

## Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies

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**Summary.** Dragonfly larvae (Odonata: Anisoptera) are often abundant in shallow freshwater habitats and frequently co-occur with predatory fish, but there is evidence that they are underutilized as prey. This suggests that species which successfully coexist with fish may exhibit behaviors that minimize their risk of predation. I conducted field and laboratory experiments to determine whether: 1) dragonfly larvae actively avoid fish, 2) microhabitat use and foraging success of larvae are sensitive to predation risk, and 3) vulnerability of larvae is correlated with microhabitat use. I experimentally manipulated the presence of adult bluegills (*Lepomis macrochirus*) in defaunated patches of littoral substrate in a small pond to test whether colonizing dragonfly larvae would avoid patches containing fish. The two dominant anisopteran species, *Tetragoneuria cynosura* and *Ladona deplanata* (Odonata: Libellulidae), both strongly avoided colonizing patches where adult bluegills were present. Laboratory experiments examined the effects of diel period and bluegills on microhabitat use and foraging success, using *Tetragoneuria*, *Ladona* and confamilial *Sympetrum semicinctum*, found in a nearby fishless pond. *Tetragoneuria* and *Ladona* generally occupied microhabitats offering cover, whereas *Sympetrum* usually occupied exposed locations. Bluegills induced increased use of cover in all three species, and use of cover also tended to be higher during the day than at night. Bluegills depressed foraging in *Tetragoneuria* and to a lesser extent in *Ladona*, but foraging in *Sympetrum* appeared unaffected. Other laboratory experiments indicated that *Sympetrum* were generally more vulnerable than *Tetragoneuria* or *Ladona* to bluegill predation, and that vulnerability was positively correlated with use of exposed microhabitats. Both fixed (generally low use of exposed microhabitats, diel microhabitat shifts) and reactive (predator avoidance, predator-sensitive microhabitat shifts) behavioral responses appear to reduce risk of predation in dragonfly larvae. Evidence indicates that vulnerability probably varies widely among species and even among instars within species, and suggests that spatial distributions of relatively vulnerable species may be limited by their inability to avoid predation.

**Key words:** Microhabitat shift – Odonata – Predator avoidance – Risk-sensitive foraging

The influence of predators on prey populations and communities continues to be a topic of enormous interest to ecologists (Sih et al. 1985). In freshwater systems, fish predation has been shown to depress abundances (Ball and Hayne 1952; Morin 1984a; Hershey 1985), reduce biomass (Crowder and Cooper 1982; Post and Cucin 1984; Pierce 1987) and alter the size structure, relative abundances, and species composition of prey communities (Brooks and Dodson 1965; Galbraith 1967; Hall et al. 1970; Petranka 1983; Morin 1984b; Lemly 1985; Bendell 1986; Hixon 1986). Increasingly, attention is being focused on more subtle aspects of predator-prey interactions such as indirect effects (Kerfoot and Sih 1986) and various other consequences of the activities of predators aside from simple removal of prey (Jeffries and Lawton 1984). One important consequence is that prey commonly possess a diversity of anti-predator defenses, many of which are behavioral (Edmunds 1974).

In aquatic systems, behavioral predator avoidance has been documented in several groups (Stein 1979; Peckarsky 1982). Fish are the conspicuous top predator in many systems, and have been shown to influence vertical migration patterns (Zaret and Suffern 1976; Stenson 1978; von Ende 1979; Gliwicz 1986), diel drift periodicity (Allan 1978), microhabitat use (Stein and Magnuson 1976; Cerri and Fraser 1983; Werner et al. 1983; Cooper 1984; Power et al. 1985; Holomuzki 1986; Kneib 1987; Wellborn and Robinson 1987), and activity (Stein and Magnuson 1976; Heads 1985; Andersson et al. 1986; Main 1987) of their prey. Some of these responses are fixed, operating at all times (or at certain times during the diel cycle) regardless if predators are actually present. Other responses are reactive, occurring only when a predator is detected. All of these behaviors appear to reduce the preys' risk of predation. However, a common cost associated with predator avoidance behavior is reduced foraging success; a consequence of reduced foraging activity (Stein and Magnuson 1976; Dill and Fraser 1984; Godin 1986; Prejs 1987), restriction to refuges with poorer food quality (Sih 1982; Holomuzki 1986), or competition for food within refuges (Mittelbach 1986).

The littoral zone of temperate ponds and lakes typically supports an abundant and diverse invertebrate fauna (Brinkhurst 1974; Rasmussen and Kalff 1987), and fish densities are usually highest there as well (Keast and Harker 1977; Werner et al. 1977). Dragonfly larvae frequently are a major component of littoral invertebrate communities (Benke and Benke 1975), accounting for roughly 25% of the biomass at the site reported on in this paper (Pierce

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1987). Larvae are readily eaten by littoral fishes in the laboratory (Wellborn and Robinson 1987; C.L. Pierce, personal observation), and their large size relative to most other littoral invertebrates should make them highly preferred prey. Dragonfly larvae are occasionally numerous in the diets of fish in the field (Sadzikowski and Wallace 1976; Martin 1986), and at least one fish exclusion experiment has demonstrated an impact of fish on densities and relative abundances of species (Morin 1984a). However, several other fish exclusion experiments produced little or no effect on dragonfly larvae (Thorpe and Bergey 1981; Gilinsky 1984; Pierce 1987), and Werner et al. (1983) reported finding very few dragonfly larvae in the diets of bluegills foraging in littoral vegetation, despite their being relatively abundant. These observations suggest that dragonfly larvae may possess effective anti-predator adaptations to reduce their risk of predation in habitats where predation pressure from fish is intense.

