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## BEHAVIOR AND ECOLOGICAL INTERACTIONS OF LARVAL ODONATA<sup>1</sup>

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**Abstract.** *Enallagma aspersum* and *E. traviatum* (Odonata: Coenagrionidae) are the most abundant larval odonates in Bays Mountain Park (Sullivan County, Tennessee, USA), although their spatial distributions are essentially nonoverlapping. *E. traviatum* coexists with insectivorous fish in a small lake, whereas *E. aspersum* is restricted to a small fishless pond nearby.

Behavioral observations revealed that *E. aspersum* larvae were more active than *E. traviatum*, and tended to occupy more conspicuous positions. *E. aspersum* also engaged in more confrontations than *E. traviatum*, especially at higher density.

In laboratory experiments with juvenile bluegills (*Lepomis macrochirus*) as predators, *E. aspersum* larvae were more vulnerable to predation than *E. traviatum*. Red-spotted newts (*Notophthalmus viridescens*) also preyed on *E. aspersum* disproportionately.

Field enclosure experiments revealed that dry mass of individual *E. aspersum* larvae was density dependent, and that increased density of *E. aspersum* or addition of *E. traviatum* produced similar reductions. Competition was asymmetrical, as *E. aspersum* appeared to have no significant effect on *E. traviatum*. The substantial increase in confrontations among *E. aspersum* larvae at higher density, and the lack of evidence for prey depletion, suggest that interference may be the mechanism of competition.

Our results suggest that the distribution of *E. aspersum* larvae may be limited by fish predation, but although competitive interactions were detected, we have no evidence that larval competition influences the distribution of either species.

**Key words:** behavior; benthic; community structure; competition; damselfly; *Enallagma*; interference; littoral; Odonata; predation.

### INTRODUCTION

Several recent studies have examined the influence of both predation (e.g., Peckarsky and Dodson 1980a, Neill 1981, Thorp and Bergy 1981a, b, Allan 1982, Crowder and Cooper 1982, Bohanan and Johnson 1983, Morin 1984a, Thorp and Cothran 1984, see Zaret 1980 for review) and competition (e.g., Benke 1978, Peckarsky and Dodson 1980b, Benke et al. 1982, Smith and Cooper 1982, Johnson et al. 1984, 1985, Morin 1984b) on the structure of aquatic invertebrate communities. Although these studies provide convincing evidence of whether the manipulated population interacts with other populations, they do not yield direct information on the mechanism of interaction (but see McAuliffe 1984 for a noteworthy exception).

Recently, Peckarsky (1983) reviewed numerous examples of how mechanisms of dispersal, competition, predation, foraging, reproduction, and habitat selection have been illuminated by careful quantification of behavior. Work with crayfish (Stein and Magnuson

1976) and notonectids (Sih 1980, 1982) has demonstrated behaviors that reduce vulnerability to predators, but also reduce foraging efficiency. Baker (1980, 1981a, b, 1982) has observed that damselfly larvae of one species (*Coenagrion resolutum*) aggressively excluded others from areas of food concentration, whereas such behavior was not observed in another species (*Lestes disjunctus*) collected from the same pond. Development of *L. disjunctus* was synchronous at this site, whereas development of *C. resolutum* was asynchronous. Delayed development of damselfly larvae associated with food reduction has been documented (Lawton et al. 1980, Baker 1982), suggesting that the asynchrony of *C. resolutum* may be due to the exclusion of some individuals from good "fishing sites," an idea originally proposed by Macan (1966).

In this paper we present results of observations and experiments with larvae of two congeneric damselflies to illustrate how behavior may influence spatial distribution and ecological relations. Although both species appear to have similar habitat preferences (Crowley and Johnson 1982b), their spatial distributions are virtually nonoverlapping at our study site (Johnson and Crowley 1980b, Crowley and Johnson 1982a). This prompted us to undertake three experiments: behav-

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ioral observations, an assessment of relative vulnerability of the two species to predators, and a field competition experiment.

#### STUDY SITE AND ORGANISMS

We studied odonate populations in a lake-pond system in Bays Mountain Park (36°31' N, 82°37' W), situated in a forested watershed in Sullivan County, Tennessee, USA. Bays Mountain Lake (BML) is a 15-ha eutrophic reservoir with a maximum depth of 7 m and a well-developed and stable littoral zone. Ecology Pond (EP) has a surface area of 0.6 ha, a maximum depth of 1.5 m, and a stable littoral zone. BML supports large populations of insectivorous fish, such as largemouth bass (*Micropterus salmoides*), bluegills (*Lepomis macrochirus*), and redear sunfish (*Lepomis microlophus*). EP contains no fish, but has a large population of adult red-spotted newts (*Notophthalmus viridescens*). Outflow from EP forms a small creek that flows into BML 100 m downstream, but fish are prevented from entering EP by a vertical overflow pipe. (For further site and habitat descriptions, see Johnson and Crowley 1980b.)

