

A seasonal shift in egg-laying behaviour in response to cues of future competition in a treehole mosquito

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Summary

1. We tested a set of hypotheses to predict egg-laying behaviour in *Aedes triseriatus* in the field in Massachusetts. These hypotheses reflect three main themes: females avoid competitive or predatory threats to their larvae; females judge larvae or eggs as cues to future permanence or productivity within a treehole; and females are either opportunistic ovipositors, or hedge their bets by scattering their eggs in multiple habitats. We predicted that mosquitoes might vary in their response depending on whether their offspring will hatch immediately or enter diapause and hatch the next year.

2. We stocked artificial treeholes with larvae at four densities ranging from 0 to 90 larvae per habitat for four trials in 1992 and eight trials in 1994. In 1992, we added predatory *Anopheles barberi* larvae to half the replicates of each density level. In 1994, we tested for an interaction between egg and larval density by stocking additional traps with eggs in batches of 0, 20 and 200, and larvae in densities as in the previous trials.

3. The population revealed a significant interaction between time of year and larval density. More eggs accumulated in traps stocked with fewer larvae (0 or 15) early in the season, but females showed a slight positive response to higher densities (45 or 90) later on, after their offspring were all likely to enter diapause. These results suggest that potential ambiguities of larval cues, with indications of habitat permanence as well as adversity of future competition, are resolved by females. Females did not respond differentially to the predatory *Anopheles barberi* larvae.

4. The estimated batch size obtained in oviposition traps did not differ from the fecundity of field-caught females allowed to oviposit under confinement in laboratory vials, suggesting that bet-hedging by scattering of eggs among multiple habitats did not occur.

5. An unexpected result, a positive response to higher egg densities, is discussed in light of studies on other insects. This result conflicts with our predictions based on females choosing less competitive environments for their larvae and also conflicts with previously published accounts of avoidance of eggs in this species. Preference for habitats with conspecific eggs might be explained if eggs reflect habitat stability or if larvae gain an advantage from being in an aggregation. Neither hypothesis is resolved by the present study.

Key-words: *Aedes*, competition, density-dependent, habitat selection, oviposition.

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Introduction

Oviposition in many insects appears non-random with respect to both abiotic and biotic factors of the

environment. Females may gather information about environmental quality, and make oviposition decisions based upon that information. Egg-laying decisions can ultimately influence the success of a female's offspring (Butkewich, Prokopy & Green 1987; Quiring & McNeil 1987; Crump 1991). Oviposition substrates differ in numerous ways that can affect larval growth and survivorship; these differences

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may provide reliable cues allowing for discrimination between favourable and unfavourable sites. Presence of competitors and predators and resource quality have all been implicated as factors assessed by egg-laying insects (see reviews in Prokopy, Roitberg & Averill 1984; Roitberg & Prokopy 1987; Thompson 1988). Many insects use oviposition-detering pheromones (Quiring & McNeil 1984) to signal that suitable hosts are already occupied (e.g. small plants, Thompson 1988; fruits, Prokopy 1981; Butkewich *et al.* 1987; seeds, Messina & Renwick 1985). Chemicals emanating from feeding larvae or other by-products of occupied sites can also act as epidiectic cues (see Prokopy *et al.* 1984; Roitberg & Prokopy 1987). Correlations have been discovered between oviposition preference and offspring performance for a number of insect species in which larvae cannot disperse (e.g. specialized herbivores and fruit feeders, parasites, and leaf and stem miners; Craig, Itami & Price 1989). This latter finding suggests that environmental cues play an important role in female choice of oviposition site. As in many herbivores and parasitoids, treehole mosquitoes (*Aedes* spp.) are dependent on restricted resources that differ in presence of intraspecific and intercohort competitors (Livdahl 1982; Edgerly & Livdahl 1992) and/or food sources (Léonard & Juliano 1995). Therefore, we expect that treehole mosquitoes will exhibit similarly choosy oviposition behaviour.

Aedes triseriatus (Say), a common treehole mosquito in the eastern United States, oviposits throughout the summer months. In the laboratory, egg-laying females are attracted to containers of water, particularly those with horizontal openings containing darkly coloured water and a high organic content (Wilton 1968). These characteristics are consistent with qualities typical of treeholes used by them in the field (Scholl & DeFoliart 1977; Sinsko & Grimstad 1977). Further laboratory studies have suggested that larva-produced compounds are also attractive to females (McDaniel *et al.* 1976). The response of *A. triseriatus* females to such cues may be species-specific; Bradshaw & Holzapfel (1988) found that water from treeholes occupied by conspecific larvae was more attractive than water from treeholes supporting other sympatric mosquitoes. Attractiveness of a treehole may be influenced further by conspecific eggs which become repellent as they accumulate in oviposition traps (Kitron, Webb & Novak 1989).

We generated hypotheses about egg-laying decisions by assuming that *Aedes* females will behave in a manner that maximizes the fitness of their offspring. These hypotheses reflect three main themes: females avoid competitive or predatory threats to their larvae; females judge larvae or eggs as cues to future permanence or productivity within a treehole; and females hedge their bets by scattering their eggs in multiple habitats (Table 1). The following sections will review predictions for each hypothesis.

POTENTIAL BIOTIC INTERACTIONS

Predators

Egg-laying mosquitoes should avoid ovipositing in sites where aquatic predators are abundant (Chesson 1984; Tietze & Mulla 1991; Blaustein & Kotler 1993). Late instar *Anopheles barberi* larvae are voracious predators of young mosquito larvae (Petersen, Chapman & Willis 1969; Livdahl 1982; Copeland & Craig 1992; Willey 1993). We predict that *A. triseriatus* females will avoid ovipositing in treeholes that contain these predators (Table 1; hypothesis 1a).