In this paper I present results from a series of experiments that demonstrate behavioral responsiveness of dragonfly larvae to fish predators, and evidence for both positive and negative consequences of the responses. First I describe a field experiment designed to test whether dragonfly larvae avoid colonizing patches of substrate where fish were present relative to fish-free patches. Then I describe laboratory experiments which examine the effects of diel period and presence of fish on microhabitat use and foraging success in dragonfly larvae. And finally I describe a laboratory experiment that quantified vulnerability of dragonfly larvae to fish predation, and permitted a test of whether microhabitat use is correlated with predation risk.

## Methods

### *Field study site and experimental animals*

I ran the field predator avoidance experiment in Farm Pond, located on the Patuxent Wildlife Research Center (U.S. Fish and Wildlife Service) (39° 2' N, 76° 47' W) in Prince George's County, Maryland, USA. Farm Pond has a surface area of 0.33 ha, and a maximum depth of 2 m. The perimeter of the pond supports a dense band of rushes (*Eleocharis quadrangulata*) and water shield (*Brasenia schreberi*) extending out to roughly the 1 m depth contour. Bluegills (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) are abundant in Farm Pond, and are the only fish species present.

*Tetragoneuria cynosura* and *Ladona deplanata* (Odonata: Libellulidae) are the most abundant dragonfly species present, accounting for over 90% of the larvae collected in Farm Pond during several studies (C.L. Pierce, unpublished data), and the only species colonizing substrates in the field experiment reported here. At this site, these species have overlapping, synchronized univoltine life cycles, as has been reported elsewhere (Benke and Benke 1975).

In the laboratory experiments, I used *Tetragoneuria*, *Ladona*, and another libellulid species, *Sympetrum semicinctum*. *Sympetrum* larvae are rare in Farm Pond, but are abundant in Goose Pond, a fishless pond of similar size approximately 1 km from Farm Pond. *Sympetrum* is also synchronized and univoltine, but emerges later than *Tetragoneuria* and *Ladona*. At this site, *S. semicinctum* appears to overwinter in the egg stage, as has been reported in *S. vicinum* (S.A. Wissinger, personal communication).

### *Predator avoidance experiment*

To test the hypothesis that dragonfly larvae avoid fish predators under field conditions, I constructed a series of cages in which natural substrate conditions could be established, larvae could readily colonize, and the presence and activities of an adult bluegill could be manipulated. The cages were chickenwire cylinders (2.5 cm mesh), 90 cm long and 25 cm in diameter, sealed at the bottoms with plastic plates, and oriented vertically with open tops extending 20–30 cm above the water surface. The plastic bottom plates had rims extending 3.5 cm upward and functioned as containers for patches of substrate that could later be easily removed for censusing larvae. The 2.5 cm mesh size was a compromise between being small enough to manipulate the presence or absence of adult fish, and being large enough to allow unrestricted entry of larvae and transmission of "signals" of the presence of fish in cages. Because of this, small juvenile fish could easily swim in and out of cages, and were assumed to occupy cages independent of treatment. Only very early instar dragonfly larvae are vulnerable to predation from such small fish (Sadzikowski and Wallace 1976; Keast 1978; Mittelbach 1981), and most larvae grew out of these small instars early in the experiment. The experiment was thus a test of effects of adult fish, with effects of small juvenile fish assumed to be equal across treatments.

I used three experimental treatments: 1) "Free fish" (F) cages contained single 9–12 cm (SL) bluegills with unrestricted access within cages; 2) "restrained fish" (R) cages were identical to F cages except that bluegills were prevented from foraging in the substrate by a chickenwire partition a few cm above the substrate; and 3) "no fish" (N) cages contained no adult bluegills. *Tetragoneuria* and *Ladona* larvae are "sprawlers", remaining on or within bottom substrates (Nestler 1980; see results of Microhabitat Use Experiment below), and thus were protected from predation by adult bluegills in R cages. Therefore, comparison of dragonfly colonization in cages with fish (F and R) to those without fish (N) provided a test of whether adult bluegills affected colonization, and comparison of F and R cages allowed me to determine whether a response to fish was indeed behavioral avoidance, or was to some extent a result of direct predation.

I randomly placed four replicate cages of each treatment in each of two shoreline locations (eight total replicates per treatment) on 26 June 1983. By this date, oviposition of *Tetragoneuria* and *Ladona* was complete, insuring that colonization of cages occurred "horizontally", or via the surrounding substrate, rather than "vertically" via oviposition. Cages were arranged linearly along the 0.6–0.7 m depth contour, approximately 0.5 m apart. Before being submerged, the bottom plates of the cages were filled with defaunated (autoclaved) sediments and detritus, providing a natural substrate for colonization. I placed the cages in locations where substrate had been previously collected for autoclaving, and secured them in place by running cords through the chickenwire meshes and tying the ends to wooden stakes.

I removed the cages on 29 October 1983, approximately four months after placement. I used a relatively long time interval to allow the defaunated substrate to recover from the disturbance and converge with the surrounding substrate through macrophyte growth and sedimentation, and to ensure recovery of middle and late instar larvae. Before

removal, a canvas sleeve with Nitex (0.5 mm mesh) panels was wrapped around each cage to retain substrate and larvae. On shore the substrate and associated organisms were washed into sample buckets and preserved in 70% ethanol. Contents of cages were washed in a 0.5 mm mesh sieve in the laboratory, and all macroinvertebrates retained were separated from the coarse substrate remaining by sugar floatation (Anderson 1959). Dragonfly larvae were counted and identified.

