

Effects of the Facultative Predator *Anopheles barberi* on Population Performance of its Prey *Aedes triseriatus* (Diptera Culicidae)

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Ann. Entomol. Soc. Am. 91(1): 33-42 (1998)

ABSTRACT We tested the hypothesis that predation by *Anopheles barberi* (Coquillett) on young larvae of *Aedes triseriatus* (Say) reduces intraspecific competition among surviving prey and thereby increases survival, mass at eclosion, and estimated rate of population increase, or decreases development time for *A. triseriatus*. In a field experiment manipulating both litter (=food) abundance and predator abundance, total survivorship of *A. triseriatus* was significantly reduced by *A. barberi* predation in tree holes, but not in tires where overall survival was extremely low. Survival to adulthood and estimated finite rate of increase (λ') were significantly lower in low-food treatments, but were unaffected by the predator. Days to and mass at eclosion were unaffected by predation. This field experiment thus provided no evidence for a positive effect of predation by *A. barberi* on *A. triseriatus* population performance. A laboratory functional response experiment yielded no asymptotic saturation of number of prey killed by *A. barberi* of any instar. Fourth-instar *A. barberi* feeding on either 1st- or 2nd-instar *A. triseriatus* had indistinguishable functional responses, but 3rd-instar *A. barberi* killed significantly fewer 1st-instar prey than did 4th-instar *A. barberi*, and did not kill 2nd-instar prey. Censuses of tree holes and tires showed limited seasonal co-occurrence of predator-prey instar combinations that can lead to predation. These data suggest that *A. barberi* has only a limited potential to reduce populations of *A. triseriatus* and that such effects are likely only during a short period in midsummer.

Aedes triseriatus (Say) and *Anopheles barberi* (Coquillett) are container-dwelling mosquitoes that co-occur in much of their range in the eastern United States (Darsie and Ward 1981). Both species occur in water-filled tree holes and artificial containers (e.g., tires) and differ in their mode and location of feeding. *A. triseriatus* feeds on detritus and bacteria within the water column and benthos, whereas *A. barberi*, like most *Anopheles*, feeds on bacteria and other organic matter caught in the surface tension of the water (Clements 1992). More interestingly, *A. barberi* is a facultative predator late in development, feeding on early instars of *A. triseriatus* (Petersen et al. 1969). In laboratory predation experiments, *A. barberi* can significantly reduce the survivorship of *A. triseriatus*, sometimes reducing the percentage emergence of *A. triseriatus* adults to roughly half that observed in the absence of *A. barberi* (Copeland and Craig 1992). Livdahl (1982) found that, in a field experiment, replicate jars contaminated with *A. barberi* yielded few if any surviving *A. triseriatus*. However, in this system where prey are vulnerable to the predator for only a short period during early development, it is possible that the predator may actually enhance the population growth of its victim if predation reduces intraspecific competition, leaving more resources available to the survivors

(Abrams and Rowe 1996). This may either allow a greater number of individuals to survive to the adult stage (Washburn et al. 1991), or may improve some other measure of population performance, such as increasing size at or decreasing time to emergence (Abrams and Rowe 1996, Washburn et al. 1991). Such an effect was demonstrated for the tree-hole species *Aedes sierrensis* (Ludlow) in a field setting using *Lambornella clarki* (Corliss & Coats), a lethal parasite of *A. sierrensis* (Washburn et al. 1991). Evidence that *A. barberi* can enhance some aspects of *A. triseriatus* population performance was provided by Copeland and Craig (1992), who showed that both male and female *A. triseriatus* were significantly larger in the presence of *A. barberi* predation. However, Copeland and Craig (1992) also documented significant mortality from predation by *A. barberi*, and it is therefore unclear if overall rate of increase of *A. triseriatus* was enhanced, reduced, or unaffected by this predator.

In this article, we pose the question: What is the total effect of the facultative predator *A. barberi* on *A. triseriatus* populations? To answer this question, we 1st conducted a field experiment designed to measure the impact of this predator when it is in the last 2 stages of larval development. In this experiment, we attempted to determine if late-instar *A. barberi* have a positive, negative, or no net effect on the performance of *A. triseriatus* populations.

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To complement the field experiment, we conducted a functional response (i.e., the relationship between prey density and number of prey eaten per predator) experiment in a laboratory setting. This study enabled us to determine how late-instar *A. barberi* behave as predators when feeding on early-instar *A. triseriatus*, whether *A. barberi* is an effective predator at the densities we used in our field experiment, and whether 1st- and 2nd-instar *A. triseriatus* are equally vulnerable to each of the 2 late-instar predator stages. Finally, we determined when the 2 species co-occur in the developmental stages that are necessary for predation by *A. barberi* on *A. triseriatus* by conducting semimonthly censuses of tires and tree holes at 2 sites. We used these data to answer a simple but important question for determining the role of predation in a natural setting: How frequently do the appropriate stages of these 2 species co-occur in space and time?

Materials and Methods

Field Experiment. *A. triseriatus* used in the experiment were progeny of individuals field-collected at Parklands Merwin Preserve (40.5° N, 89.1° W) and adjacent woodlands (collectively referred to as Parklands) located north of Normal, IL (see Munstermann and Wasmuth 1985, Juliano 1989, and Juliano et al. 1993 for rearing methods). At this latitude there appears to be >2 generations per year. *A. barberi* larvae were field collected at Parklands 1–14 d before the start of the experiment and were held in a water-filled tub until the start of the experiment. They were not provided any macroscopic food during this time. The experiment was initiated on 25 August 1994 and ended on 11 November 1994.