Competitors

The presence of older conspecific larvae may be unfavourable to a cohort of newly hatched larvae. Laboratory studies suggest that many *A. triseriatus* eggs hatch upon inundation with rainwater in the spring, while others delay hatching until repeated immersions have occurred (Livdahl & Koenekoop 1985). The resulting multiple cohort structure of *A. triseriatus* larval populations leads to complex and often detrimental interactions. For example, in simulated treeholes placed in the field, younger cohorts suffered adverse consequences of competition, increasing in severity as larval density increased (Livdahl 1982; Edgerly & Livdahl 1992). In these studies, detrimental effects of density were reflected in decreased sizes of adults, delayed development, and increased mortality. Of note is that the experimental densities were based on naturally occurring densities of 28, 44 and 60 larvae per 100 mL (see Livdahl 1982; Edgerly & Livdahl 1992). Newly hatched larvae may also risk cannibalism by older larvae (Koenekoop & Livdahl 1986; but see Edgerly & Livdahl 1992). We suggested that *A. triseriatus* eggs delay hatching under conditions of high larval density to avoid such competitive penalties (Livdahl, Koenekoop & Futterweit 1984; Livdahl & Edgerly 1987; Edgerly, Willey & Livdahl 1993). The inhibition appears to result from larvae grazing micro-organisms from the egg surfaces, thereby removing agents of oxygen consumption, which would otherwise promote egg hatching (Edgerly & Marvier 1992). Another possible mechanism for avoiding potentially competitive habitats, tested in the present study, is selective oviposition in response to larval density (Table 1; hypothesis 1b).

The repercussions of delayed hatching may depend on the time of year. If ovipositing females do respond to larvae, it seems also likely that their response could vary with season. During June and July, a female deposits eggs that can hatch and reach adulthood during that growing season. However, in northern areas, eggs enter diapause in response to a short photophase later in the summer, and hatch the following spring (Shroyer & Craig 1980). Females ovipositing in late summer may therefore face constraints different from those ovipositing early in the season. If

Table 1. Predictions, derived from previously published accounts of *Aedes* ecology (see text for details), about oviposition choices by the eastern treehole mosquito

Hypotheses	Predictions
1. <i>Potential biotic interactions</i>	
1a. Females avoid predators of larvae	Females will not lay eggs near <i>Anopheles</i> larvae
1b. Females avoid habitats with high larval densities because of competition between larvae	Females will lay eggs in less crowded habitats
1b1. Response to larval density is influenced by timing of egg diapause	If eggs are able to hatch immediately, females will avoid competitive habitats
1c. Females avoid eggs which reflect potential competition in the future	Females will avoid laying eggs in habitats containing a relatively large number of eggs
2. <i>Habitat quality</i>	
2a. Presence of larvae indicates treehole permanence	When larvae are present, females will lay eggs into the habitat
2b. Eggs indicate that treehole held water in recent past	Eggs attract and/or stimulate egg-laying females
2c. Larval density reflects treehole productivity	Females will be differentially attracted to treeholes with more larvae
3. <i>Bet-hedging</i>	
3a. Catastrophes within individual habitats occur asynchronously, and risk of movement among habitats is low	Females will lay eggs in multiple habitats; minimum batch size < potential batch size
3b. Catastrophes are uncommon, or occur synchronously within a region; risk of movement among habitats is high	Females will lay all eggs within a single habitat; minimum batch size = potential batch size

a female in early summer oviposits into a crowded habitat, her eggs may delay hatch long enough to enter diapause, and delay development for nearly a year. If she rejects crowded habitats and instead oviposits into less populated treeholes, her eggs may hatch, thereby increasing her fitness in two ways: generation time of her offspring will be reduced, and by avoiding winter mortality, survivorship of her offspring will be increased. Although the former advantage applies specifically to growing populations, the second should apply to all populations that experience mortality during an extended period of dormancy. In contrast, a female in late summer may not reject crowded habitats, especially if the presence of larvae reflects a treehole's qualities of permanence or nutrition as argued below. Competition, while imminent early in the season, will not occur between a late summer female's progeny and those presently in the treehole because the former enter diapause, while the latter emerge as adults or die at the onset of freezing weather. Based on this logic, we predict a negative relationship between the number of eggs added during the trial and the number of larvae already present in early summer. In contrast, late summer females should not discriminate between the artificial treeholes based

on number of larvae present (Table 1: hypothesis 1b and 1b1).

Future competitors

Clusters of eggs may portend a future, rather than immediate, competitive environment (Table 1: hypothesis 1c). Potential competition among emerging larvae may explain why abundant eggs apparently repelled females searching for oviposition sites at an Illinois field site (Kitron *et al.* 1989). Egg density may be a more important signal of future competition than present larval density, and we predict that the number of eggs added to ovitraps will be an inverse function of the number of eggs already present.

HABITAT QUALITY

Habitat permanence

Females should choose treeholes with water-holding ability (Table 1: hypotheses 2a, 2b). If so, then early and late summer females should choose treeholes with older larvae, regardless of density. The presence of these older larvae indicates relative habitat perma-

nence. We would expect significantly more eggs in habitats with larvae than without, regardless of density if habitat permanence underlies a female's response to larvae.

Eggs may accumulate over time in a treehole and their numbers may reflect relative permanence. Despite the report that eggs repel ovipositing females (Kitron *et al.* 1989), we predict that females could use relatively high numbers of eggs as a reflection of past water-holding capabilities of the treehole. Females are known to lay their eggs into water-filled cavities (Wilton 1968). The possibility exists that if they locate a dry treehole with eggs along the inner wall of a treehole, the eggs reflect a conspecific's response to water that evaporated in the recent past. Eggs might then be a reliable cue to water-holding. Therefore, eggs might accumulate at a higher rate in habitats that already have eggs (Table 1: hypothesis 2b). This prediction is the opposite of that predicted by the competition hypothesis 1c.

Habitat productivity

In addition to variation in tendency to desiccate, treeholes also vary in quantity and quality of stemflow, a source of water and nutrients, and organic matter necessary for development of larvae (Walker & Merritt 1988; Léonard & Juliano 1995). If a nutrient-rich habitat is key to the survival of larvae, then egg-laying females may select treeholes occupied by larvae, particularly in late instars (Table 1: hypothesis 2c). By this hypothesis, we would expect the number of eggs to increase linearly as number of larvae increases, independent of seasonal variation.

HEDGING BETS

In a risky habitat, we may expect females to adopt different strategies of oviposition, depending on when the risks are most intense during the life cycle, and whether the risks are spatially distributed in a patchy or homogeneous manner. The possible evolutionary outcomes include at least two conditions in which eggs should accumulate without regard to the presence or abundance of larvae. We set forth the following hypotheses to account for the possible observation of no response to larvae.