The response variable was number of larvae per cage, and I used a two-way ANOVA (location  $\times$  treatment) to test for effects of bluegills. Variances were similar between treatments, so data were not transformed. Three F cages and one R cage were discarded from the analysis because the bluegills had either died or escaped during the experiment. Treatment means were compared using the GT2 test, which is designed for uneven replication among treatments (Sokal and Rohlf 1981). Analysis was performed using the GLM procedure of SAS (Ray 1982).

#### Microhabitat use experiment

This experiment was designed to quantify microhabitat use patterns in the three dragonfly species, examining effects of diel period and presence of bluegills. All larvae and fish were maintained for at least one week prior to experiments in a controlled environment chamber, on a 12:12 h (light : dark) diel cycle at 20° C. Larvae were kept in 10 l aquaria with a substrate of dead leaves, and fed *Daphnia magna* and lumbricid worms ad lib several times per week. Bluegills were kept in a 260 l plexiglass tank and fed a variety of live prey or pellets daily.

Microhabitat use observations were made in 31  $\times$  16 cm clear plastic tanks, containing 9.3 l of aged, filtered tap water. Small wooden dowels (diameter = 6 mm), spaced 5 cm apart in regular rows, extended from the bottom of the tanks to the surface of the water, simulating the natural rushes in Farm Pond. I placed five or six dead leaves on the bottom and then poured in 100 ml of a well-mixed, standard mixture of sediments (particle size < 1 mm) collected from Farm Pond. Tanks were prepared in this manner 12–18 h prior to experiments, and sediments settled out of the water column to a depth of 2–3 mm on the bottom. This provided a substrate that mimicked the structurally complex littoral zone of Farm Pond, but allowed me to observe positions of most larvae during experiments.

I ran the experiments in a controlled environment chamber, set for a 12:12 h diel cycle and 20° C. Light intensity in the tanks during the day period was approximately 520 lux. Dim red overhead lights ( $\sim$  10 lux) were on continuously during the night period to permit observation of larvae, and a flashlight with red filter was frequently used to provide additional light ( $\sim$  30 lux) to locate larvae.

The species and instars used in all laboratory experiments are listed in Table 1. Within each species  $\times$  instar combination, the experiment was designed as a 2  $\times$  2 factorial (day/night vs. fish/no fish), with four replicates of each treatment combination. A replicate consisted of ten larvae of the same species and instar.

For observations with fish present, I placed single 5–6 cm (SL) bluegills in tanks after the sediment mixture was poured in. Beforehand, I temporarily tied the fishes' mouths shut with fine monofilament fishing line threaded through the thin membranes of their protrusible jaws, pre-

**Table 1.** Species and instars of dragonfly larvae used in laboratory experiments

Species	Instar <sup>a</sup>	Mean body length (mm)	Mean dry mass (mg)
<i>Tetragoneuria cynosura</i>	F-0	16.9	36.6
	F-1	11.7	12.2
	F-3	7.2	2.2
<i>Ladona deplanata</i>	F-0	19.5	24.5
	F-1	14.1	10.5
	F-3	8.4	2.7
<i>Sympetrum semicinctum</i>	F-0	13.6	17.6
	F-1	9.7	9.4

<sup>a</sup> F-0 = last larval instar, F-1 = next to last, etc

venting them from eating larvae (or other prey – see below). After 30–60 min in a separate holding tank, behavior of these fish appeared normal and they were frequently seen attempting (unsuccessfully) to strike prey in experimental tanks.

For the day observations, larvae were placed in individual tanks 1 h after lights-off in the evening. After a 12 h acclimation period (1 h after lights-on), I recorded the positions of all larvae exposed (visible) from above or through the sides of the tanks. Exposed larvae were categorized as being fully exposed on the bottom (on open bottom or leaf covering bottom), partially exposed on the bottom (partially covered by leaf with at least 25% of body visible from above), or perched on a dowel above the bottom. Larvae not exposed (invisible from above) during observations were underneath leaves. Night experiments were run in reverse order, with positions recorded 1 h after lights-off. Individual larvae were used only once for this experiment.

The response variables analyzed were proportions of larvae exposed (fully or partially), and proportions perched on dowels. Data were transformed as arcsine ( $\sqrt{p}$ ), and analyzed by two-way ANOVA using the GLM procedure of SAS (Ray 1982).

#### Foraging experiment

This experiment was designed to examine the effects of diel period and presence of bluegills on foraging success of larvae. The species and instars used (Table 1), temperature, photoperiod, tanks, substrate set-up and factorial design were the same as in the microhabitat use experiment described above. I ran eight replicates of each treatment combination, and larvae were used only once. Only one larva was used in each replicate trial.

I standardized feeding history by allowing larvae to feed ad lib on *Daphnia magna* and lumbricid worms for one hour, and then starved them for 48 h to insure gut clearance before experiments. I used 20 *Daphnia* (2.2/l) and 20 lumbricid worms (400/m<sup>2</sup>) as prey in each replicate trial, assuring that prey were available to larvae perched on dowels (primarily *Daphnia*) as well as on the bottom underneath cover (primarily worms). Bluegills were prevented from consuming prey as in the previous experiment, and I observed no differences in prey distribution or behavior when fish were present.

The time course in this experiment was the reverse of the microhabitat experiment: day experiments ran from 1 h after lights-on to 1 h after lights-off, and the night experiments vice versa. I attempted to make a 15 min observation at the end of each experiment to record larval movements, but this was only possible when larvae were exposed from above or very near a side of the tank, and could be located without use of a flashlight. I obtained behavior observations on about one third of the larvae.