The experiment was conducted in cylindrical cages (30 mm diameter, 250 mm long) constructed from 250- μ m nylon mesh, and suspended in large natural basal rot holes ($n = 3$ holes) and tires ($n = 5$) at Parklands. Tires had been in place for 3 yr. The volume of water held by these cages when in a vertical position in the field was 141.03 ± 2.71 ml (mean \pm SE) in tree holes and 115.18 ± 4.15 ml in tires. A plastic vial at the bottom of the cage made up 50 mm of the total length and held ≈ 20 ml of water when the cages were removed from the tires or tree holes to check for adults. The cages contained either 0.1 or 0.5 g of leaf litter (*Quercus alba*), collected from the forest floor at Parklands and sorted and dried at 55°C. Cages with litter were placed in tires or tree holes at Parklands 3 d before the start of the experiment to allow the leaf litter to soak and to be colonized by microorganisms. Tires and tree holes were covered with 6-mm² wire mesh to prevent disturbance by vertebrates. Different amounts of leaf litter (and the associated microorganisms) have been used in other experiments to vary food availability (Léonard and Juliano 1995). Different quantities of food were used so that the effect of *A. barberi* on *A. triseriatus* could be ob-

served under conditions of both limited and severe resource competition.

To start the experiment, *A. triseriatus* eggs were hatched 24 h before the start of the experiment using the synchronous hatching technique (Novak and Shroyer 1978). The newly hatched larvae were then transferred to the experimental cages in tires and tree holes at Parklands. Each cage held 40 newly hatched *A. triseriatus* larvae and no predator, one 3rd-instar, or one 4th-instar *A. barberi* larva. At the start of the experiment, the *A. barberi* larvae were taken to the field site in individual containers and placed into appropriate treatment cages.

Water levels in the experimental containers were maintained at maximal levels by weekly additions of deionized water. Each cage was checked daily for the eclosion of adults, and container, treatment, sex, days to eclosion, and dry mass (determined using a Cahn 31 microbalance) of each individual were recorded. At the end of the experiment, all remaining larvae in each cage were counted and identified.

Analysis of variance (ANOVA) was done separately on tires and tree holes because different experimental designs were necessary in the 2 habitats. Tires had a single replicate per tire, whereas tree holes had multiple replicates per tree hole. ANOVA included effects of container (individual tree holes or tires used as blocks), predator, food, and predator–food interaction. When the predator effect was significant, we tested 2 a priori contrasts, 1 comparing the no-predator treatment with the averaged predator treatments, and a 2nd comparing the 2 predator treatments. Contrasts were done using the Bonferroni approach to control type I experiment-wise error. Survivorship was measured in the following 2 ways: (1) survivorship to adulthood, in which only individuals emerging as adults by the end of the experiment were counted, and (2) total survivorship, which included both adult survivors and those larvae surviving to the end of the experiment. Survivorship to adulthood, total survivorship (both arcsine transformed to meet the assumptions of normality and homogeneous variance), time to eclosion, and mass at eclosion were analyzed using ANOVA to test for food, predator, and interaction effects, and for significant variation among tires and tree holes. Along with analyzing these variables individually, survivorship to adulthood, mass at eclosion, and time to eclosion were combined to obtain a composite estimate of cohort rate of increase, r' (Livdahl and Sugihara 1984, Fisher et al. 1990). The value r' is determined as follows:

$$r' = \frac{\ln \left[(1/N_0) \sum_x A_x f(w_x) \right]}{D + \left[\sum_x x A_x f(w_x) / \sum_x A_x f(w_x) \right]}$$

where N_0 is the original number of females (assumed to be 50% of the initial number of larvae in the cohort), A_x is the number of females eclosing on

day x , w_x is the mean dry mass of females eclosing on day x , $f(w_x)$ is the function relating production of female progeny to female dry mass, and D is the time between adult eclosion and reproduction. A_x and w_x were determined for each cage. D was assumed to be 12 d (Léonard and Juliano 1995, Grill and Juliano 1996). The regression relating number of female eggs laid to dry mass at eclosion was

$$f(w_x) = (1/2)\exp[4.5801 + 0.8926(\ln w_x)] - 1$$

$$r^2 = 0.5377 \quad n = 36.$$

To obtain this regression, we determined fecundities $f(w_x)$ of females fed to repletion and allowed to oviposit at 24°C and a photoperiod of 16:8 (L:D) h. We measured wing length and estimated dry masses for these females, using the regression equation dry mass = 0.21 (wing length)³ - 0.099 = 0.67 (Nasci 1990). When no females in a cohort survive to adulthood $r' = -\infty$, a value that is very difficult to use in analyses. Instead, a related measure of cohort performance, the estimated finite rate of increase (λ') (Léonard and Juliano 1995, Grill and Juliano 1996), was analyzed. Finite rate of increase, $\lambda = e^{r'}$, is the multiplicative increase in population size in 1 time unit (days in this case) (Pianka 1983), and may be estimated by $\lambda = e^{r'}$. If $\lambda' > 1.0$, the cohorts in question are, on average, increasing. If $\lambda' \approx 1.0$, the cohorts are, on average, just replacing themselves. Finally, if $\lambda' < 1.0$, cohorts are, on average, decreasing.

Predictions for the Field Experiment. If predation by *A. barberi* lowers density sufficiently to reduce competition among early-instar *A. triseriatus*, the predator treatments should yield greater λ' , mass at eclosion, survivorship, or lower time to eclosion (Copeland and Craig 1992). Because resource competition will be more intense in the low-food treatment, predator treatments may have stronger positive effects (i.e., relatively greater enhancement of λ' , survivorship, mass, or reduction of days to eclosion) in the low-food treatment than in the high-food treatment (i.e., a predator \times food interaction) (Hard et al. 1989, Léonard and Juliano 1995).