We focused on two congeneric zygopteran species, *Enallagma aspersum* (Hagen) and *E. traviatum* (Selys) (Odonata: Coenagrionidae). These species are univoltine, similar in size, and have life cycles that overlap considerably at Bays Mountain Park (Crowley and Johnson 1982a). *E. traviatum* is the most abundant odonate species in BML, found primarily in allochthonous detritus and submersed macrophytes of the littoral zone. *E. aspersum* is the most abundant odonate species in similar habitats in EP. A few *E. traviatum* larvae are routinely found in EP, but in 6 yr of monthly sampling, only one *E. aspersum* larva has been collected from BML.

#### METHODS

##### *Behavior experiment*

The purpose of this experiment was to compare larval behavior of the two *Enallagma* species with respect to aggressiveness, prey capture, and potential susceptibility to other predators under varying conditions of conspecific density, prey availability, and "light" (described below).

We collected larvae from BML and EP, maintained them in vials in an incubator on a 12:12 h (light : dark) cycle at 20°C, and fed them 5–10 *Daphnia magna* three times per week. To standardize physiological condition, we observed larvae during the first 3 d of the final instar. We allowed larvae to feed ad lib on *Daphnia* for 1 h, then transferred them to the observational aquarium for an adjustment period of 17–23 h before beginning each observation period.

We observed larvae in a small (6-L) glass aquarium, filled with 2 L of filtered tap water, and maintained at 20°. The aquarium was illuminated from above by a

circular fluorescent magnifying lamp, and larvae were observed through the magnifying lens of the lamp. We simulated allochthonous detritus with multiple layers of fiberglass window screen cut into various shapes, such that larvae were always visible. Preliminary observations indicated no obvious differences in behavior of larvae on natural and artificial detritus. Mesh openings in the screen were too small for the larvae to crawl through (<2 mm), but gaps between layers were accessible (3–6 mm). Light intensities on the aquarium bottom were estimated to be 2130 lx in the open, 1380 lx under one layer of screen, and 900 lx under two layers of screen.

We recorded the amount of time spent in the following behaviors and orientations: crawling, swimming, abdominal waving, cleaning, and occupying locations visible from above (i.e., more than half of the larva exposed). We recorded the frequencies of occurrence of labial strikes at prey, prey captures, approaches toward and retreats from other larvae. Approaches and retreats were summed to yield the number of confrontations. All observations were recorded using an eight-channel event recorder.

The experiment followed a completely randomized 2<sup>4</sup> factorial design, with two replicates of each of 16 treatment combinations. Treatments were as follows: species (*E. aspersum* vs. *E. traviatum*), density (176 larvae/m<sup>2</sup> [or 8 larvae/aquarium] vs. 44 larvae/m<sup>2</sup> [or 2 larvae/aquarium]), prey availability (220 *Daphnia magna*/m<sup>2</sup> [or 10 *Daphnia*/aquarium] vs. none), and light (illuminated as described above vs. "dark," simulated by covering eyes and ocelli of larvae with black enamel paint). Each larva was observed for 3 h. We analyzed the data for each variable separately by four-way ANOVAs using the GLM procedure of SAS (Ray 1982).

##### *Predation experiment*

We tested the hypothesis that the two *Enallagma* species differ in vulnerability to predation with laboratory feeding trials using two abundant vertebrate predators from Bays Mountain Park: adult red-spotted newts and juvenile bluegills. Predators and prey were collected from BML and EP. Damselfly larvae were maintained in the manner described in the previous section; bluegills and newts were maintained in small aquaria at room temperature and fed a variety of items several times per week.

We conducted the experiment in 38-L aquaria containing filtered tap water and a substrate of allochthonous detritus previously sorted to remove all macroinvertebrates. Aquaria were covered with tents of black polyethylene to minimize disturbances and illuminated from above on a 14:10 h (light : dark) cycle. Light intensity at the substrate was ≈1200 lx.

For each foraging trial, 10 larvae, five of each species, were placed in an aquarium 18–24 h before introducing a predator. We standardized within-trial larval size by

randomly selecting five of each species from a group of similar size. Three bluegills (63, 68, and 68 mm standard length) and three newts (42, 44, and 45 mm snout-vent length) were used as predators. In each foraging trial a solitary predator foraged for a specified period of time. Preliminary observations indicated that bluegills were more efficient predators than newts. For this reason we used a 12-h foraging period for bluegills (0800 to 2000, lights on entire period), and a 24-h foraging period for newts (lights on from 0800 to 2100, dark from 2100 to 0800). These time periods were sufficiently long that enough larvae were eaten by each species of predator to resolve differences in vulnerability, but were short enough to prevent switching from one species to the other as the more vulnerable species became depleted. We then removed the predator and thoroughly sorted the substrate to recover surviving larvae. We ran four replicate trials with each individual predator. Predator-free trials controlled for either intraodonate predation or incomplete retrieval of larvae. Data (numbers eaten) were analyzed with the binomial test (Daniel 1978), which tested the hypothesis that of all the larvae eaten, more of one species were taken than the other.