I removed larvae from tanks immediately after the experiments and isolated them in vials for collection of fecal pellets. Fecal pellet mass (FPM) generally correlates well with food intake (Folsom and Collins 1982a, b; see below), and was used as an index of foraging success. Based on gut clearance experiments (see below) I isolated larvae for 48 h after experiments, checking periodically for fecal pellets. All fecal material produced by individual larvae was pooled, dried (60° C, 24 h), and weighed to the nearest  $\mu\text{g}$  on a digital electrobalance.

The response variable was FPM (dry), and data were transformed as  $\log_e(x+1)$  to stabilize variances and analyzed by two-way ANOVA using the GLM procedure of SAS (Ray 1982).

#### Vulnerability experiment

This experiment quantified vulnerability of larvae to bluegill predation, using the same species and instars as the two previous experiments (Table 1). Trials were run in 100 × 60 cm plexiglass tanks, containing 260 l of dechlorinated tap water. Substrates were set up as in the other lab experiments, and larvae were allowed a 12–18 h adjustment period prior to introducing fish. Temperature and photoperiod were the same as in the other lab experiments, but light levels in the larger tanks were lower (day = 240 lux, night = <1 lux). Ten larvae of the same species and instar were used in each replicate trial, and larvae were used only once.

I started experiments at approximately 1000 h and ran them for 48 h. Single, 8–10 cm (SL) bluegills were used as predators, and fish were selected randomly from a group of 20–30 in a separate holding tank. At the end of each trial, the fish was removed and the entire contents of the tank was sorted carefully to recover surviving larvae. Recovery in fish-free control trials was 100% for all species, indicating that losses during experiments were due only to bluegill predation. I ran four replicate trials with each species × instar combination.

The response variable was proportion of larvae eaten, and data were transformed as arcsine ( $\sqrt{p}$ ). Differences among species/instar combinations were analyzed by ANOVA and an SNK test using the GLM procedure of SAS (Ray 1982).

## Results

#### Predator avoidance experiment

Dragonfly larvae responded strongly to the presence of adult bluegills in experimental substrate patches in Farm Pond ( $F_{2,16} = 27.52$ ,  $P < 0.0001$ ); abundances in cages containing fish averaged just 15% of levels in fishless cages (Fig. 1). Responses of *Tetragoneuria* and *Ladona* were similar, with significantly higher densities in N cages than either

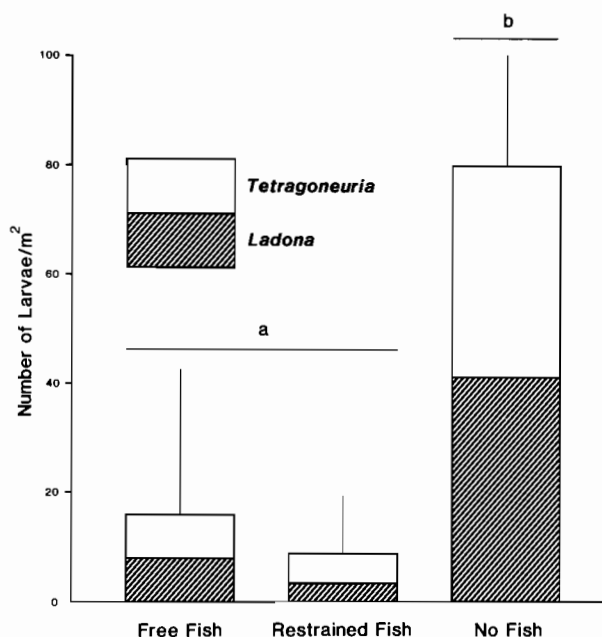


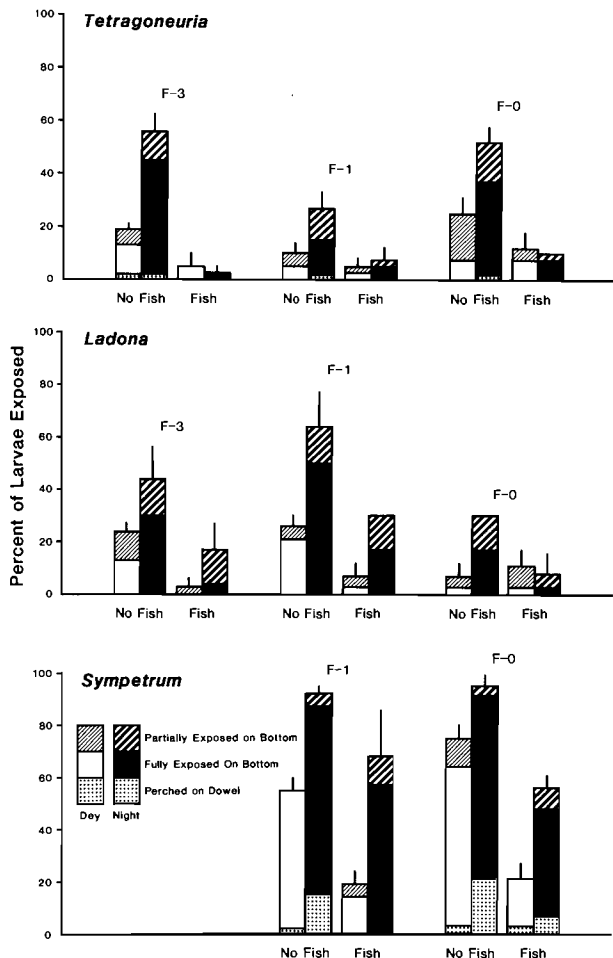
Fig. 1. Effect of bluegills on colonization of experimental substrate patches by larval *Tetragoneuria cynosura* and *Ladona deplanata* in Farm Pond. Histograms represent mean densities (+95% C.I.); shading indicates species composition. Means sharing a common horizontal bar and letter are not significantly different ( $\alpha=0.05$ , GT2 test). (Note: statistical comparisons similar for both species individually and combined)