In contrast, if *A. barberi* predation is so intense that fewer individuals survive to the adult stage than if predation were absent, and this effect outweighs any benefit from reduced competition, predation by *A. barberi* should have a negative effect on *A. triseriatus* survival, rate of increase (λ'), mass, or development. Finally, if predation causes significant mortality but in the absence of predation competition leads to reduced survival, growth, and development rate, the rate of increase (λ') may be unaffected by predation. The specific case of mortality from predation being roughly equivalent to mortality from density dependence in the absence of predation is known as compensatory mortality (Washburn et al. 1991).

Functional Response. Functional response experiments were conducted in 250-ml plastic beakers that contained 200 ml of deionized water. The ex-

periment consisted of the following 4 treatments: (1) 4th-instar *A. barberi* feeding on 1st-instar prey, (2) 4th-instar *A. barberi* feeding on 2nd-instar prey, (3) 3rd-instar *A. barberi* feeding on 1st-instar prey, and (4) 3rd-instar *A. barberi* feeding on 2nd-instar prey. Controls without *A. barberi* were used to estimate nonpredatory mortality of *A. triseriatus* larvae. Only 1st- and 2nd-instar prey were used because 3rd- and 4th-instar prey are apparently too large for *A. barberi* to consume (Petersen et al. 1969, Copeland and Craig 1992). Prey were hatched synchronously using hatching tubes (Novak and Shroyer 1978). *A. barberi* were collected from the field and the number of replicates of each treatment was determined by the number of *A. barberi* larvae collected. Hunger levels of *A. barberi* larvae were standardized by placing the predators in water containing 1 g/liter of food (see Copeland [1987] for composition of food) at 24°C and a photoperiod of 18:6 (L:D) h 2 d before the initiation of the experiment. When not being used in an experiment, *A. barberi* larvae were maintained as described by Copeland (1987).

Twenty-four hours after an *A. triseriatus* hatch, the 1st-instars were allotted to treatments in the densities of 10, 20, 40, 60, 80, 100, 150, 200, and 250 per 200 ml. One *A. barberi* larva of the appropriate instar was placed in the appropriate replicate. After 24 h at 24°C and with a photoperiod of 18:6 (L:D) h, the *A. barberi* were removed and the numbers of *A. triseriatus* remaining in each replicate were counted. When 2nd-instar *A. triseriatus* were used, 24 h after a hatch all 1st-instars were counted out in groups of 500, placed in 500 ml of deionized water, and given 0.05 g of liver powder. The larvae were then placed in an environmental chamber at 24°C and a photoperiod of 18:6 (L:D) h, for 2 d, when most had molted to the 2nd-instar. These 2nd-instars were then allocated to treatments, and the experiment was conducted in the same manner as with 1st instars.

These data were analyzed to determine the shape of *A. barberi*'s functional response to *A. triseriatus* (Juliano 1993). The data did not fit any of the usual functional response relationships (see Juliano 1993 for details), and a linear relationship on a double log scale (i.e., a power function) yielded the best fit of these data. Therefore, a simple analysis of covariance (ANCOVA) (after testing for equality of slopes) was used to analyze the log-transformed functional response data and to compare functional responses of these predator-prey combinations.

Censuses of Containers. Tree holes and tires were censused at Parklands, and additional tree holes were censused at another nearby site, Moraine View State Park (which lacked tires). The 2nd site was added to determine whether patterns of co-occurrence were similar at 2 sites within the area. Tree holes at both sites were low rotholes. Tires at Parklands had been in place since 1991. Both sites were censused monthly from May to August 1995 and bimonthly from August to November 1995, when *A.*

Table 1. ANOVA for effects of container (=block), predator treatment, and food availability on survival of *A. triseriatus* in both tires and tree holes in the field experiment

	Tree holes					Tires				
	df	Total survivorship		Survivorship to adult		df	Total survivorship		Survivorship to adult	
		F	P > F	F	P > F		F	P > F	F	P > F
Container	2	5.83	0.0089	20.35	0.0001	4	0.62	0.6556	1.53	0.2328
Predator	2	4.54	0.0218	0.33	0.7207	2	0.62	0.5504	0.48	0.6278
Food	1	1.61	0.2166	6.79	0.0158	1	13.77	0.0014	5.91	0.0246
Predator-Food	2	0.75	0.4816	0.19	0.8292	2	0.17	0.8430	0.33	0.7218
Error	23	—	—	—	—	20	—	—	—	—

barberi appears to increase in abundance (Cope-land and Craig 1990). Collection techniques differed between tires and tree holes. Tires were censused more effectively by collecting all of the water and detritus, transporting it to the laboratory, and sorting the contents until no more larvae were found. Tire volume also was measured at each census. Larvae in tree holes were collected by siphoning the water and detritus into a 500- μ m mesh sieve.

Water from each container was returned and the process was repeated to increase the likelihood of removing all of the larvae. Larvae retained in the sieve were taken to the laboratory, where they were counted. Only the maximal water volume was measured for tree holes. It is likely that some 1st-instars passed through the 500- μ m sieve. Because only maximum water volume was measured and all 1st-instars may not have been accounted for, data from tree holes were used only for qualitative comparison with the tire data. In the laboratory, larvae were