A bet-hedging approach, which might be anticipated in a low-risk environment for adults and a high-risk environment for larvae, is to scatter their offspring among as many habitats as possible, thereby minimizing the likelihood of losing all offspring due to a catastrophe in the larval habitat. This strategy should be most advantageous in situations when the larval habitats vary greatly in their permanence, or when catastrophes occur asynchronously among larval habitats, and when the females have no reliable means of discriminating between temporary and permanent habitats or anticipating future catastrophes (Table 1:

hypothesis 3a). This approach may also prevent a detectable response to larval density. However, bet-hedging females are more likely to encounter multiple habitats during repeated searches, and are therefore more likely to be able to make choices among them. Therefore, if bet-hedging occurs within an ovarian cycle, some response to cues about habitat quality might be anticipated.

A contrasting approach is more likely if females travel in a low-risk environment, when they may have much to gain by inspecting a variety of habitats before finalizing their decision about where to oviposit. In this instance, a response of females to larval density may be advantageous. However, if there is substantial risk of mortality during additional searching, or of not finding another suitable habitat, oviposition of all eggs into the first suitable larval habitat discovered, independently of larval abundance, may be the most successful strategy (Table 1: hypothesis 3b).

Adult female *Aedes triseriatus* experience a moderate risk of dying while searching for oviposition sites and blood-meals (daily survival ranges from 0.78 to 0.95; references in Pumpuni & Walker 1989); risk of pre-reproductive death may have led to the evolution of less choosy oviposition behaviour than that exhibited in laboratory tests, where alternative sites are nearby (references in Bentley & Day 1989).

Materials and methods

INFLUENCE OF LARVAL DENSITY AND PREDATOR PRESENCE

We established 40 ovitraps for each of four trials during July–September 1992 in Moore State Park, a wooded area in Paxton, Massachusetts, USA. We chose this site and sampling period after discovering egg-laying females there, beginning the third week of June. We fashioned ovitraps from plastic cups painted black and lined with beige paper towel. These were suspended, facing west, on nails ≈ 60 cm from the ground, on sugar maple (*Acer saccharum*) and red oak (*Quercus rubra*). Ovitrap traps were placed along a pair of north–south transects, one 200 m and the other 100 m in length. The distance between ovitraps ranged from 4 m to 50 m (mean distance = 9.8 m). Because of the possibility that site-specific attributes may differentially attract females (Beehler & DeFoliart 1990), we randomly varied the position of each treatment combination with each trial. To provide all traps with an aqueous solution to facilitate larval growth and to attract ovipositing females, we collected water from treeholes located within ≈ 2 m of the ground, demonstrated to be preferred habitats for northern populations of *A. triseriatus* (Scholl & DeFoliart 1977). We removed particles by filtering treehole water through a mesh (0.5 mm), and autoclaved the liquid in hopes of destroying larval-produced attractants, which appear to lose activity when heated (Bentley *et al.*

1976; McDaniel *et al.* 1979). At the outset of a trial, each ovitrap received 100 mL of this homogeneous liquid, an oak leaf from the forest floor at the study site, plus 5 mL of stemflow, previously collected from an individual sugar maple tree and stored for 12 months at 5 °C prior to and during the experiment. These materials provided a source of bacteria and nutrients (Walker & Merritt 1988) for the larvae and potential oviposition attractants as described above.

On the first day of each 1-week trial, we stocked the ovitraps with third and fourth instar *A. triseriatus* at four densities based on an estimated carrying capacity (K) of 60 larvae per 100 mL (estimated as the density at which experimental cohorts achieved a per capita growth rate of zero, Livdahl 1982): zero as a control, $1/4K$, $3/4 K$, and $3/2 K$ (0, 15, 45, and 90 larvae per 100 mL, respectively). The range of densities provided low, moderate and high density treatments. Predators, third and fourth instar *Anopheles barberi*, were added in pairs to five replicates of each density level, and five replicates received no predators. Trials were conducted 14–21 July, 23–30 July, 17–24 August and 26 August–2 September 1992. We tested the effect of larval density on oviposition behaviour more extensively in 1994 by replicating the above experiment but without predators and with more trials through the season. We established ovitraps as described above except for the addition of a black plastic roof affixed with caulking to the tree ≈ 15 cm above the ovitrap to prevent rain water or extra stemflow from entering the ovitraps. Larval densities as described above were replicated 10 times each on 8, 15, 22, 29 July and 5, 12, 19, 31 August 1994. We collected the paper liners at the end of each 1-week trial and counted all *Aedes* eggs affixed to them.

Because seasonality may influence a female's choice of an oviposition site, we needed to determine the prevalence of diapausing eggs throughout summer. To do so, we collected a sample of eggs at the field site and left them to develop on the forest floor in ziplock bags for 7 days. They were then submerged in nutrient broth, which acts as a hatching medium, and the proportion hatching was determined. Hatch rate declined from 0.5 to 0.15 for eggs laid during trials started on 8 July through 22 July. No hatching was obtained for eggs produced thereafter; trials started after 22 July were therefore considered to be during egg diapause. Thus, our design for 1992 included three factors: predator presence (with two levels), larval density (with four levels) and seasonality (with two levels – prediapause or diapause). In 1994, we omitted predators from the design, but tested for differences between years (1992 and 1994) as well as for effects of larval density and seasonality.

After counting the eggs in 1992, we exposed a sample of 11 paper liners to a hatching stimulus so we could identify larvae from the eggs and verify that they were indeed *A. triseriatus* and not *A. hendersoni*, a possible resident in the area (Loor & DeFoliart

1969). Using relative length of anal glands as the distinguishing character (Darsie & Ward 1981) we found that all larvae in our sample ($n = 222$) were *A. triseriatus*.

THE IMPACT OF EGGS AND LARVAL DENSITY ON OVIPOSITION

Ovitraps for this test were shielded by a black plastic cup lid propped open at ≈ 35 degrees to each cup's opening. The lids were designed to prevent direct rainfall from dislodging experimental egg batches. The cups were hung on large trees (≥ 20 cm d.b.h.) 1 km from the previous trials, but within the same continuous stand of red oak and sugar maple.