F or R cages, which did not differ (GT2 test,  $\alpha=0.05$ ). Since bluegills prevented from foraging in the substrate (where the larvae occur) produced essentially the same effect as unrestrained fish, the reduction of colonization in F and R cages can be attributed solely to behavioral avoidance, and is strong evidence that *Tetragoneuria* and *Ladona* larvae can detect and avoid fish predators in their natural environment. The lack of a significant additional effect of direct predation in F cages is not surprising, since densities of larvae were already very low due to avoidance.

#### Microhabitat use experiment

Microhabitat use of all three species varied significantly with diel period and the presence or absence of fish (Fig. 2, Table 2). Exposure was generally lower during the day and/or when fish were present, indicating a tendency for larvae to shift away from vulnerable positions when risk of predation in those areas was greatest. In F-0 and F-1 *Tetragoneuria*, exposure was significantly reduced in the presence of fish (Table 2). A significant fish × time interaction in F-3 *Tetragoneuria* indicated reduced daytime exposure only when fish were absent; when fish were present, exposure was uniformly low. This trend was also apparent in F-0 and F-1 *Tetragoneuria* as well, but was not statistically significant (Fig. 2, Table 2).

The same trend was evident in F-0 *Ladona*, indicated by a significant fish × time interaction (Fig. 2, Table 2). Exposure in both F-1 and F-3 *Ladona* was significantly reduced in the presence of fish, and daytime exposure was significantly reduced in the F-1 instar. A similar diel trend in the F-3 instar was not statistically significant (Fig. 2, Table 2).



**Fig. 2.** Effects of bluegills and diel period on microhabitat use by larval *Tetragnoneuria cynosura*, *Ladona deplanata*, and *Sympetrum semicinctorum* in laboratory experiments. Histograms represent mean percent of larvae exposed ( $+1$  SE); shading indicates time of day and position (see bottom panel). Histograms clustered by instar (see Table 1). Statistical comparisons in Table 2

F-0 and F-1 *Sympetrum* showed nearly identical microhabitat shifts in response to the treatments; exposure was significantly reduced both in the presence of fish and during daytime (Fig. 2, Table 2).

Across all treatments and instars, *Sympetrum* larvae occupied exposed microhabitats significantly more frequently (60%) than either *Tetragnoneuria* (19%) or *Ladona* (23%), which did not differ significantly ( $\alpha=0.05$ , GT2 test) (Fig. 2). *Sympetrum* also perched on dowels above the substrate more frequently (6%) than either *Tetragnoneuria* (<1%) or *Ladona* (0%) ( $\alpha=0.05$ , GT2 test). Thus, although *Sympetrum* exhibited the same kind of microhabitat shifts in response to diel period and fish predators as *Tetragnoneuria* and *Ladona*, they generally occupied high-risk (exposed) microhabitats such as the top surface of the substrate and simulated rushes much more frequently than the other two species.