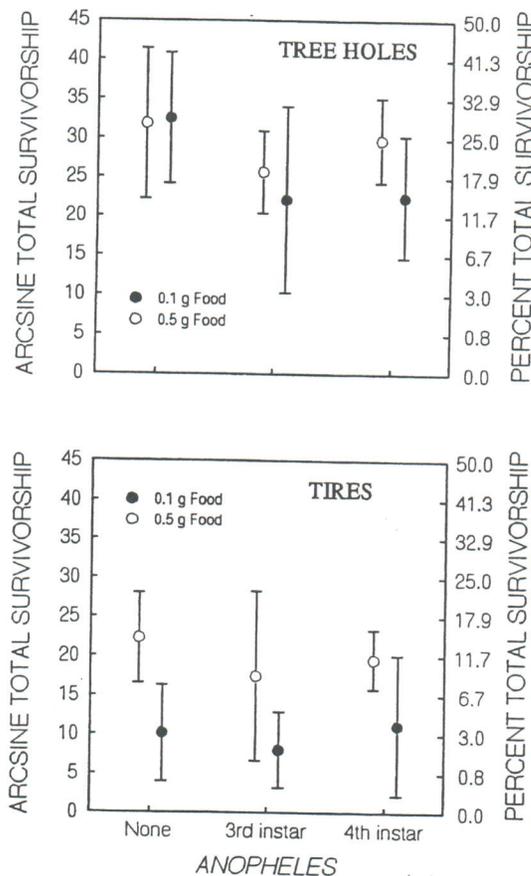


Fig. 1. Arcsine-transformed total survivorship (mean \pm SE) for both tires and tree holes. Significant differences exist between predator treatments and control for tree holes. Significant differences also exist between food levels for tires. No predator \times food interaction exists for either tree holes or tires.

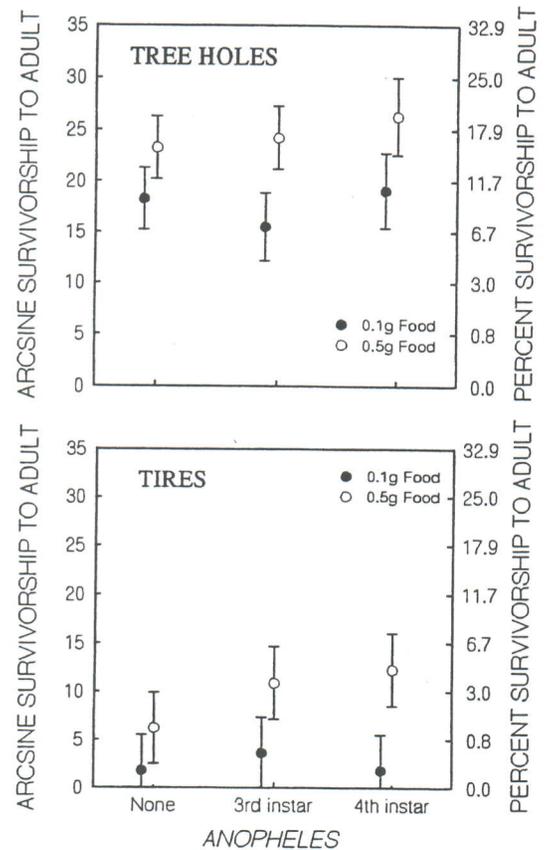


Fig. 2. Arcsine-transformed adult survivorship (mean \pm SE) for both tires and tree holes. Significant differences exist between food levels for both tires and tree holes, but no predator effect or predator \times food interaction exists.

Table 2. ANOVA testing for effects of container (=block), predator treatment, and food availability for median days to and mean mass at eclosion of male and female *A. triseriatus* in tree holes

	df	Median, d		Mean mass	
		F	P > F	F	P > F
Females					
Container	2	8.46	0.0031	15.33	0.0002
Predator	2	2.53	0.1109	0.27	0.7651
Food	1	1.11	0.3067	0.70	0.4162
Predator-Food	2	0.165	0.8529	1.94	0.1765
Error	16	—	—	—	—
Males					
Container	2	0.25	0.7854	1.30	0.3234
Predator	2	0.38	0.6938	1.32	0.3199
Food	1	1.68	0.2308	0.02	0.8859
Predator-Food	2	1.48	0.2841	0.86	0.4585
Error	8	—	—	—	—

enumerated by species and instar. All larvae were returned to the appropriate container the following day.

From our field data we calculated the mean interspecific crowding (Lloyd 1967) between the following: (1) 4th-instar *A. barberi* and 1st-instar *A. triseriatus*, (2) 4th-instar *A. barberi* and 2nd-instar *A. triseriatus*, (3) 3rd-instar *A. barberi* and 1st-instar *A. triseriatus*, and (4) 3rd-instar *A. barberi* and 2nd-instar *A. triseriatus*. Mean interspecific crowding per 200 ml volume is calculated as follows:

$$\left[\sum_{i=1}^n (y_i z_i / v_i) / y_i \right] 200 \text{ ml},$$

where y_i is the number of individuals of a particular instar of species y , z_i is the number of individuals of a particular instar of species z , v_i is the volume of water in the i th tree hole or tire, and the summation is done over n tires or tree holes. Mean interspecific crowding values may be interpreted as the mean number of a particular instar of species z encountered per 200 ml by the average individual of a particular instar of species y (Bradshaw and Holzapfel 1983).

Results

Field Experiment. Total Survivorship. When all individuals surviving to the end of the experiment were analyzed, there was a significant predator effect for tree holes (Table 1). There were significantly more survivors in the no-predator treatment than averaged predator treatments (contrast, $t_{23} =$

2.97, $P = 0.0069$) (Fig. 1). There was no significant difference in total survivorship between the 2 predator treatments (contrast, $t_{23} = 0.18$, $P = 0.8593$) (Fig. 1). For tree holes, there were no food or interaction effects. For tires there was no significant predator effect (Table 1). There was a food effect, with 0.5-g food treatments yielding significantly greater total survivorship than the 0.1-g food treatments (Fig. 1). There was no significant interaction effect for total survivorship in tires.

Survivorship to Adulthood. Within both tire and tree holes, effects on survivorship to adulthood (arcsine transformed) were similar. There was no significant predator effect, nor was there a significant predator-food interaction in either habitat (Table 1). However there was a significant food effect in both habitats (Table 1), with greater survivorship in the higher food treatment (Fig. 2). Experimental cages appeared to yield more adults in tree holes than in tires (Fig. 2).