Each replicate, stocked as in the above experiment, received a randomly chosen combination of *A. triseriatus* larval and egg densities. The larval densities were 0, 15, 45 and 90, while the egg densities were 0, 20 and 200. This factorial experimental design yielded 12 different combinations of treatment levels, with 8 replicates for each combination. Experimental eggs were laid by females caught in the field and brought to the laboratory for feeding and oviposition. Polygons (≈ 6 cm²) of the original oviposition paper, cut to produce batches of 20 or 200 eggs, were affixed to the paper towel that lined the inside of the cup using a hot melt adhesive (Master Mechanic®). As an oversight, no such polygons were added to control cups, and therefore no control existed for the additional paper and adhesive.

Ovitraps were set out on 21 July 1994. After 7 days, the paper towel liners were returned to the laboratory. We counted the total number of eggs on each paper, and subtracted the initial number of eggs to obtain the number of eggs deposited during the trial.

DISTINGUISHING BETWEEN BET-HEDGING AND RISK AVERSION BY OVIPOSITING FEMALES

If females oviposit opportunistically to minimize risks of mortality during a search for additional habitats, they should lay all of their eggs in a single batch. The alternative scattering strategy should be reflected by a batch size that is lower than the total fecundity of females for a given ovarian cycle. We tested for that difference by estimating the minimum batch size per oviposition trap, for comparison with batch sizes obtained by forcing females to lay all of their eggs in isolated vials.

The data from all of the trials described above provided 13 estimates of mean density (eggs per trap for each trial), as well as 13 estimates of mean crowding (Lloyd 1967), which estimates mean number of neighbouring individuals per sampling unit per individual (other eggs per individual per trap). As mean density approaches zero, mean crowding should approach the minimum batch size minus 1 (Iwao 1968; Kitron *et al.* 1989). Therefore, we used these two estimates of abun-

dance, obtained in 13 censuses, to estimate the minimum batch size, obtained as the y -intercept of the regression of (mean crowding + 1) on mean density. This estimate of minimum batch size was compared with batch sizes obtained from 261 females caught in the field in 1989, fed to repletion in the laboratory, held within cages for 5 days without an oviposition site, then isolated within 30 mL vials lined with damp strips of paper towel. Oviposition ensued within a 1-day period, but females were left in the vials for an additional 2 days. Retention of eggs has not been observed in previous studies using comparable methods with *A. triseriatus* (Livdahl 1982; P. Grimstad, personal communication). After deleting 11 vials in which no oviposition occurred, a t -test was constructed using the mean batch size and its standard error for the laboratory group and the minimum batch size estimate and the standard error of the y -intercept obtained from the field census data.

Results

OVERALL RESULTS

The following section details results as they relate to each hypothesis described in Table 1. Table 2 summarizes the hypotheses that gained support based on the statistical analyses.

OVIPOSITION RESPONSE TO LARVAL DENSITY

We used regression methods (JMP v. 3.1.5, SAS Institute Inc. 1995) to examine the three main effects and all possible interactions among factors to test the remaining hypotheses. A square-root transformation

of the number of eggs, the dependent variable, was used to achieve homogeneity of variance.

1992 data

A preliminary analysis of oviposition data from 1992, using a full factorial design, showed non-significant interactions for all interaction terms involving the *Anopheles* treatment ($P > 0.4$ for all interactions). Because none of these interactions (*Anopheles* × Trial, *Anopheles* × *A. triseriatus* density, and *Anopheles* × *A. triseriatus* density × Trial) were relevant to the hypotheses of this study, these terms were combined with the error sum of squares. Analysis of a simplified model (Table 3) revealed that the densities of *A. triseriatus* had no significant influence on oviposition as main effects. These results justified the inclusion of 1992 data with those of 1994, in which no *Anopheles* larvae were added.

The only significant main effect was due to time of year (Trial); substantially more eggs were laid per week during the first collection of 1992 than during the last three collections. This effect was complicated by a significant interaction with the density of *A. triseriatus*. Analyses of subsets of the data, excluding each trial in turn, revealed that this interaction was due to a negative response of oviposition to *A. triseriatus* density in the initial trial (subsets that included the initial trial consistently retained the significant interaction), and a consistent positive response during the latter three trials (the subset excluding the initial trial yielded no significant interaction). This interaction was examined more extensively with an additional set of eight trials in 1994, in

Table 2. Hypotheses on oviposition choices in *Aedes triseriatus* that gained support from field results. Numbering system corresponds with Table 1

Hypotheses	Results
1. <i>Potential biotic interactions</i>	
1b1. Response to larval density is influenced by timing of egg diapause	The number of eggs accumulated in response to larval density as a function of seasonality, with a slight preference for less dense habitats in the prediapause season and a slight preference for more crowded habitats in the diapause season
2. <i>Habitat quality</i>	
2b. Eggs reflect water-holding ability of the treehole	Eggs attracted and/or stimulated egg-laying females, irrespective of larval density, and therefore this hypothesis cannot be rejected.
2c. Larval density reflects treehole productivity	Females were differentially attracted to treeholes with more larvae only during the diapause season, lending support for this hypothesis. However, this hypothesis must be considered in conjunction with hypothesis 1b1 to explain the variability across the summer. The support for this hypothesis is relatively weak.
3. <i>Bet-hedging</i>	
3a. Bet-hedging by scattering eggs among habitats does not occur	Females laid the same number of eggs within laboratory vials as the estimated minimum batch size obtained from the 13 censuses. However, spatial bet-hedging could still occur between ovarian cycles.

Table 3. Analysis of variance testing for the response of *Aedes triseriatus* oviposition to three factors in 1992 (Trial, *Anopheles barberi* density, *A. triseriatus* density), and to the interaction between Trial and *A. triseriatus* density. This analysis treats all factors as continuous variables

Source	d.f.	M.Sq.	F	P
Trial	1	540.8	13.3	<0.01
<i>Anopheles barberi</i> density	1	101.1	2.5	NS
<i>A. triseriatus</i> density	1	114.2	2.8	NS
Trial * <i>A. triseriatus</i> density	1	167.3	4.1087	<0.05
Error	177	40.7		

NS, $P > 0.05$.

which the density of *A. triseriatus* was manipulated at the same densities as the 1992 trials.