#### Competition experiment

To test the hypothesis that competition occurs, we conducted a field enclosure experiment in BML for  $\approx 1$  mo (24 October to 21 November 1981). The relatively short duration was chosen to minimize enclosure effects (see Crowley et al. 1983). The experiment was designed to detect and compare both intraspecific and interspecific interactions as well as responses of prey resources to treatments. Competition was evaluated by two measures: (1) survival, and (2) dry mass.

We used cylindrical Nitex mesh (0.5 mm) enclosures, 20.3 cm in diameter, and 30.5 cm high. The enclosures contained a natural substrate of littoral detritus with its associated invertebrate fauna, and were staked to the lake bottom at a depth of 0.5 m. Except for removal of odonate larvae other than the experimental individuals, we attempted to mimic natural conditions of the shallow littoral zone as closely as possible in the enclosures. Comparisons of conditions and invertebrate populations inside our enclosures with unenclosed areas, and details of enclosure construction, placement, substrate preparation, and sampling have been published elsewhere (Crowley et al. 1983: see third experiment). Cladocerans, copepods, ostracods, and rotifers were sampled by placing inverted-funnel traps (Brakke 1976) inside the enclosures 24 h before removal from the lake. Macroinvertebrates, including the experimental odonate larvae, were censused directly by sorting the entire contents of enclosures in sugar solution (Anderson 1959).

We used size distributions of odonate larvae that closely resembled ambient distributions, based on the large collection of individuals obtained before starting

the experiment. We also included equal numbers (3 larvae per enclosure, or 92/m<sup>2</sup>) of dragonfly larvae (*Tetragoneuria cynosura*) in all treatments. Dragonfly larvae, most of which grow larger than damselfly larvae and are known to prey on them, are common in both BML and EP (Johnson and Crowley 1980b). Thus, their inclusion in our experimental design permitted evaluation of competition among the damselfly larvae in the context of a natural invertebrate assemblage.

We used a randomized complete block experimental design, with shoreline location as the blocking factor (two blocks). The design included low (one-half natural) and high (natural) density treatments of each species alone, and a high-density treatment with equal biomass of the two species (Table 1). There were two replicates of each treatment per block, or a total of four replicate enclosures for each treatment.

Survival of damselfly larvae was analyzed by a two-way ANOVA with blocks and damselfly treatments as the main effects. Our analysis of dry mass was somewhat more involved. We reasoned that either reduced food intake or increased energy expenditure would result in reduced biomass of individual larvae. Because morphological dimensions such as head width remain fixed between molts, we expected individuals involved in competitive interactions to weigh less, for a given head width, than individuals not engaged in competition. For this reason we analyzed dry mass of individuals by ANCOVA, effectively removing the variance due to the relationship of dry mass with head width (Sokal and Rohlf 1981). This also reduced the variance associated with our use of natural size distributions (initially determined by head-width measurements). The treatments described in Table 1 permitted three unambiguous tests for each species with each of the two response variables. (1) Did intraspecific competition occur? (2) Did interspecific competition occur? (3) Was one form of competition greater than the other? These questions were evaluated by the following non-orthogonal a priori contrasts in respective order: A vs. AA and T vs. TT, A vs. AT and T vs. TA, AA vs. AT and TT vs. TA (see Table 4).

We analyzed prey responses to the damselfly treatments by separate two-way ANOVAs for each taxon, with blocks and damselfly treatments as the main effects. Data were transformed [ $\log_e(x + 1)$ ] for analysis. The GLM procedure of SAS (Ray 1982) was used for all statistical analyses.

## RESULTS

### Behavior experiment

*E. aspersum* larvae were much more active than *E. triviatum* larvae (Fig. 1). The most obvious difference in activity (Fig. 1, Table 2) between the two species was in abdominal waving behavior (a side-to-side motion of the abdomen) which was often exhibited by *E. aspersum* larvae for several minutes at a time. Also

TABLE 1. Description of treatments from the field competition experiment.

Treatment	Abbreviation*	Number of larvae per enclosure†	Larval density (no./m <sup>2</sup> )
<i>E. aspersum</i> , 1/2 natural density	A	15	460
<i>E. aspersum</i> , natural density	AA	30	920
<i>E. traviatum</i> , 1/2 natural density	T	9	280
<i>E. traviatum</i> , natural density	TT	18	560
Both species, natural density	AT and TA	24	740

\* The AT abbreviation refers to the *E. aspersum* component of the mixed-species treatment, and TA refers to the *E. traviatum* component.