Days to and Mass at Eclosion. There were no significant treatment effects on median days to eclosion (Table 2) or on mean mass at eclosion (Table 2) for both males and females in tree holes. Mean mass and median days to eclosion for both males and females in tree holes are given in Table 3. In tires, production of adults was so low (Fig. 2), often 0, that analyses of mass at and days to eclosion were uninformative and were therefore omitted.

Another way of testing the effects of *A. barberi* on development rate of *A. triseriatus* is to analyze the proportion of surviving individuals that completed development by the end of the experiment. The effect of predation was the only significant factor

Table 3. Least-squared means and SE for both mean mass at and median time to eclosion for both males and females in tree holes

Predator treatment	Males			Females		
	None	3rd instar	4th instar	None	3rd instar	4th instar
Mean mass, mg	0.1212	0.1408	0.1604	0.2489	0.2590	0.2596
SE	0.0140	0.0181	0.0174	0.0120	0.0106	0.0136
Median, d	32.00	35.58	35.43	48.89	40.04	43.73
SE	2.81	3.62	3.48	2.62	2.32	2.96

Table 4. ANOVA for effects of container (=block), predator treatment, and food availability on λ' for *A. triseriatus* in both tires and tree holes in the field experiment

	Tree holes			Tires		
	df	F	P > F	df	F	P > F
Container	2	4.01	0.0320	4	1.75	0.1786
Predator	2	0.88	0.4289	2	0.15	0.8617
Food	1	7.43	0.0121	1	4.11	0.0562
Predator-Food	2	0.27	0.7648	2	1.11	0.3493
Error	23	—	—	20	—	—

affecting proportion of survivors that completed development ($F = 4.37$; $df = 2, 23$; $P = 0.0245$). A contrast between the predator treatments and the no-predator control indicates that this proportion was significantly greater for treatments in which predators were present ($0.736 + 0.090$ for predator treatments versus $0.489 + 0.080$ for control treatments, $t_{23} = 23.784$, $P = 0.0071$). A contrast between the 2 predator treatments was not significant.

Estimated Finite Rate of Increase. In tree holes, there was a significant effect of food treatment on λ' , (Table 4), the higher food treatment yielding a greater value of λ' (Fig. 3). In tires, the effect of food treatments on λ' approached significance (Table 4), the higher food treatment yielding a greater mean λ' than the lower food treatment (Fig. 3). For both tires and tree holes, there was no effect of predator and no predator \times food interaction (Table 4).

Functional Response. Third-instar *A. barberi* were unable to consume 2nd-instar *A. triseriatus*, hence this combination was not included in the analysis of functional responses. Data from the remaining instar combinations were fit by a power function (i.e., linear on a log-log scale) as well as, or better than, by any of the standard functional response relationships. However, the slope (\pm SE) of 0.891 ± 0.075 , estimated from ANCOVA, did not differ significantly from 1.0 ($t_{136} = -1.463$, $P > 0.05$), indicating that this relationship between the number eaten and prey density was not significantly different from linear. The data were analyzed as a simple ANCOVA to test for differences among instar combinations. Slopes for each predator-prey combination did not differ significantly from one another ($F = 0.76$; $df = 2, 136$; $P = 0.4679$). ANCOVA revealed a significant effect of instar combination ($F = 25.28$; $df = 2, 136$; $P = 0.0001$). Comparisons among least square means of number of prey consumed indicated that numbers of 1st- and 2nd-instar *A. triseriatus* consumed by 4th-instar *A. barberi* did not differ significantly (Fig. 4), but that both of these instar combinations yielded significantly greater consumption than did 3rd-instar *A. barberi* feeding on 1st-instar *A. triseriatus* (Fig. 4). Consumption by 4th-instar *A. barberi* was ≈ 3 times that of 3rd-instar *A. barberi* (Fig. 4).

Censuses of Containers. Mean interspecific crowding between each of the *Anopheles-Aedes* instar combinations indicated a seasonal trend in vulnerability to predation for *A. triseriatus* (Table

5). Early in the season (May and June), 1st- and 2nd-instar *A. triseriatus* were abundant but 3rd- and 4th-instar *A. barberi* were not detected. However, in July, both 1st- and 2nd-instar *A. triseriatus* and 3rd- and 4th-instar *A. barberi* were present with the highest mean interspecific crowding observed

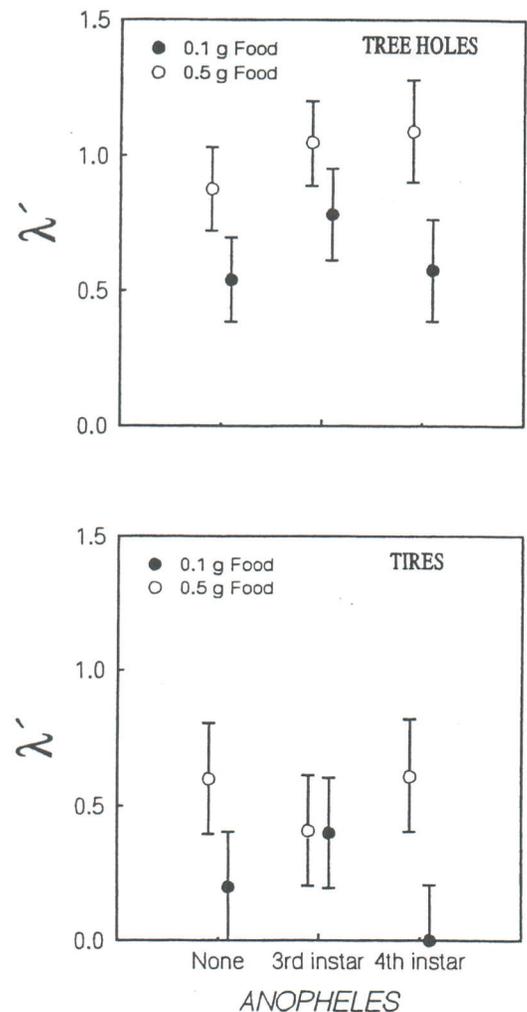


Fig. 3. λ' (mean \pm SE) for both tires and tree holes. Significant differences exist between food levels for both tires and tree holes, but no predator effect or predator \times food interaction exists.