Combined analyses: 1992 and 1994

The full analysis includes one new main effect (Year), as well as interactions between Year and *A. triseriatus* density and between Year and Trial; the effect of *Anopheles* and associated interactions of 1992 are excluded. Because we had no expectations of differences in any particular direction, the influence of Year was treated as a random factor, along with its associated interaction terms. An initial analysis revealed non-significant interactions which did not bear on our hypotheses (Year \times Trial, Year \times *A. triseriatus* density). An important result of the initial analysis was the non-significance of the three-way interaction (*A. triseriatus* density \times Trial \times Year, $F_{1,585} = 0.15$, $P > 0.70$), indicating that the season-dependent response to *A. triseriatus* larvae did not change appreciably between the two years. We eliminated those interaction terms from the statistical model to obtain a simplified model summarized in Table 4. The relevant result for our initial hypothesis (Table 1: hypothesis 1b1), that oviposition response to density may differ with time of year, did not change from the analysis of 1992 data: the interaction between *A. triseriatus* larval density and week of trial remained significant (Table 4), and warrants against generalizations concerning the significant *A. triseriatus* density effect,

which was negative. The results are summarized in Figs 1, 2 and 3.

The nature of the interaction is clarified by pooling data from the eight trials into two groups, organized according to whether some of the eggs laid during the trial were likely to have the opportunity to hatch during the same year (prediapause, trials 1–3) or whether they were all likely to enter diapause (trials 4–8) (Fig. 2). The interaction is also clarified by examining the slopes of individual linear regressions of oviposition on larval density for each week of each year of the study (Fig. 3): significant negative responses to larvae were seen only during the first three trials; results for the later trials were all non-significant individually, although it is possible to obtain significant positive results by pooling the later groups.

Response to the presence or absence of larvae

One hypothesis (Tables 1, 2a) predicted that larvae might provide a signal about the relative permanence of a habitat. If so, then a small number of larvae should convey the same degree of information about permanence as a large number. Females should respond positively to any number of larvae. Using methods consistent with those described above, we tested this by pooling all larval densities greater than zero, and comparing these against the controls. In this analysis, Year and Trial remained as significant

Table 4. Analysis of variance testing for the response of *Aedes triseriatus* oviposition to three factors (Trial, *A. triseriatus* density, and Year), and to the interaction between Trial and *A. triseriatus* density. This analysis treats Trial and *A. triseriatus* density as continuous variables, and treats the influence of Year as a random, nominal factor

Source	d.f.	M.Sq.	F	P
Trial	1	382.7	10.1	<0.01
<i>A. triseriatus</i> density	1	174.9	4.6	<0.05
Year	1	859.1	22.7	<0.01
Trial * <i>A. triseriatus</i> density	1	188.8	5.0	<0.05
Error	588	37.8		

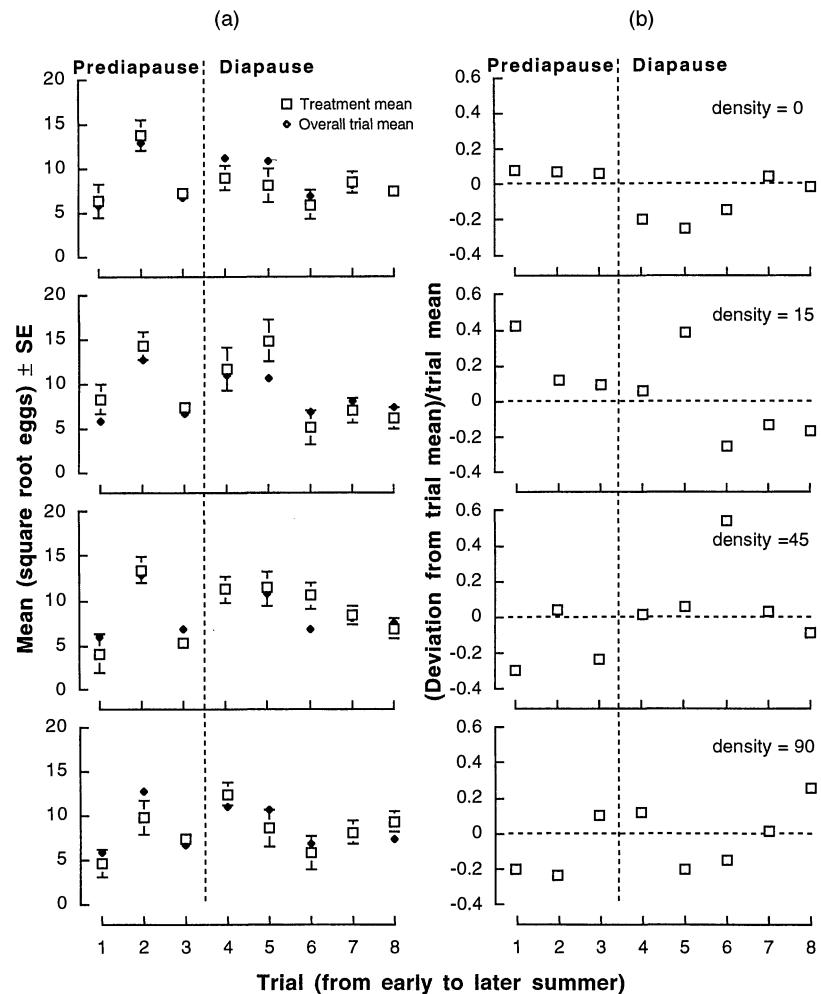


Fig. 1. (a) Scatter plot showing trial means as a function of larval density (0, 15, 45 and 90). The overall trial mean was added at each trial ($x = 1-8$ indicate weeks after 1 July) for comparison purposes. Means, based on the square root transformation of number of eggs, were calculated after pooling 1992 and 1994 of the study, as well as both levels of the *Anopheles* treatment for 1992. The standard error of each mean is shown as an error bar. A vertical line divides the graph into prediapauses (trials before July 21) and diapause seasons. (b) Scatter plot obtained by standardizing for differences among trials. Values represent deviations of cell means from the mean for each trial date, divided by the mean for each trial date. All other notations are as in Fig. 1a.

factors, but all other effects were non-significant, including the terms most relevant to this hypothesis, *A. triseriatus* presence or absence ($F_{1,588} = 0.19$, $P > 0.60$) and the interaction between larval presence and Trial ($F_{1,588} = 0.40$, $P > 0.5$).