† The difference in number of individuals between the A and T treatments is a reflection of larger average size of *E. traviatum* in late autumn, as species biomasses rather than numbers were equal.

significant was a higher incidence of swimming by *E. aspersum* (Table 2). The two species spent similar proportions of time cleaning various portions of the body.

Although the two species spent similar proportions of time crawling, averaged over all treatment combinations (Table 2), there was a significant species × density interaction (Fig. 2, Table 2). Crawling among *E. traviatum* larvae was depressed at higher density, whereas *E. aspersum* larvae crawled somewhat more at higher density.

*E. aspersum* larvae spent a significantly greater proportion of time perched in locations visible from above (Fig. 3, Table 2). Although the species × light interaction was not significant, exposure of *E. traviatum* larvae was sharply curtailed in the light, whereas *E. aspersum* was relatively unaffected.

The frequency of confrontations increased for both species at higher density (Fig. 4). *E. aspersum* larvae tended to engage in more confrontations than *E. traviatum* (Fig. 4, Table 2).

*E. aspersum* larvae struck at roughly three times as many prey and captured twice as many prey as *E. traviatum* during our observations, although neither difference was statistically significant (Table 2).

TABLE 2. Summary of ANOVAs on time spent in or frequency of several larval behaviors.

Sources of variation†	Behaviors‡						
	VA	CR	AW	SW	CL	CO	SP
Species (S)	*	NS	***	**	NS	*	NS
Density (D)	NS	NS	NS	NS	NS	**	NS
Light (L)	*	NS	NS	NS	NS	NS	NS
S × D	NS	*	NS	NS	NS	NS	NS

\* .05 > P > .01, \*\* .01 > P > .001, \*\*\* P < .001, NS = P > .05.

† Although all four treatments and all possible interactions were tested, only those main effects and interactions involving species that significantly affected one or more of the behaviors are included here.

‡ VA = visible from above, CR = crawling, AW = abdominal waving, SW = swimming, CL = cleaning, CO = confrontations, SP = strikes at prey. Temporal data (VA, CR, AW, SW, CL) were transformed as arcsine ( $\sqrt{p}$ ), where p was the proportion of the 3-h observation period occupied by particular behaviors. Frequency data (CO, SP) were not transformed.

Predation experiment

*E. aspersum* larvae were clearly more vulnerable to vertebrate predation than *E. traviatum* larvae (Fig. 5). Two out of three bluegills ate significantly more *E. aspersum* than *E. traviatum* during laboratory feeding trials. Overall, bluegills ate three times as many *E. aspersum* larvae as they did *E. traviatum* larvae. Only one of the three red-spotted newts ate a significantly greater proportion of *E. aspersum*; however, the difference in numbers of the two species eaten pooled over all newts was significant. In only 1 of a total of 24 feeding trials (newt B) were more *E. traviatum* larvae eaten than *E. aspersum* larvae. Although newts were allowed a longer foraging period than bluegills, they consumed roughly half as many larvae.

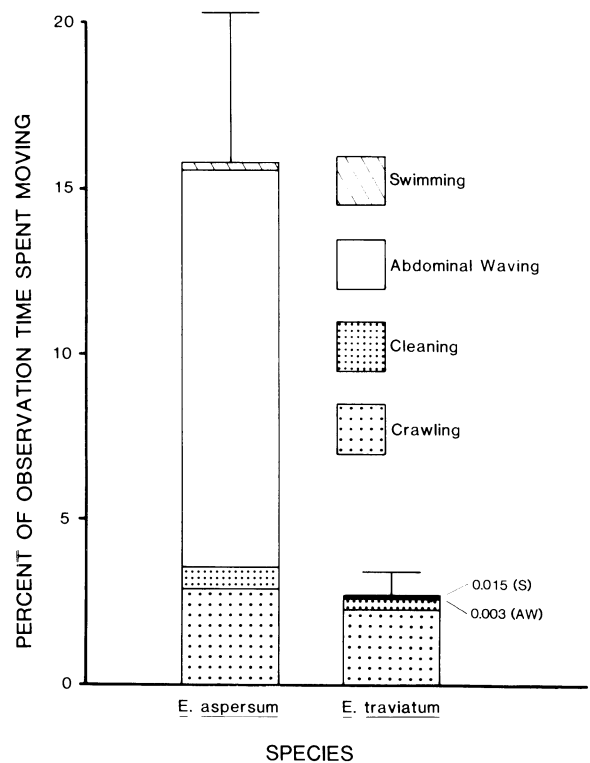


FIG. 1. Percent of observation time spent moving (means + 1 SE). Data are averaged over all treatment combinations.