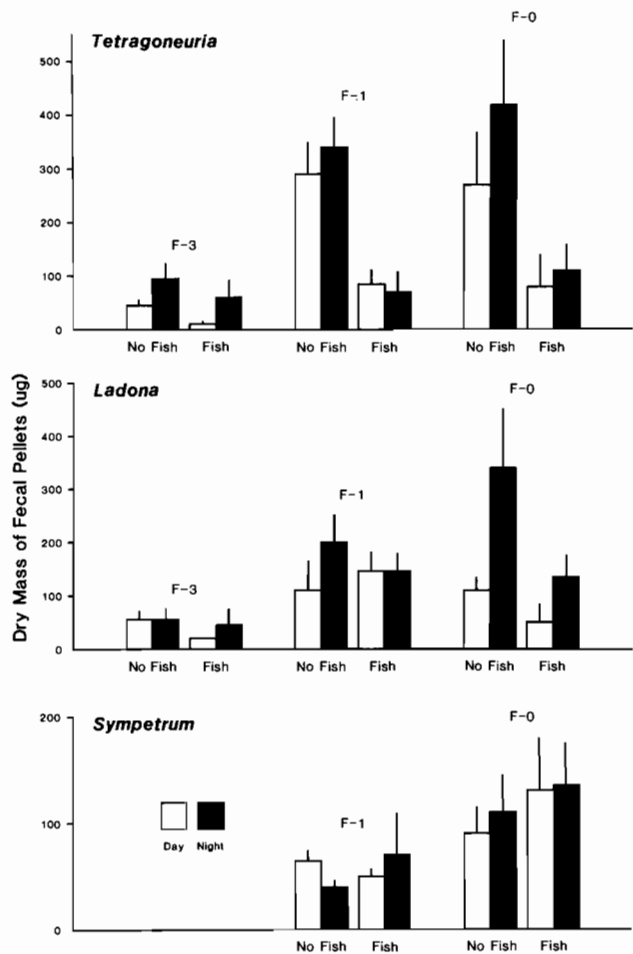
#### Foraging experiment

I made three assumptions in using fecal pellet production as an index of foraging success: 1) fecal pellet mass is positively correlated with food intake, 2) food intake explains most of the variation in fecal pellet mass (FPM), and 3) gut passage time is slow enough that little or no fecal material is expelled before the end of the 12 h experiment. Preliminary experiments indicated positive correlations between FPM and number of *Daphnia magna* eaten in all three species (Pierce 1987). Number of *Daphnia* eaten explained large percentages of FPM variation in *Tetragnoneuria* (96%) and *Ladona* (88%), but not in *Sympetrum* (15%). Many of the *Daphnia* killed by *Sympetrum* larvae in these preliminary experiments were only partially consumed, whereas *Tetragnoneuria* and *Ladona* consumed 100% of prey killed. Because of this, I could only estimate the number of *Daphnia* eaten by *Sympetrum* from examination of the remaining fragments, which probably explains the poor correlation between FPM and number of *Daphnia* eaten. It seems reasonable to assume that FPM is a good predictor of the actual amount of food ingested in *Sympetrum*, just as it is in *Tetragnoneuria*, *Ladona*, and in other species (Folsom and Collins 1982a, b). Other preliminary experiments indicated that gut passage time was indeed slow enough that most of the total fecal output would occur during the period when larvae were isolated, averaging 83%, 83%, and 100% for *Tetragnoneuria*, *Ladona* and *Sympetrum*, respectively (Pierce 1987).

Bluegills reduced foraging success in all three instars of *Tetragnoneuria* and F-0 *Ladona*, but there was no evidence

**Table 2.** Summary of ANOVAs testing the effects of bluegills and diel period on exposure in *Tetragnoneuria*, *Ladona*, and *Sympetrum*. Asterisks indicate significant effects: \* $0.05 > P > 0.01$ , \*\* $0.01 > P > 0.001$ , \*\*\* $P < 0.001$

Species	Source	Instar					
		F-3		F-1		F-0	
		F	P	F	P	F	P
<i>Tetragnoneuria cynosura</i>	Fish	46.30	<0.001***	5.60	0.036*	19.96	<0.001***
	Time	5.22	0.041*	2.38	0.149	4.09	0.066
	F $\times$ T	7.41	0.019*	1.38	0.262	3.30	0.094
<i>Ladona deplanata</i>	Fish	13.12	0.003**	14.76	0.002**	2.24	0.160
	Time	3.54	0.082	19.23	<0.001***	1.23	0.289
	F $\times$ T	0.00	0.966	0.03	0.857	5.67	0.035*
<i>Sympetrum semicinctorum</i>	Fish			6.65	0.024*	50.30	<0.001***
	Time			17.91	0.001**	21.93	<0.001***
	F $\times$ T			0.18	0.681	0.00	0.945



**Fig. 3.** Effects of bluegills and diel period on foraging success of larval dragonflies in laboratory experiments. Histograms represent mean fecal pellet dry mass (+1 SE); shading indicates time of day (see bottom panel). Histograms clustered by instar (see Table 1). Statistical comparisons in Table 3

of reduction in *Sympetrum* or F-1 and F-3 *Ladona* (Fig. 3, Table 3). FPM in F-0 and F-1 *Tetragoneuria* was strongly depressed when fish were present, averaging 28% and 25% of trials without fish, respectively. In general, foraging success was similar in day and night experiments for all species,

although daytime FPM was significantly lower than at night in F-0 *Ladona*. Similar, but nonsignificant diel trends were also seen in F-0 and F-3 *Tetragoneuria*. Baker (1986) has recently reported higher FPM in damselfly larvae fed ad lib on enchytraeid worms than in those fed on *Daphnia*. Despite evidence to the contrary (Folsom and Collins 1982a, b), if this bias applies to the dragonfly larvae used in the present experiment, FPM should be negatively correlated with exposure, since the proportion of *Daphnia* eaten was probably higher when exposure was higher. There was no indication of this in any of the three species (Figs. 2, 3), which suggests that FPM bias due to prey type either did not occur or was at least very small relative to the effect of predation risk. Thus, it appears that foraging success of some dragonfly larvae is sensitive to predation risk, but the degree of risk-sensitivity varies both among species and instars within species.

Behavioral observations indicated very low rates of movement, averaging 0.8, 0.3, and 1.7 movements/h in *Tetragoneuria*, *Ladona*, and *Sympetrum*, respectively. Similarly low movement rates for *Tetragoneuria* have been reported previously (Crowley et al. 1987). Movement rates did not differ significantly between species ( $\alpha=0.05$ , GT2 test), and there were no differences due to fish or diel period within species (instars pooled) ( $P>0.05$ , ANOVA). The few movements that were observed generally consisted of brief crawling moves, usually less than one body length. *Tetragoneuria* and *Ladona* larvae were never observed to swim, but *Sympetrum* occasionally swam in very short, rapid bursts.

#### Vulnerability experiment

Vulnerability to bluegill predation varied greatly among the eight species/instar groups, ranging from 8 to 73% of the larvae being eaten (Table 4). The eight groups fell into two fairly distinct categories: a relatively vulnerable group suffering 60% or greater losses, and a relatively less vulnerable group experiencing losses of less than 25% (Table 4).

