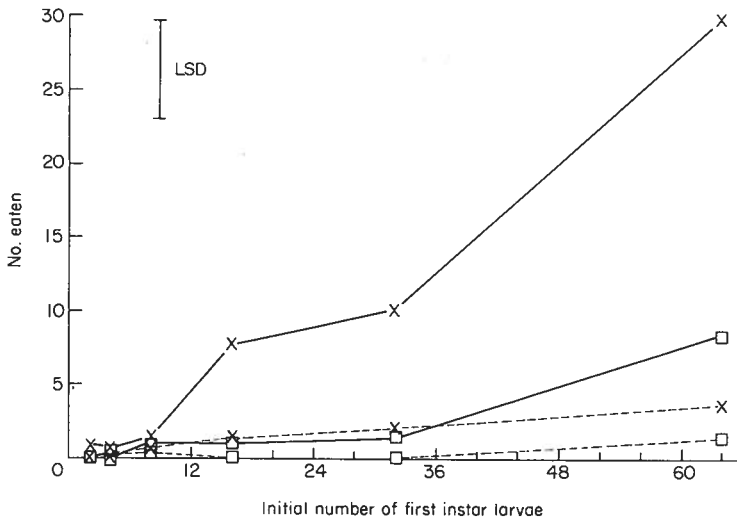


FIG. 1. The functional response of fourth instar larvae to density of newly hatched larvae. The points represent the means of three replicates in each treatment combination. Solid lines indicate no food; dashed lines, food added; ×, 1.5-h-old larvae; □, 24-h-old larvae. Tukey's LSD is shown for visual comparison of the cell means.

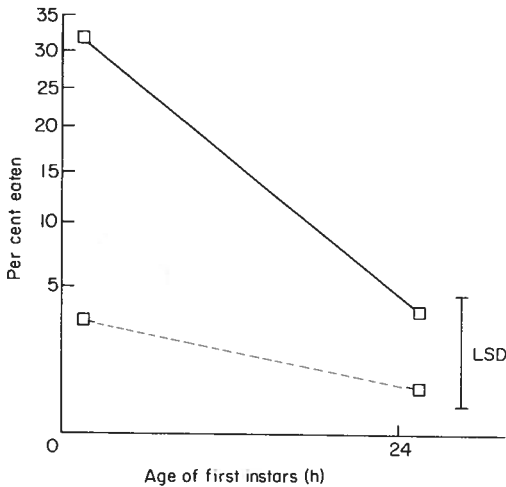


FIG. 2. The effect of the interaction between the age of the first instar and the availability of an alternate food source on the fourth instar attack rate. Solid line, no food; dashed line, food added. The points represent the means summed across all density levels. Tukey's LSD is shown for comparison of the means. The vertical scale converts attack rate into the more appropriate angular transformation.

(Table 1). This result is supported by regressions of fraction eaten on density, all of which were not significant.

The facultative nature of cannibalism. The availability of a yeast food source reduces the frequency of cannibalism (Table 1) for both ages of first instars, but cannibalism was not eliminated at any combination of food, density and age treatment levels.

The influence of first instar development. The vulnerability of first instars to cannibalism declines dramatically during the first 24 h of larval life (Table 1, Fig. 2). When the first instars are more than 24 h old, the cannibalism rate declines to less than 10%. At least two hypotheses may explain this decline: an increase in size during the first 24 h might increase the time required for the cannibal to subdue, ingest or digest its victims (i.e. the handling time increases); alternatively, larvae might gain substantial agility within their first 24 h, reducing the rate of successful attack. We can eliminate one of these alternatives by examining the interaction between the density and age factors (Table 1). This interaction is nonsignificant, indicating that the responses of cannibalism rates to density are similar for 1.5-h and 24-h-old larvae; thus we detect no

difference in handling time. The decrease in cannibalism rate of 24-h-old larvae results more likely from their greater agility. Inspection of the attack rates (number eaten/initial number) confirms this possibility. Without the additional food source, the attack rate averaged 0.6 for the 1.5-h-old larvae, and 0.2 for the 24-h-old larvae. This difference is significant (Tukey's Least Significant Difference = 0.17).

These results provide the first documentation of cannibalism in *Aedes triseriatus*. A few studies have reported cannibalism in other mosquito species: *Aedes aegypti* (MacGregor, 1915), *Eratmapodites* (Haddow, 1946; Gillett, 1972), *Anopheles stephensi* (Reisen & Emory, 1976), *Culex tritaeniorhynchus* (Mogi, 1978) and *Toxorhynchites rutilus* (MacRary, 1965). *A priori*, one would not expect cannibalism to occur in *Aedes* larvae, partly because they are filter-feeding detritivores. However, cannibalism has been recorded in a number of typical filter-feeders such as Copepod nauplii (Landry, 1978), Rotifers (Gilbert, 1980), *Notonecta* (Fox, 1975), Pismo clams (Fitch, 1964) and others (Polis, 1981). According to Polis (1981) and Fox (1975), cannibalism or intraspecific predation is an overlooked, probably very important, and certainly widespread phenomenon in animals. They conclude that the notion of cannibalism as abnormal or unnatural behaviour should be dismissed.

The significant interaction between first instar age and food may be interpreted in two ways (Fig. 2). Fourth instar larvae may increase their filtering rate under conditions of food scarcity, rendering the more vulnerable young first instars particularly susceptible to cannibalism during such periods. Alternatively, the youngest first instars are able to grow out of their vulnerability quite rapidly when food is abundant, thus diminishing the difference between attack rates on old and young first instars. This experiment was not designed to distinguish between the two explanations of this unanticipated result. By either mechanism the result is the same: cannibalism is a food dependent, facultative process in *Aedes triseriatus*.

There may be at least two reasons why *Aedes* eggs avoid hatching into an environment that contains abundant larvae. A density induced hatching delay would have definite

adaptive rewards that could outweigh the cost to fitness of the increase in generation time. We now know that density-dependent hatching inhibitions can occur in this species (Livdahl *et al.*, 1984). Our data show that facultative cannibalism might have been a strong factor in the evolution of egg hatching inhibition by larvae. An additional benefit to eggs that refrain from hatching into crowded habitats results from the avoidance of severe competitive effects of larger larvae (Livdahl, 1982).

While cannibalism should have clear potential importance to population regulation, it could be completely overlooked during a *posteriori* analyses of field census data in which pupal biomass is regressed against earlier larval biomass (e.g. Bradshaw & Holtzapfel, 1983) because of the short interval in which cannibalism operates. The same possibility exists for a density-induced inhibition of egg hatching (Livdahl *et al.*, 1984). Where these and other short-term regulatory processes are possible, negative results in such a search for density-dependent effects within or between species (as reported by Bradshaw & Holtzapfel (1983) for *Aedes triseriatus* and other treehole mosquito inhabitants) should be viewed as incomplete until direct experiments to detect intra- and interspecific competition have been performed.

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