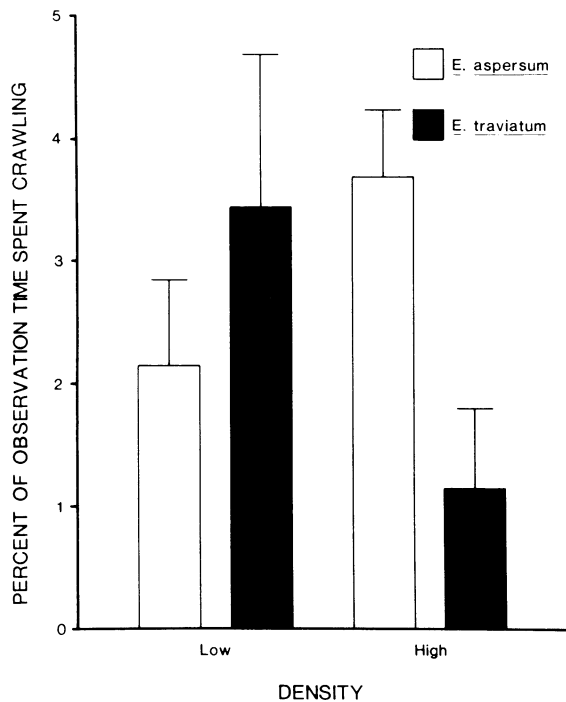


FIG. 2. Percent of observation time spent crawling (means + 1 SE). Density levels explained in Methods: Behavior Experiment.

#### Competition experiment

No competition was detected by analysis of larval survival of either species (Table 4). Average survival over all treatments was 59% for *E. aspersum* and 68% for *E. traviatum* (Table 3).

Although we detected no competitive effects on dry mass of *E. traviatum* larvae, both increased conspecific density and the presence of *E. traviatum* significantly reduced the adjusted mean dry mass of *E. aspersum* larvae (Tables 3 and 4, Fig. 6). Increased conspecific density decreased dry mass by 32%, whereas a 25% decrease was associated with the presence of *E. traviatum* larvae (Table 3). However, the difference between these effects was not statistically significant (Table 4), indicating that *E. aspersum* experienced intraspecific and interspecific competition of approximately equal severity.

Damselfly larvae had no significant effects on any of the 11 prey taxa examined (ANOVA,  $P > .05$ ), suggesting that prey resources were not limiting at higher damselfly density. Treatment means and standard errors (Table 5) illustrate large variances among replicates for all taxa. Blocking accounted for a significant proportion of variation for chydorids ( $P < .001$ ), daphnids ( $P < .001$ ), ceratopogonids ( $P < .001$ ), and ephemeropterans ( $P < .01$ ). The cladocerans were more abundant in one block, while the insects were more abundant in the other.

TABLE 3. Treatment means and standard errors for proportion of larvae surviving the experiment and individual dry mass of survivors.

Treatment*	Survival			Dry mass (mg)		
	n†	Mean	SE	n‡	Adjusted mean§	SE
A	4	0.55	0.07	15	0.1812	0.0204
AA	4	0.70	0.08	50	0.1226	0.0111
AT	4	0.53	0.05	21	0.1353	0.0172
T	4	0.65	0.20	19	0.1847	0.0179
TT	4	0.72	0.10	48	0.2060	0.0114
TA	4	0.68	0.11	21	0.1722	0.0170

\* Treatments are described in Table 1.

† Number of replicate enclosures.

‡ Number of unfragmented larvae recovered at the end of the experiment.

§ Adjusted means were generated by ANCOVA on head width.

#### DISCUSSION

Our behavioral observations have indicated differences between the two *Enallagma* species that are clearly consistent with the hypothesis that fish predation may play an important role in determining local distributions of odonate larvae. *E. aspersum* larvae spent over five times as much time moving as *E. traviatum* larvae, and the significant differences occurred in behaviors (abdominal waving and swimming) that would be likely to attract efficient visual predators. During observations of predators foraging on larvae, we often observed *E. aspersum* swimming as an escape response to approaching predators. Larvae never successfully

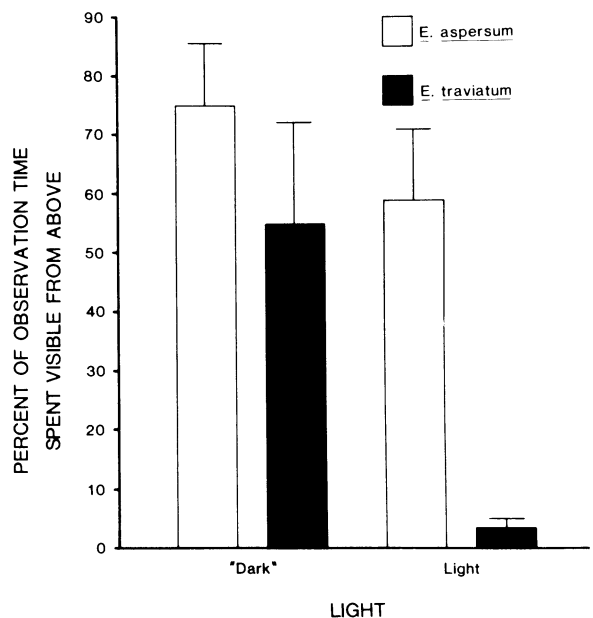


FIG. 3. Percent of observation time spent visible from above under each of the two light treatments (means + 1 SE). The "dark" treatment involved painting the eyes and ocelli of larvae with black enamel paint.