Comparison of the mean vulnerability values for each of the eight species/instar groups with mean values of % exposure, % of larvae moving during behavioral observations, magnitude of predator-induced microhabitat shift (away from exposed locations), and magnitude of diel microhabitat shift indicated that vulnerability was most close-

**Table 3.** Summary of ANOVAs testing the effects of bluegills and diel period on foraging success in *Tetragoneuria*, *Ladona*, and *Sympetrum*. Asterisks indicate significant effects: \* $0.05 > P > 0.01$ , \*\* $0.01 > P > 0.001$ , \*\*\* $P < 0.001$

Species	Source	Instar					
		F-3		F-1		F-0	
		F	P	F	P	F	P
<i>Tetragoneuria cynosura</i>	Fish	6.76	0.015*	29.68	<0.001***	9.06	0.006**
	Time	1.53	0.227	0.28	0.599	0.79	0.383
	F × T	0.09	0.765	1.09	0.306	0.00	0.974
<i>Ladona deplanata</i>	Fish	1.25	0.286	0.47	0.497	7.83	0.010*
	Time	0.00	0.985	1.25	0.273	6.09	0.020*
	F × T	0.00	0.991	0.85	0.365	0.90	0.351
<i>Sympetrum semicinctum</i>	Fish			0.51	0.482	1.21	0.281
	Time			3.27	0.082	1.03	0.319
	F × T			0.13	0.719	0.22	0.640

**Table 4.** Vulnerability (% eaten) of dragonfly larvae to bluegill predation in laboratory experiments, and relationship with behavioral attributes. Values for behavioral attributes are means averaged over all treatment combinations (fish  $\times$  time). Species/instar groups are listed in descending order according to vulnerability

Species/Instar	%Eaten <sup>1</sup>	Behavioral attribute			
		%Exposed	%Moved <sup>2</sup>	Predator-induced microhabitat shift <sup>3</sup>	Diel microhabitat shift <sup>4</sup>
<i>Sympetrum</i> /F-0	73 <sup>a</sup> $\pm$ 6	60	14	56	37
<i>Sympetrum</i> /F-1	60 <sup>a</sup> $\pm$ 12	59	13	41	54
<i>Ladona</i> /F-3	60 <sup>a</sup> $\pm$ 7	21	0	71	58
<i>Ladona</i> /F-1	23 <sup>b</sup> $\pm$ 11	31	0	54	60
<i>Tetragoneuria</i> /F-1	15 <sup>b</sup> $\pm$ 9	13	0	68	56
<i>Tetragoneuria</i> /F-3	13 <sup>b</sup> $\pm$ 3	21	0	89	59
<i>Ladona</i> /F-0	10 <sup>b</sup> $\pm$ 7	14	9	47	53
<i>Tetragoneuria</i> /F-0	8 <sup>b</sup> $\pm$ 3	25	20	72	39
Correlation with %Eaten <sup>5</sup>		0.76 (0.027)	0.14 (0.737)	-0.36 (0.386)	-0.22 (0.604)

<sup>1</sup> Untransformed mean percentages ( $\pm 1$  SE) of larvae eaten by bluegills in the vulnerability experiment. Means sharing a common superscript are not significantly different ( $\alpha=0.05$ , SNK test)

<sup>2</sup> Percentage of larvae that moved at least once during behavioral observations

<sup>3</sup> Percent reduction of larvae exposed when bluegills were present relative to when no fish were present

<sup>4</sup> Percent reduction of larvae exposed during the day period relative to the night period

<sup>5</sup> Correlation coefficients (probability that  $r=0$  in parentheses) for vulnerability to bluegill predation with behavioral attributes

ly related to exposure (Table 4). Vulnerability to bluegill predation was positively correlated with % exposure, but not significantly correlated with the other behavioral attributes. Larval size (body length) also appeared to be unrelated to vulnerability ( $r = -0.41$ ,  $P = 0.314$ ). These results suggest that microhabitat use is an important determinant of vulnerability of dragonfly larvae to fish predation.

## Discussion

Predator avoidance behaviors may be categorized as either fixed or reactive (Stein 1979). (Edmunds (1974) referred to these as primary and secondary responses, respectively.) Fixed behaviors are “hard-wired”, occurring regardless if predators are actually present. Use of microhabitats that provide refuge, infrequent movement, and diel microhabitat shifts away from dangerous areas during periods of predator activity are common examples of fixed antipredator behaviors. Reactive behaviors occur only when prey sense the presence of a predator. Moving away from predators, predator-induced microhabitat shifts, and predator-induced reductions in movement are common examples of reactive antipredator behaviors. The link between predation as a selective pressure and prey behavior as an evolutionary response is clearer for reactive behaviors, especially in cases where prey have been shown to react less vigorously to nonpredatory organisms that are morphologically similar to predators (Peckarsky 1980; Fraser and Mottolese 1984; Heads 1985). Cause and effect is more difficult to ascertain with fixed behaviors, as they may be merely fortuitous “exaptations” (Gould and Vrba 1982), having evolved in response to selection pressures other than predation. Despite the problems with evolutionary interpretations of fixed “antipredator” behaviors, there are many examples documenting their functional significance (Stein 1979; Peckarsky 1982) and there is abundant evidence to suggest that both fixed and reactive behaviors are important in reducing risk of predation in many prey species.

My results demonstrate both fixed and reactive behavioral responses to fish predators, and suggest that these responses may be important in predator-prey interactions between fish and dragonfly larvae by, 1) reducing vulnerability of species that co-occur with fish, and 2) determining which species successfully coexist with fish. *Tetragoneuria* and *Ladona* showed a strong tendency to avoid fish in the field, and in laboratory experiments exhibited general microhabitat preferences and both diel and predator-induced microhabitat shifts that should reduce their risk of fish predation. With the exception of F-3 *Ladona*, vulnerability experiments confirmed that risk of predation was relatively low in these species. Wellborn and Robinson (1987) have demonstrated that microhabitat choice is an important determinant of vulnerability of another libellulid species to bluegill predation as well. Recent evidence suggests that littoral zone fishes exploit only a very small fraction of the available invertebrate prey biomass (Boisclair and Leggett 1985), implying that “real” prey availability (the amount of prey that can actually be captured by fish) may be much less than “potential” prey availability (the density of prey in the habitat). Risk-reducing behavioral patterns in prey such as dragonfly larvae along with the considerable structural complexity of the littoral zone no doubt account for this disparity in large measure.