OVIPOSITION RESPONSE TO THE DENSITY OF LARVAE, EGGS, AND THE INTERACTION BETWEEN LARVAL AND EGG DENSITY

These effects were tested with a regression model incorporating coefficients for egg density, larval density, and a coefficient for the product of egg and larval density. An initial analysis indicated that eggs and larvae operate as independent factors (Egg \times Larva coefficient: $F_{1,92} = 0.01$, $P > 0.90$). This interaction term was deleted from the regression model. During this trial, larvae inhibited oviposition

(Fig. 4, $F_{1,93} = 5.9$, $P < 0.05$), and eggs had a stimulatory effect (Fig. 5, $F_{1,93} = 4.6$, $P < 0.05$).

TESTING FOR SCATTERING OF EGGS

The minimum batch size was estimated as the y-intercept of the regression of (mean crowding + 1) on mean density for the 13 censuses conducted during this study (Fig. 6). This estimate (predicted value = 57.6, SE = 15.8) was quite similar to the batch size obtained from females isolated in laboratory vials (mean = 56.1, SE = 1.5), and the difference was not significant ($t_{260} = 0.2$, $P > 0.8$).

Discussion

RESPONSE TO POTENTIAL PREDATION

Female *A. triseriatus* did not discriminate between habitats based on the presence or absence of predatory

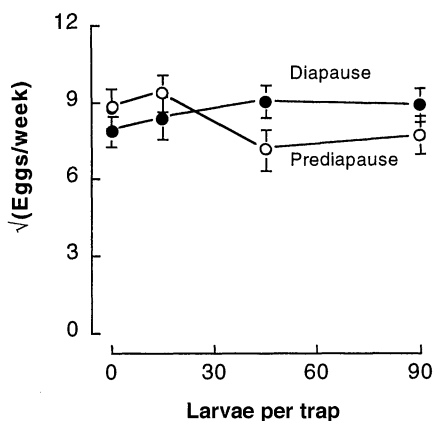


Fig. 2. Response of oviposition by *Aedes triseriatus* to the density of *Aedes triseriatus* fourth instar larvae. Data from eight trials (beginning in the first week of July) during the 2 years of the study are grouped according to whether the eggs laid during each trial had some prospect of hatching, or were all likely to enter diapause. The data have been pooled across both levels of the *Anopheles barberi* treatment, which was not a significant main effect and produced no significant interaction effect. Mean values, based on a square root transformation, are shown ± 1 standard error. Grouping of trials was performed as follows: weeks 1–3 = prediapause, weeks 4–8 = diapause.

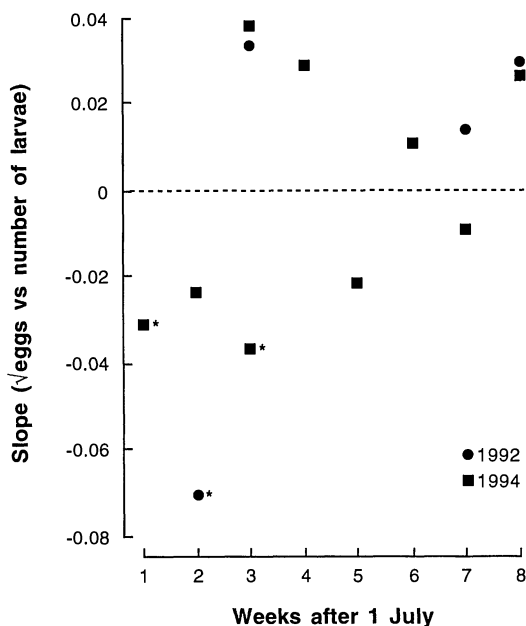


Fig. 3. Regression coefficients of oviposition to larval density for each trial during the 2 years of the study, beginning in the first week of July (* $P < 0.05$).

larvae (*Anopheles*). Although these results are suggestive, they do not mean conclusively that a response has not evolved to this predator. Cues found to be attractive to *A. triseriatus* in previous studies (Wilton 1968) – characteristics typical of basal treeholes – may effectively isolate their larvae from *Anopheles* in Massachusetts where the latter tend to be restricted to rot-holes located higher on the tree (personal obser-

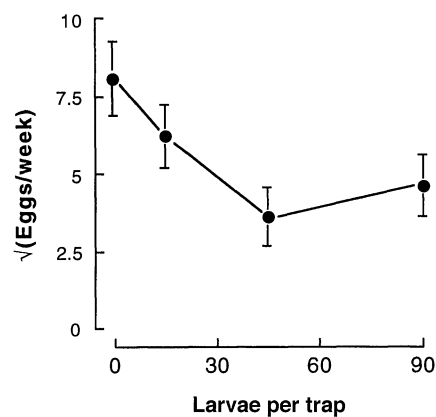


Fig. 4. Response to larval density in the egg \times larva study, conducted in trial week 3, 1994. Mean values of counts are shown with standard errors, obtained after a square root transformation and pooling across all egg density treatment levels.

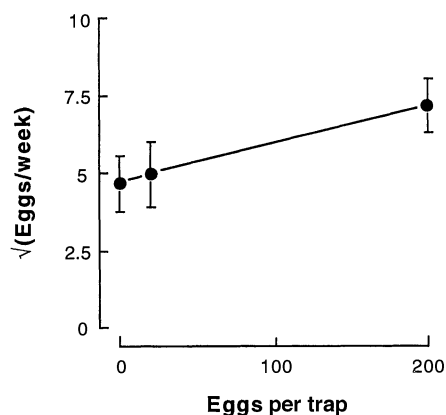


Fig. 5. Influence of conspecific eggs placed in ovitraps on subsequent oviposition by *Aedes triseriatus*. These data come from the egg \times larva study, conducted in trial week 3, 1994. Mean values of counts, transformed as square root, and standard errors are shown for each level of initial egg density, obtained after pooling across all larval density treatment levels.

vation). Cues from our experimental water, derived from basal holes, may have overwhelmed cues emanating from the two individual predators per ovitrap. As suggested by Bradshaw & Holzapfel's (1988) experiment in Florida, *A. triseriatus* may be sensitive to water from treeholes harbouring predators, perhaps only when a suite of relevant cues is intact. Alternatively, the density of *A. barberi* may not have been high enough to elicit a detectable response, although two fourth instar larvae of this species can consume hundreds of newly hatched *A. triseriatus* larvae per day (Willey 1993).