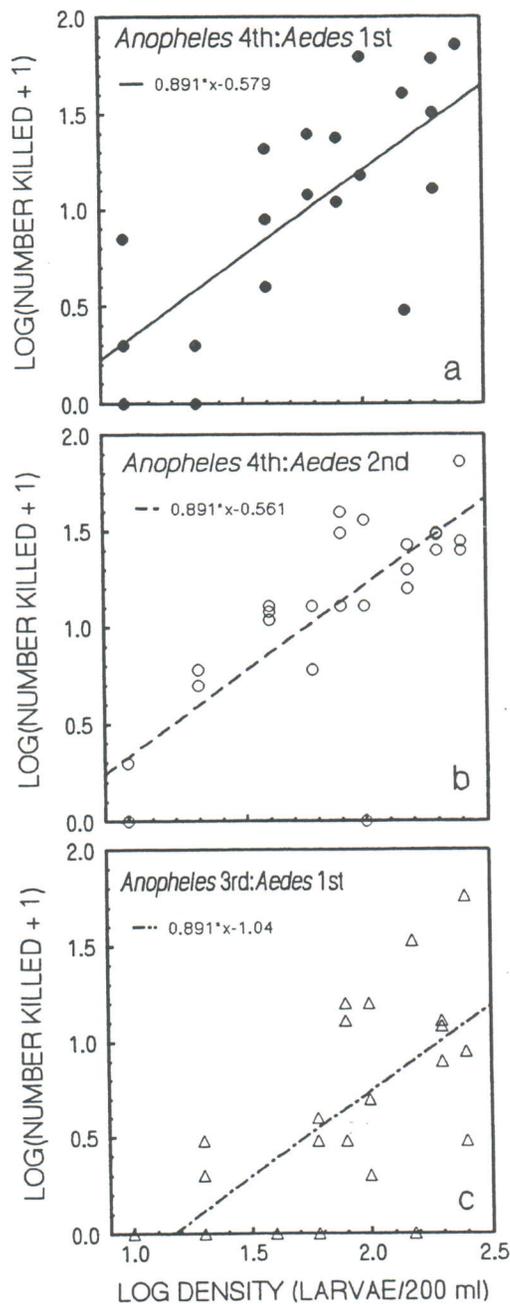


Fig. 4. The log (mean number of larvae killed + 1) as a function of the log of the initial density of prey. (a) 4th-instar *A. barberi* feeding on 1st-instar *A. triseriatus*, (b) 4th-instar *A. barberi* feeding on 2nd-instar *A. triseriatus*, (c) 3rd-instar *A. barberi* feeding on 1st-instar *A. triseriatus*. Data in a and b do not differ significantly; data in c differs significantly from those in a and b.

throughout the censusing period for both the number of *A. triseriatus* larvae per 200 ml per *A. barberi* larva and the number of *A. barberi* larvae per 200 ml per *A. triseriatus* larva (Table 5). After July, the

mean interspecific crowding of early-instar *A. triseriatus* and late-instar *A. barberi* decreased greatly (Table 5). In September and October, young *A. triseriatus* were very rare or absent (Table 5).

Discussion

The results from the field experiment provide no support for the hypothesis that predation by *A. barberi* can enhance performance of *A. triseriatus* significantly. This experiment was designed specifically so that the potential for *A. barberi* to have a positive effect on population performance of *A. triseriatus* was high. The experiment was done at high densities and low resource levels. At low food levels, survivorship to adulthood was significantly reduced in both tree holes and tires (Fig. 2), and λ' was reduced significantly in tree holes and nearly so in tires (Fig. 3). If we assume that these effects are products of density-dependent food limitation, predation by *A. barberi* acting early should have alleviated that density-dependence and produced an increase in survivorship and λ' . The lack of such effects is strong evidence that *A. barberi* does not affect *A. triseriatus* populations in a positive manner. There is, however, evidence that *A. barberi* does have an effect on *A. triseriatus*. *A. barberi* reduced total survivorship of *A. triseriatus* in tree holes compared with controls where the predator was absent, consistent with results of Copeland and Craig (1992), Livdahl (1982), and Petersen et al. (1969). Therefore, there is considerable evidence that late-instar *A. barberi* can consume a substantial number of early-instar *A. triseriatus*. The lack of any significant predator effects in tires probably results from the extremely low success of *A. triseriatus* in tires (Fig. 1). Insufficient resources seems the most likely cause of high mortality in the tires (Carpenter 1983, Léonard and Juliano 1995).

Although total survivorship of *A. triseriatus* in tree holes was reduced by *A. barberi* predation, the total effect on *A. triseriatus* population performance remains unclear because the overall finite rate of increase can be calculated only by using survivorship to adulthood. In this experiment, survivorship to adulthood did not differ between predator treatments for either tires or tree holes, and consequently λ' also did not differ between predator treatments. If it is assumed that all or most of the *A. triseriatus* larvae remaining at the end of the experiment would not survive through the winter (Sims 1982), the lack of a difference between predator treatments and control treatments implies that *A. barberi* causes compensatory mortality, by simply replacing mortality caused by other factors (i.e., density dependence and freezing conditions) operating in the absence of predation (Washburn et al. 1991). However, compensatory mortality demonstrated in this field experiment is likely in nature only if conditions are right, with late-instar *A. barberi* encountering a fairly high density of early-

Table 5. Mean interspecific crowding values for tires and tree holes from Parklands, and Moraine View State Park