*Sympetrum* larvae from fishless Goose Pond showed similar diel and predator-induced microhabitat shifts, but generally tended to favor more exposed (and presumably risky) microhabitats than either *Tetragoneuria* or *Ladona*, and were correspondingly more vulnerable to fish predation. Odonate species assemblages in fishless habitats are quite different from those where fish occur (Wright 1943; Kime 1974; Nestler 1980; Johnson and Crowley 1980; Henrikson 1981; M.A. McPeck, personal communication; S.A. Wissinger, personal communication; personal observations), and there is evidence that fish may exclude species that do not possess effective antipredator behavioral patterns (Henrikson 1981; Pierce et al. 1985). It is not surpris-



ing that *Sympetrum* exhibit some degree of response to fish predators, since they probably co-occur to a limited extent presently and may have overlapped broadly in the past. Indeed, Sih (1986) documented predator avoidance responses in a species of mosquito larvae that had no previous contact with the notonectid predator, suggesting that some apparent predator avoidance responses are really generalized responses to any large organism. Successful coexistence of relatively large, profitable prey such as dragonfly larvae with fish predators may depend on either highly precise antipredator responses (e.g., Sih 1986) or a more general but effective combination of fixed and reactive responses, such as appears to be the case with *Tetragoneuria* and *Ladona*. The greater tendency of *Sympetrum* to occupy exposed microhabitats was correlated with increased risk of fish predation, which may partially explain the rarity of *Sympetrum* in Farm Pond while being abundant in nearby Goose Pond.

Compromising foraging success in favor of reduced risk of predation is a commonly observed behavioral "decision" in many prey species (Dill 1987). In my experiments, bluegills significantly reduced both foraging success and use of exposed microhabitats in *Tetragoneuria* larvae, which might suggest that the "decision" to move to a safer microhabitat necessarily leads to reduced foraging. However, there are at least two reasons to doubt the strength of this link in dragonfly larvae. First, *Sympetrum* underwent a similarly sharp microhabitat shift in the presence of fish, yet there was no evidence of reduced foraging. Secondly, micro-distributions of dragonfly prey in littoral habitats are unknown, and there is no reason to believe that fewer prey are available in safe microhabitats than in risky ones. It seems more likely that fish reduce foraging in some species by intimidation, making larvae less likely to strike at prey or perhaps inhibiting them from moving to more profitable "fishing sites" (Heads 1985; Dixon and Baker 1987). Crowley et al. (1987) have shown that small *Tetragoneuria* respond behaviorally to larger, cannibalistic conspecifics by "freezing", which supports the hypothesis that foraging reductions are the result of intimidation rather than microhabitat shift. Of course, in nature fish not only distract dragonfly larvae from foraging, but they also exploit some of the same prey populations. Recent field experiments suggest that juvenile fish and *Tetragoneuria* engage in a complex network of interactions involving both exploitative competition and intimidation (Moore 1985).

Recent experiments with mayfly (Peckarsky 1980, 1987; Peckarsky and Dodson 1980; L.A. Martinez, personal communication) and mosquito larvae (Sih 1986) indicate that predators are detected through a combination of tactile and chemical cues. The mechanisms of predator recognition in larval dragonflies have not been investigated, but the relative importance of sensory mechanisms can be inferred from morphology and studies of stimuli eliciting foraging responses. Dragonfly eyes are very well developed relative to many other aquatic insects; ommatidial numbers in late instar larvae of many anisopteran species are comparable to those of other terrestrial insects known to have good vision (Sherk 1977). In species with the greatest compound eye development (Aeshnids), vision is the most important sense directing prey capture (Corbet 1962; Pritchard 1965; Sherk 1977). The libellulids used in this study have intermediate compound eye development (Sherk 1977, personal communication), and species of this type generally depend

on both visual and mechanical stimulation in foraging (Pritchard 1965; Richard 1970). Chemical stimuli are apparently unimportant. Thus, it seems likely that visual and/or mechanical cues are the basis for predator detection in dragonfly larvae. Direct tactile cues (e.g., Peckarsky 1980, 1987) are probably of limited value other than for large larvae in escaping repeated attacks from small fish. However, mechanical stimulation in the form of water displacements generated by the fanning movements of a fish's fins may be important. Underwater vibrations are known to attract *Chaoborus* to zooplankton prey (Autrum 1964; Giguere and Dill 1979), and predatory caddisfly larvae to benthic prey (Tachet 1977).

It is probably incorrect to postulate that the sensory mechanisms enabling predator avoidance behavior in dragonfly larvae evolved solely for that reason, since many of the species with clearly superior senses do not commonly co-occur with fish (Wright 1943; Kime 1974; Johnson and Crowley 1980; personal observation). However, in prey species that do coexist with fish, predator detection and avoidance may be an important component in reducing their risk, and further experimental studies will be necessary to compare the relative importance of fixed versus reactive antipredator behaviors in minimizing risk of fish predation, and to determine the influence of predator avoidance on prey availability to fishes.

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