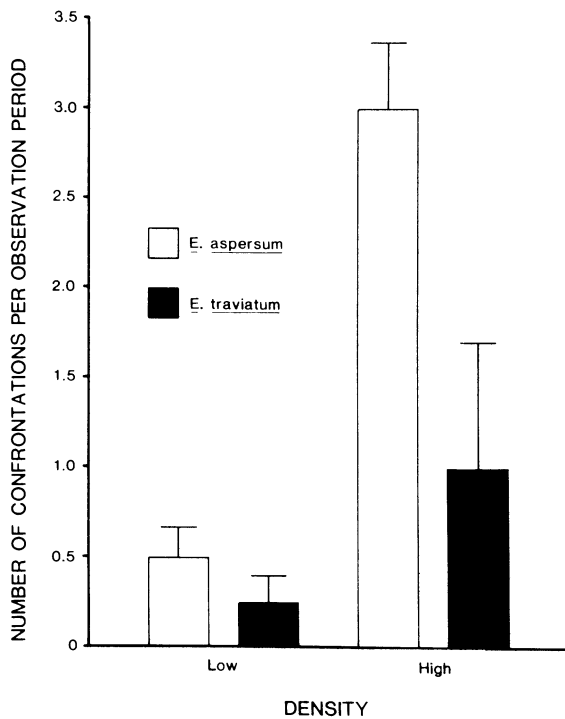


FIG. 4. Number of confrontations per observation period (means + 1 SE). Density levels as in Fig. 2.

escaped from bluegills by swimming, but newts were frequently eluded in this manner. In contrast, *E. traviatum* larvae remained motionless when predators were near and they often went undetected (C. L. Pierce et al., *personal observations*). *E. aspersum* also spent more time perched in exposed locations than *E. traviatum*, a difference that was especially pronounced in the light. These differences all suggest that *E. aspersum* should be more vulnerable than *E. traviatum* to highly efficient visual predators such as bluegills. The results of our predation experiment lend further support to this hypothesis. Thus two lines of evidence suggest that the absence of *E. aspersum* from BML may be due in part

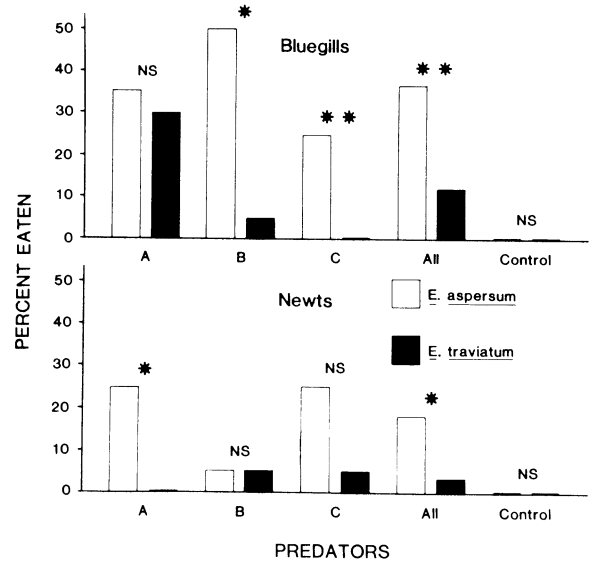


FIG. 5. Percent of available larvae eaten by bluegills and red-spotted newts. Data are presented for individual predators, predator types, and predator-free controls. Significance levels from binomial tests (Daniel 1978) of differences in proportions eaten: NS =  $P > .05$ , \* $.05 > P > .01$ , \*\* $P < .01$ .

to behavior that is incompatible with fish predation. It is interesting that, although *E. aspersum* were also more vulnerable than *E. traviatum* to red-spotted newt predation, newts do not exclude *E. aspersum* from EP. Apparently this is because newts are much less efficient (Fig. 5; C. L. Pierce et al., *personal observations*) predators than bluegills.

Several previous studies have illustrated the influence of fish on odonate populations. In large-scale experiments, Ball and Hayne (1952), Macan (1966), Hall et al. (1970), and Crowder and Cooper (1982) demonstrated reductions in odonate density that were associated with the presence of fish. Kime (1974), Johnson and Crowley (1980a), and Henrikson (1981) have reported cases where active species were abundant in fishless areas, but were replaced by more cryptic species

TABLE 4. Tests of the effects of competition on proportion of larvae surviving the experiment and individual dry mass of unfragmented survivors.