Sample date	Parklands tires			Parklands tree holes				Moraine View tree holes				
	n	4th-1st	4th-2nd	3rd-1st	n	4th-1st	4th-2nd	3rd-1st	n	4th-1st	4th-2nd	3rd-1st
No. <i>Aedes</i> /200 ml/ <i>Anopheles</i> ^a												
15 May	8	NAn	NAn	NAn	7	NAn	NAn	NAn	—	—	—	—
15 June	8	NAn	NAn	NAn	5	NAn	NAn	NAn	6	NAn	NAn	NAn
15 July	8	23.92	15.26	42.94	4	0.00	0.62	0.00	6	0.00	4.58	0.00
1 Aug.	—	—	—	—	6	18.32	3.16	21.96	6	NAn	NAn	NAn
15 Aug.	8	0.06	4.22	0.06	6	0.04	1.56	0.08	4	0.00	0.96	0.00
1 Sept.	—	—	—	—	5	0.00	0.00	0.00	2	NE	NE	NE
15 Sept.	8	0.00	0.00	0.00	4	0.00	0.00	NE	4	NAn	NAn	NAn
1 Oct.	—	—	—	—	4	0.00	2.68	NE	2	NE	NE	0.00
15 Oct.	8	NE	NE	NE	2	NE	NAn	NE	3	NAn	NAn	NAn
No. <i>Anopheles</i> /200 ml/ <i>Aedes</i> ^b												
15 May	8	0.00	0.00	0.00	7	0.00	0.00	0.00	—	—	—	—
15 June	8	0.00	0.00	0.00	5	0.00	0.00	0.00	6	0.00	0.00	0.00
15 July	8	1.67	2.44	3.42	4	NAe	0.03	NAe	6	NAe	0.72	NAe
1 Aug.	—	—	—	—	6	0.17	0.01	0.05	6	0.00	0.00	0.00
15 Aug.	8	0.01	0.09	0.03	6	0.01	0.06	0.02	4	NAe	0.32	NAe
1 Sept.	—	—	—	—	5	NAe	NAe	NAe	2	NE	NE	NE
15 Sept.	8	NAe	NAe	NAe	4	NAe	NAe	NE	4	0.00	0.00	0.00
1 Oct.	—	—	—	—	4	NAe	1.34	NE	2	NE	NE	NAe
15 Oct.	8	NE	NE	NE	2	NE	0.00	NE	3	0.00	0.00	0.00

Instar combinations (*Anopheles*-*Aedes*) are indicated at the top of each column; —, no census was taken at that date; n = number of containers. NAn, absence of *A. barberi* larvae of a particular instar on a sample date; NAe, absence of *A. triseriatus* larvae of a particular instar on a sample date; NE, absence of both *A. barberi* and *A. triseriatus* of a particular instar combination on a sample date.

^a Mean interspecific crowding values: number of *A. triseriatus* larvae per 200 ml per *A. barberi* larvae.

^b Mean interspecific crowding values: number of *A. barberi* larvae per 200 ml per *A. triseriatus* larvae.

instar *A. triseriatus* late in the season. If, however, overlap of the right developmental stages occurred earlier in the year, the net effect of *A. barberi* on *A. triseriatus* population performance would be likely to be more negative because some fraction of the larvae alive at the end of the experiment may have survived to become adults, increasing the difference in survivorship and λ' between the predator and no-predator treatments.

The results for the proportion of surviving individuals that completed development by the end of the experiment suggest a tendency for increased development rate in the presence of *A. barberi*. This suggests that more surviving *A. triseriatus* larvae in the predator treatments were able to develop sufficiently quickly to emerge as adults before the end of the experiment than were individuals in the absence of a predator. An increase in the development rate would be consistent with a reduction of intraspecific competition caused by *A. barberi*-induced mortality. *A. triseriatus* has a greater development rate when released from intraspecific competition (Carpenter 1983, Fish and Carpenter 1982, Copeland and Craig 1992, Léonard and Juliano 1995), but such an increased development rate would not likely offset the negative effects of higher mortality caused by *A. barberi* predation if that increase occurred earlier in the season. Although a greater proportion of adults emerged in the predator treatments, there were no significant differences between predator and no-predator treatments in the number of eclosing adults, or in mass at eclosion, both of which can be affected by a release from intraspecific competition (Carpenter

1983, Fish and Carpenter 1982, Copeland and Craig 1992, Léonard and Juliano 1995).

Functional responses of 4th-instar *A. barberi* to 1st- and 2nd-instar *A. triseriatus* were statistically indistinguishable. This was, however, clearly not the case for 3rd-instar *A. barberi*, which could not consume 2nd-instar *A. triseriatus*, and which killed significantly fewer 1st-instar *A. triseriatus* than did 4th-instar *A. barberi*. This result is important, suggesting that if *A. barberi* is to have an effect on *A. triseriatus* populations, the 2 species must co-occur in the right developmental stages. Such co-occurrence is likely only at certain times of the year, so these functional response results also suggest a seasonal change in the effect of *A. barberi* on *A. triseriatus*.

The relationship between the number killed and density followed a power function, as opposed to the usual asymptotic type II or type III functional response curves documented in most studies on the functional response of predators (Juliano 1993). This inability to fit standard functional response relationships could arise for statistical reasons (i.e., highly variable data, insufficient densities). However, there are biological hypotheses that could account for the lack of an asymptote. *A. barberi* may change its behavior in response to changing densities of prey, consuming more of each individual when the density of prey is low and consuming less of each individual when the density of prey is high. Such partial consumption in response to increasing prey densities has been observed in other predator-prey systems (Johnson et al. 1975). Given that *A. barberi* is a facultative predator, able to survive

without prey, and given that prey are likely to become suddenly abundant (e.g., after rainfall), this behavior would seem to be advantageous for this predator.