FEMALE RESPONSE TO LARVAL DENSITY

Our field results support the hypothesis that egg-laying *A. triseriatus* respond to immature conspecifics occupying oviposition sites. The mosquitoes displayed

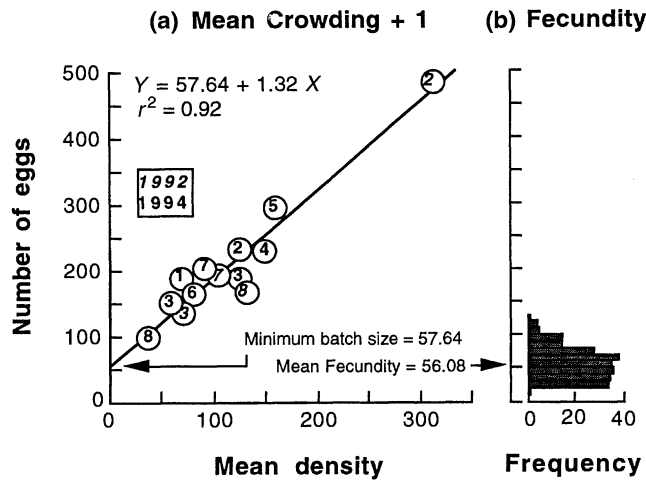


Fig. 6. A test for scattering of eggs among multiple oviposition sites. (a) Minimum batch size is estimated by the y -intercept of the regression of (mean crowding + 1) on mean density for 13 censuses conducted in this study; the minimum batch size is similar to the fecundity (b) of field-caught female *A. triseriatus* confined within vials during oviposition. Census data are distinguished by trial (numbers depicting weeks after 1 July) and by year (italicized numbers 1992, others 1994).

a statistical response to larval density that varied over the season during both years of the study (the Trial \times Larval Density Interaction, Table 4) lending support to hypothesis 1b1 (Table 2). The results suggest a relatively strong negative response to crowded habitats early in the season when newly laid eggs are able to hatch. The significant negative slopes for the relationship of eggs laid as a function of larval density reflect this behaviour (Fig. 3). Results from the experiment investigating the interaction between eggs and larval density also yielded a significant negative response to density in ovipositing females in early summer (Fig. 4). The negative consequences of larval competition and larva-imposed hatch inhibition, more severe in the crowded treeholes (as described earlier), may have selected for sensitivity to larval density in egg-laying females early in the season. In contrast, the more extensive experiment on larval density revealed a tendency for females to accept all water-filled habitats (occupied or not) from approximately the end of July through the remainder of the summer. A slight positive response to density was apparent in these late season results, again as reflected in the slopes (Figs 2 and 3). These results support the hypothesis (2c in Table 2) that occupied habitats may reflect positive, long-term habitat productivity. Eggs deposited later in the season will enter diapause and hatch next summer, thus not encountering the present competitive situation. The resulting larvae may, however, accrue benefits from a treehole with adequate resources next season. Despite the statistical support for the hypothesis that females are choosy in these ways, a great deal of unexplained variability remains. There appear to be other important factors determining extent of oviposition at sites at given times.

Interpreting the data in light of competing hypotheses (1b1 and 2c, Table 2) remains ambiguous in some ways. For example, an acceptance of habitats with

larvae later in the season may reflect the loss of a negative response to larvae that was apparent early in the summer rather than an overt preference for larvae. The difference is subtle but may reflect different selective pressures: in the former case, greater numbers of larvae may represent competition in the early summer and tend to be avoided; in the latter, larvae are of little consequence to eggs in the late summer and therefore, eggs accumulate in occupied habitats. An alternative interpretation is that larvae reflect habitat quality later in the summer and therefore eggs accumulate in occupied habitats. The positive response to density in later trials was less intense than the negative response in trials 1–3 (Fig. 3). Therefore, a strong case cannot be made for the latter hypothesis (hypothesis 2c).

Support for hypotheses related to larval density does not preclude the possibility that some females may simply take the first habitat they encounter or hedge their bets by ovipositing in multiple sites. We can reject the bet-hedging possibility, as defined in Table 1, on the basis of the similarity of mean fecundity and minimum batch size estimates (Fig. 6), which provides a strong indication that females lay all their eggs when the decision to oviposit has been made. Other forms of minimizing risks of erroneous habitat selection remain possible; females must do some travelling to find the blood source for their next ovarian cycle, which may result in their selection of different sites.

Responses to larval density by egg-laying females occur in many insects (e.g. Prokopy 1981; Fitt 1984; Butkewich *et al.* 1987; Quiring & McNeil 1987; Hilker & Weitzel 1991), including mosquitoes (Soman & Reuben 1970; Benzon & Apperson 1988; Consoli & Teixeira 1988; Bentley & Day 1989; Heard 1994). In a recent field study, Heard (1994) gathered field evidence that pitcher plant mosquitoes (*Wyeomyia smithii*) are sensitive to larval density and resource qual-

ity. In that case, females laid more eggs into pitcher plants containing intermediate numbers of larvae, either conspecifics or midge larvae, and fewer eggs into pitchers containing no larvae or higher numbers of larvae. Larger pitchers were preferred overall, perhaps because of their higher resource levels and/or more stable water supplies.

In addition to questions about the mechanism of attraction or inhibition of oviposition, our results raise questions about factors that account for a seasonal change in oviposition behaviour. At the individual level, female response to larvae could be influenced by female age, or by the number of egg batches the female has already produced. Such endogenous factors were shown to influence female parasitic wasps in a laboratory study investigating the impact on egg laying of seasonal dynamics and variable host quality (Roitberg *et al.* 1992). In that study, female wasps responded to host quality (non-parasitized fly larvae = high quality; previously parasitized = low quality) in a manner that depended on previous foraging experience and on photoperiod. Wasps reared under summer photoperiods would search for high quality hosts longer than those reared under fall photoperiods. The authors suggested that the summer-reared females had a longer life expectancy, and were more sensitive and/or responsive to host (or habitat) quality. The females' response depended on their experience with hosts: if these females were previously exposed to parasitized larvae, they stayed in a low quality patch longer and were more likely to superparasitize their hosts. Under autumn photoperiodicity, females previously exposed to high quality hosts also engaged in a high rate of superparasitism. This latter result might reflect a willingness by females to accept any host at the end of the season when the risk of female death is relatively high because of limited resources and/or a killing frost. Female mosquitoes may also modify their preferences in response to changing weather conditions or photoperiod. Alternatively, if the attraction or repulsion results from larval products, these substances could vary in quantity or quality at different times of the year. At the population level, the seasonal change in preference could result from differences in preference among cohorts developing and emerging at different times. Females emerging late in the season may differ from early emerging females due to seasonal variation in nutritional quality of their larval habitat. Eggs hatching at different times in the growing season may produce groups of larvae with intrinsically different properties (Livdahl & Koenekoop 1985) and this hatching asynchrony could yield seasonal differences in oviposition preferences as adults.