Contrast†	Survival‡				Dry mass§			
	df	ss	F	P	df	ss	F	P
A vs. AA	1	0.0506	0.62	0.9703	1	2.1525	15.49	0.0006*
A vs. AT	1	0.0009	0.01	1	1	1.3175	9.48	0.0143*
AA vs. AT	1	0.0651	0.79	0.9464	1	0.0332	0.24	0.9972
T vs. TT	1	0.0193	0.23	0.9976	1	0.1979	1.42	0.7986
T vs. TA	1	0.0001	0	1	1	0.0007	0.01	1
TT vs. TA	1	0.0226	0.28	0.9963	1	0.1830	1.32	0.8261

† Treatments are described in Table 1.

‡ Survival data were arcsine-square root transformed and analyzed by ANOVA.

§ Dry mass data were log<sub>e</sub> transformed and analyzed by ANCOVA.

|| P values of planned, nonorthogonal contrasts were adjusted by the Dunn-Šidák method to maintain a 5% type 1 experimentwise error rate (Sokal and Rohlf 1981). Asterisks indicate significant contrasts.

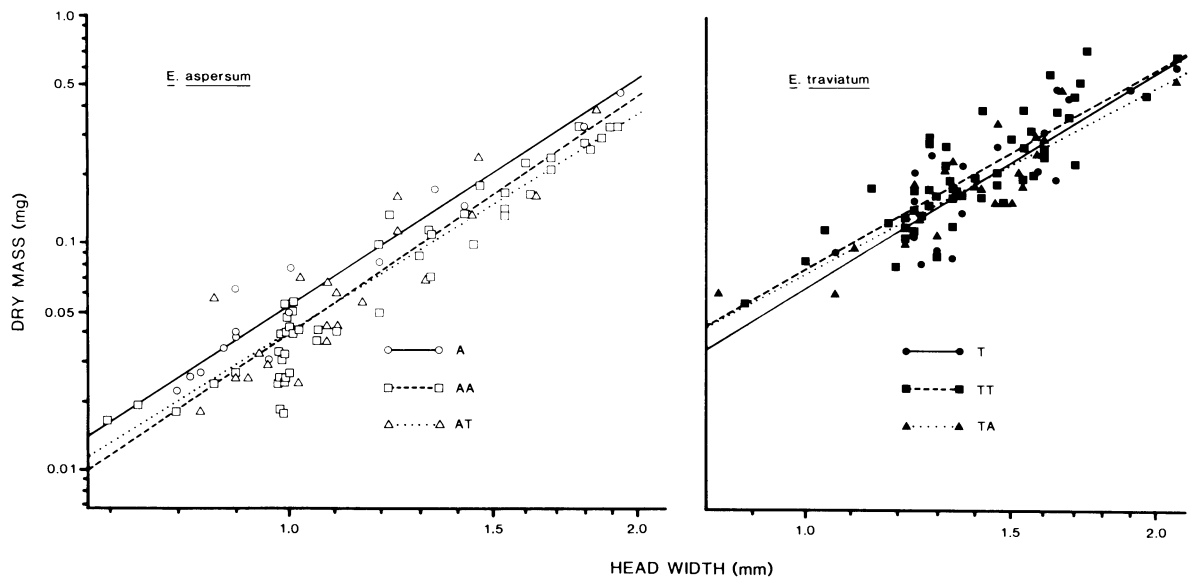


FIG. 6. Regressions of dry mass on head width of larvae surviving the competition experiment. (A few individuals were fragmented during sample processing and are not included here.) Both variables were log<sub>e</sub> transformed to facilitate linear regression and ANCOVA. For the general power function, dry mass =  $a(\text{head width})^b$ , parameter values and coefficients of determination are as follows: (A)  $a = 0.0537$ ,  $b = 3.3571$ ,  $r^2 = 0.94$ ; (AA)  $a = 0.0409$ ,  $b = 3.2089$ ,  $r^2 = 0.94$ ; (AT)  $a = 0.0400$ ,  $b = 3.5195$ ,  $r^2 = 0.77$ ; (T)  $a = 0.0644$ ,  $b = 3.2017$ ,  $r^2 = 0.60$ ; (TT)  $a = 0.0784$ ,  $b = 2.9724$ ,  $r^2 = 0.67$ ; (TA)  $a = 0.0748$ ,  $b = 2.7598$ ,  $r^2 = 0.72$ . No significant differences exist among slopes ( $P = .6633$ ), an assumption of ANCOVA (Sokal and Rohlf 1981). Tests for differences among adjusted dry mass means are presented in Table 4.

where fish were present. Recently, Morin (1984a) has documented significant effects of fish predation on both overall density and relative abundance of species in a littoral assemblage of pond-dwelling odonates. Exclusion of fish resulted in a substantial increase in odonate density in small-mesh enclosures, and shifted numerical dominance from the smaller species present to species of intermediate size. There seems little doubt that fish predation does exert substantial influence on odonate community structure in many instances, although there is at least one experimental study that found fish to have little or no impact on odonates (Thorp and Bergey 1981a).