Anopheles barberi's lack of a substantial negative impact on *A. triseriatus* population performance seems surprising given the functional responses to prey density for *A. barberi*. Other mosquito predators—*Corethrella appendiculata* (Grabham) and *Toxorhynchites rutilus* (Coquillett)—that significantly affect *A. triseriatus* reach an asymptotic number of prey eaten in a 24-h period that is far lower than the maximal number of prey killed in a 24-h period for *A. barberi* (Livdahl 1979, Lounibos 1985). *T. rutilus* differs from *A. barberi* by being an obligate predator capable of eating all stages of *A. triseriatus* (Steffan and Evenhuis 1981). Therefore, mortality from predation by *T. rutilus* occurs throughout the entire larval life of *A. triseriatus*, and may result in extremely high cumulative mortality by the time *A. triseriatus* pupates. *C. appendiculata*, however, is more similar to *A. barberi* in that it preys primarily on early-instar *A. triseriatus* (Lounibos 1983). Given this similarity, it is surprising how different these 2 species are in the maximal number of early instars consumed in a 24-h period. Functional response experiments with *C. appendiculata* indicate an asymptote at ≈ 10 larvae in a 24-h period (Lounibos 1985). *A. barberi* in our experiment, on the other hand, killed ≈ 65 larvae in a 24-h period, apparently without reaching an asymptote characteristic of a type II functional response.

Natural co-occurrence of late-instar *A. barberi* with early-instar *A. triseriatus* is both seasonal (mid-July) and brief (Table 5). This limited co-occurrence of viable combinations of predator and prey larvae declines as the summer and fall progress, meaning that if *A. barberi* does have an effect on *A. triseriatus* populations, this effect is likely to occur only in mid-summer, particularly in July. We conducted the field experiment (in late August) at a time when the critical photoperiod for egg diapause in *A. triseriatus* had been reached (Sims 1982), which probably accounts for the absence of early-instar *A. triseriatus* observed by the mid-September census. Copeland and Craig (1989) observed that 2nd-instar *A. barberi* were better able to withstand cold, and to overwinter, than were 3rd-instar *A. barberi*, which suggests that late-instar *A. barberi* do not perform well in cooler weather. This effect of temperature may have contributed to the low impact of *A. barberi* in the experiment.

The highest mean interspecific crowding values, obtained in mid-July, were at the low end of densities used in the functional response experiment, and were about half that of densities used in the field experiment, which were on average 56.8 *A. triseriatus* per 200 ml for tree holes and 69.4 *A. triseriatus* per 200 ml for the tires. The mean number killed at this density under laboratory conditions is still high compared with that killed by *C. appendiculata* ($\approx 4/24$ h) and *T. rutilus* ($\approx 5/24$ h) at the same

density (Lounibos 1985). The number of early-instar *A. triseriatus* larvae actually eaten in the field experiment may have been lower than this value because of the presence of leaf litter, which may provide cover for larvae and may make it more difficult for *A. barberi* to capture prey. Leaf litter may also act as a barrier, possibly reducing the number of encounters between *A. barberi* and *A. triseriatus*. Therefore, differences between the high attack rates in the functional response experiment (where leaf litter was not present) and the limited predator impact in the field experiment (where leaf litter was present) may be caused in part by the differences in habitat complexity.

Mean interspecific crowding of *A. barberi* on *A. triseriatus* followed the same seasonal pattern as the mean interspecific crowding of *A. triseriatus* on *A. barberi*. This is important because this indicates that *A. triseriatus* faces the most dangerous conditions (i.e., the highest number of predators per larva) in mid-July, when *A. barberi* has enough prey available to make *A. triseriatus* a worthwhile source of food. Therefore, it seems likely that mid-July represents the time when *A. barberi* is most likely to have an impact on *A. triseriatus* populations.

The 3 components of our study (the field experiment, the census data, and the functional response studies) along with other experimental studies, suggest that this predator may have a negative impact on *A. triseriatus* populations (Livdahl 1982, Copeland and Craig 1992). However, evidence from our study suggests that the time window for such effects is small and seasonal. Any effect of *A. barberi* on *A. triseriatus* may also be limited by habitat differences beyond the scope of this experiment. Bradshaw and Holzapfel (1988) and Copeland and Craig (1990) found that *A. triseriatus* and *A. barberi* are negatively associated among tree holes, *A. triseriatus* being found more often in more ephemeral basal pan tree holes and *A. barberi* found more often in more permanent rot holes. Whether this relationship holds true for these species in this northern part of their range is unclear. Although Copeland and Craig's (1990) study was conducted in the northern part of the ranges of these species, they did not include large basal rot holes such as those used in our experiment nor did they include tires, which were the sites of highest mean interspecific crowding in our study. In the southern part of the range of these species, the pattern of co-occurrence of these 2 species is complicated by the presence of *T. rutilus* (Bradshaw and Holzapfel 1988). In addition to the negative association between *A. triseriatus* and *A. barberi*, Bradshaw and Holzapfel (1988), found that *T. rutilus* was positively associated with *A. barberi* and negatively associated *A. triseriatus*. Therefore, the observed negative association between *A. triseriatus* and *A. barberi* could be an effect of heavy predation by *T. rutilus* on *A. triseriatus*.

Acknowledgments

We thank S. Clesen, M. E. Gravel, L. M. Turek, A. S. Aspbury, and H. Grimes for their help with both field and laboratory work, and C. F. Thompson and S. S. Loew for their helpful comments on the manuscript. We also thank the Parklands Foundation, D. Sears, and the Illinois Department of Conservation for access to sites where the field experiment and censuses were conducted. This research was supported by grants from NIH (R 15 AI34139-011) to S.A.J., and the Beta Lambda chapter of Phi Sigma Biological Honor Society to M.A.N.

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Received for publication 20 January 1997; accepted 3 October 1997.