A POSITIVE RESPONSE BY FEMALES TO EGGS: GROUP EFFECT OR HABITAT QUALITY?

Egg-laying females showed a positive response to the presence of relatively abundant conspecific eggs

(Fig. 5). This result was predicted by the hypothesis that eggs reflect the water-holding capability of the treehole (hypothesis 2b), but is also consistent with a group effect hypothesis that would predict that females prefer to group their eggs with those of other females because larvae gain by being in an aggregation. This latter hypothesis was not considered in our experimental design because previous reports stress the importance of competitive, rather than facilitative, larval interactions in *A. triseriatus*.

Other aquatic insects also choose habitats with conspecific eggs. For example, sandfly females (*Lutzomyia longipalpis*) are stimulated or attracted by the presence of eggs (Dia-Eldin & Ward 1991). Oviposition attractants have also been found in eggs of mosquitoes in the genus *Culex*, as previously mentioned. These mosquitoes, which reside in larger pools than do *Aedes*, apparently produce an oviposition pheromone which promotes aggregation. The resulting larvae are gregarious and may better prevent scum from forming on the pool of water and may reduce chances of larval predation and parasitism (Pile 1987 as cited in Dia-Eldin & Ward 1991). In contrast, larval competition for *A. triseriatus* can be severe when larvae are in groups. Furthermore, the generally negative response to larval density early in the season in the present study suggests that larvae are relatively unattractive to egg-laying females. Therefore, based on these results, the larval competition hypothesis (with its seasonal component reflected in the significant statistical interaction shown in Table 4) emerges as a better model than a group effect model for understanding the response of females to larval density.

Although attraction to conspecific eggs might seem to promote competition, egg hatching dynamics in *Aedes* may prevent overt competition among larvae that hatch from clustered eggs. For example, in a previous study (Edgerly & Livdahl 1992), eggs (allowed to hatch on their own schedule) were exposed to varying densities of older larvae. The resultant larvae ultimately performed significantly better than experimentally synchronized cohorts held at similar densities for a number of measures of success, including an estimate of per capita growth for each experimental population. If attraction to eggs evolved because eggs reflect habitat permanence, the ability of pharate larvae to detect habitat quality and to hatch in a staggered manner (Livdahl *et al.* 1984; Livdahl & Koenekoop 1985; Livdahl & Edgerly 1987; Edgerly & Marvier 1992) might prevent competitive interactions so often detected in experiments where larval cohorts are tightly and artificially synchronized (Livdahl 1982). In sum, females in the present field study may have avoided crowded habitats early in the season because of larval competition and the problems of hatch inhibition which is induced by high larval density. They may have preferred habitats with eggs because eggs reflect the water-holding ability of the treehole and do not represent an immediate source of competition.

The positive response to eggs in our study conflicts directly with an account of oviposition in *A. triseriatus* in Illinois (Kitron *et al.* 1989) which claimed that females avoid high densities of eggs, and with a laboratory study of *A. aegypti* (Chadee, Corbet & Greenwood 1990). Kitron's *et al.* (1989) conclusion was based on a failure to find a difference between the number of eggs found on fresh substrates relative to substrates that had received eggs during the preceding trial. However, that analysis was based on 'intensity' (number of eggs per positive trap) rather than density, and the study made no attempt to determine the number of eggs added to each trap. In addition, Kitron *et al.* counted only the eggs found on a balsa strip 2.5 cm in width. This limited water margin (about 12% of the trap's perimeter) could have produced a bias, because eggs could have been laid elsewhere within each trap. Our study used substrates that covered the entire margin of water within the trap. This difference in methodology may also account for the lower batch size estimates obtained in the other study, which, after comparison to fecundity of mosquitoes reared under laboratory conditions, led Kitron *et al.* to conclude that females lay their eggs in multiple sites. We suggest that the remaining eggs from small batches could have been found elsewhere in the trap, at locations other than the balsa strips. Other methodological and population differences may have contributed to the differences between their study and ours.

Conclusions

A considerable number of herbivorous insects produce pheromones, signalling degree of crowding and host exploitation and eliciting dispersal from occupied resources (Prokopy 1981). Our field results suggest that a treehole mosquito may respond to cues that reflect the competitive environment within larval habitats, which are relatively limited and exploitable as are small host plants and seeds for specialist herbivores. In previous studies, mosquitoes have been found to respond to a variety of chemical cues at oviposition sites, some of which are produced by larvae (see references in Maire 1983; Bentley & Day 1989) and others by bacteria associated with larvae (e.g. Benzon & Apperson 1988). By taking an evolutionary approach to empirically assess mosquito oviposition behaviour in the field, we investigated aspects of a complex behaviour apparently subject to selective pressures similar to those in other resource-limited insects. The seasonal shift in response to larval density was predicted by two hypotheses: (i) that larvae represent a source of competition for other larvae early in the season; and (ii) larvae reflect habitat quality later in the season, when eggs enter diapause rather hatch into a competitive situation. Despite the theoretical possibility, the positive response to eggs was not expected because of published accounts of a negative

response to eggs in this species (Kitron *et al.* 1989). Clustering of eggs, however, was predicted by the hypothesis that eggs reflect the water-holding capability of the treehole. The apparent negative response to larval density early in the season, the positive response to eggs, and the slight positive response to treeholes with larvae later in the season suggest that female choice and egg hatch dynamics (previously reported for this species) combine to produce subtle population dynamics within treeholes. Clearly, more fine-tuned experimental work will be required to understand the advantages of clustering eggs in treeholes and to unravel as yet unexplained variability in response to larval density apparent in this field population.

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