In contrast, the mechanisms by which fish alter odo-

nate communities are not well understood. Morin's (1984a) results, and numerous demonstrations of this phenomenon in other systems (Brooks and Dodson 1965, Allan 1981, Newman and Waters 1984, review in Zaret 1980) led to the suggestion that the effect of fish predation on odonates may be size dependent (Morin 1984a). Our study indicates that the effects of fish predation on odonate species may also be strongly associated with behavioral patterns. Size-selective and "behavior-selective" predation could have fundamentally different implications for the structure of prey communities, and carefully designed experiments will be necessary to determine the relative importance of these two processes.

TABLE 5. Densities (number/m<sup>2</sup>) of prey. Table entries are means ( $\pm 1$  SE) from the four replicate enclosures for each treatment. The C (control) treatment contained no damselflies. Other treatments are described in Table 1.

Prey taxon	Treatment					
	A	AA	T	TT	AT and TA	C
Chironomidae	2340 $\pm$ 266	1861 $\pm$ 550	2186 $\pm$ 726	1097 $\pm$ 306	1691 $\pm$ 516	2579 $\pm$ 411
Chydoridae	2433 $\pm$ 1710	1782 $\pm$ 769	764 $\pm$ 376	1160 $\pm$ 271	1245 $\pm$ 457	1160 $\pm$ 697
Copepoda	1019 $\pm$ 212	990 $\pm$ 286	792 $\pm$ 139	651 $\pm$ 214	792 $\pm$ 190	1019 $\pm$ 80
Ephemeroptera	587 $\pm$ 196	572 $\pm$ 248	664 $\pm$ 378	572 $\pm$ 228	579 $\pm$ 405	502 $\pm$ 280
Rotifera	368 $\pm$ 97	594 $\pm$ 156	509 $\pm$ 108	368 $\pm$ 117	538 $\pm$ 54	255 $\pm$ 28
Ceratopogonidae	178 $\pm$ 118	278 $\pm$ 106	471 $\pm$ 212	85 $\pm$ 75	147 $\pm$ 70	247 $\pm$ 135
Daphnidae	198 $\pm$ 134	396 $\pm$ 199	283 $\pm$ 188	170 $\pm$ 33	340 $\pm$ 179	198 $\pm$ 54
Ostracoda	141 $\pm$ 107	368 $\pm$ 117	57 $\pm$ 33	85 $\pm$ 28	368 $\pm$ 169	198 $\pm$ 71
Bosminidae	113 $\pm$ 65	85 $\pm$ 54	28 $\pm$ 28	85 $\pm$ 85	170 $\pm$ 98	0
Trichoptera	93 $\pm$ 33	100 $\pm$ 44	93 $\pm$ 66	85 $\pm$ 43	108 $\pm$ 37	70 $\pm$ 41
Oligochaeta	31 $\pm$ 18	62 $\pm$ 13	23 $\pm$ 15	23 $\pm$ 15	8 $\pm$ 8	31 $\pm$ 22



The competitive interactions detected by our field experiment appear to be the result of interference for two reasons. (1) No prey depletion was detected at higher larval densities. (2) Our behavior observations indicated that the species experiencing density-dependent biomass reductions (*E. aspersum*) moved about more and engaged in more confrontations than the other species, especially at high density.

We initially hypothesized that fish predation was a likely reason for the absence of *E. aspersum* in BML, but that the rarity of *E. traviatum* in EP was due, in part, to competitive exclusion by *E. aspersum*. We found no evidence for the latter hypothesis, and in fact detected competitive effects in the opposite direction. That we cannot explain the absence of *E. traviatum* from EP on the basis of larval competition is, perhaps, not surprising. Diffuse competition involving several taxa and adult oviposition preferences based on the size or other characteristics of bodies of water are also plausible alternative possibilities, as yet untested.

The evidence available at present suggests that competition occurs among odonate larvae (Benke 1978, Benke et al. 1982, Johnson et al. 1984, Morin 1984b, Johnson et al. 1985, and the present study), but there is no indication that these interactions are intense enough to influence spatial distributions. Perhaps other constraints such as oviposition site suitability, microhabitat requirements, or the influence of predators swamp out the effects of competition. In Morin's (1984b) experiment, competition among dragonfly larvae occurred only at elevated densities produced by excluding fish, suggesting that fish predation may keep dragonfly densities below the level where competitive interactions are detectable. If this phenomenon is a general one, we might expect that competition among larval odonates would be more prevalent in small, temporary, or otherwise fishless ponds.

Clearly, interactions among odonates and with their predators are complex, and more experiments will be necessary to assess the relative roles of biotic interactions in these communities. We also suggest that, by clarifying mechanisms of interaction, behavioral studies are a valuable complement to manipulative experiments and will greatly enhance our understanding of the influence of such interactions on community structure.

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