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BEHAVIOR OF ZYGOPTERAN NYMPHS IN A SIMULATED WEED BED

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The results are reported of some laboratory experiments intended to (1) gather baseline behavioral observations of zygopteran nymphs in a simulated rush bed, (2) test a hypothesis to account for switching by nymphs between alternative prey in the laboratory, and (3) quantify some components of nymph predation on cladoceran prey. The predators were *Ischnura verticalis* nymphs in the 2nd day of their final instar; their movements (strikes, captures, ignores, discards) were measured during 1-hr observation periods using event recorders. The experiments were designed as a factorial with 3 main treatments (hunger: starved 24 hr, fed; — illumination: light, dark; — prey: *Daphnia*, *Simocephalus*, none) and 7 replicates of each treatment combination. Analyses of variance and orthogonal contrasts performed on the data indicate that nymphs move around more when hungry, in the light, and in the absence of prey, and that predation rates are higher for starved nymphs, in the light and with *Daphnia* present. The data are consistent with the switching hypothesis, but a "dispersal" interpretation is offered as an alternative explanation. These results and other evidence also imply that vision can be important in prey capture; that actively swimming prey are much more vulnerable to this classic sit-and-wait predator; and that prey ingestion depends more strongly on the frequency of predator-prey encounters than on predation efficiencies.

INTRODUCTION

Remarkably little is known about lake littoral zones in general and about the odonate nymphs living there in particular (CORBET, 1962). It is known that these nymphs are often abundant (GERKING, 1962; MACAN, 1964; BENKE, 1976); that they occupy detritus, mud, rocks, and especially weeds in shallow water (WALKER, 1956; CORBET, 1962; JOHNSON &

CROWLEY, 1979); and that they prey heavily on Cladocera, midges, and other littoral invertebrates (MACAN, 1964; FISCHER, 1966; LAWTON, 1970; PEARLSTONE, 1971). And it now appears quite possible that odonate nymphs may often exert an important stabilizing influence on their prey populations, damping their density fluctuations, and extending persistence (see CROWLEY, 1975; JOHNSON et al., 1975; BENKE, 1978; JOHNSON & CROWLEY, 1979; AKRE & JOHNSON, 1979). To investigate this latter possibility and to begin filling the gap in our knowledge of the littoral zone, some baseline quantitative observations must be made.

Recent studies of the functional response of zygopterans to the Cladocera *Daphnia* and *Simocephalus* (LAWTON et al., 1974, AKRE & JOHNSON, 1979) demonstrate that these nymphs can "switch" the brunt of their predation to the relatively most abundant prey. (The possible stabilizing implication of such behavior is well recognized (MURDOCH, 1969; LAWTON et al., 1974)). Though their experiments include no direct observations of this interaction, Akre and Johnson suggest that *Anomalagrion hastatum* exhibits two distinct search modes: (1) When *Daphnia* are relatively abundant, the nymphs "sit and wait" for moving prey to mechanically stimulate the antennae or mouthparts, triggering a labial "strike"; — (2) when *Simocephalus* are relatively abundant, the nymphs move around in their container, contacting and consuming the sessile *Simocephalus* disproportionately (cf. also JOHNSON & CROWLEY, 1979). Experiments reported in the present paper, carried out with a closely related predator (*Ischnura verticalis*) under similar experimental conditions, provide a test of Akre and Johnson's suggested behavioral shift for weed-dwelling zygopterans: Do the nymphs move around more at lower prey densities? Are they more active when hungry? Is this amount of movement influenced by light intensity?

Other *a priori* hypotheses are also addressed in these experiments: Swimming nymphs are probably much more vulnerable to fish predators than are other nymphs, suggesting that swimming may be a relatively drastic means of longer range dispersal. Do nymphs therefore swim more when hungry, in the dark, and with no prey available? Do they swim more in the presence of the relatively inactive *Simocephalus* than with *Daphnia*? Certain components of nymph predation (encounters with prey, labial strikes, prey capture, prey ingestion) can be observed and quantified under the experimental conditions. Are the active *Daphnia* easier prey than *Simocephalus*, even at a lower density? Do light and hunger increase the predation rate? Does the number of prey ingested per nymph depend on the encounter frequency or on the handling efficiencies in the different treatment combinations?

MATERIAL AND METHODS

The experimental design is a 3 x 2 x 2 factorial with seven replicates: three prey regimes (*Daphnia pulex* at 25 l^{-1}, *Simocephalus vetulus* at 50 l^{-1}, and none), two nymph hunger levels (starved 24 hr, fed *ad lib*), and two light regimes ("dark": red light < 10 lux, "light": around 750 lux — see below). (For the predation components, the design is 2 x 2 x 2, since the "no prey" experiments are not applicable). This approach permits the results to be evaluated by a balanced three-way analysis of variance (using Statistical Analysis System release 76.6B on IBM 360 computer), with most of the questions at the end of the introduction answered as designed orthogonal contrasts.

Daphnia pulex was cultured in a series of 1.5 gal (5.7 l) glass aquaria, to which freeze-dried brewer's yeast was added daily and the motile green alga *Chlamydomonas reinhardii* every two or three days. Two 0.5 mm mesh screen baskets containing egg-bearing *D. pulex* were placed in each aquarium for about 24 hr; adults were retained by the fine mesh, but neonates were released into the aquarium. In this way these daphnids, used in experiments seven days later, were known to be age 7 ± 0.5 days. Unfortunately, this method proved an ineffective means of standardizing daphnid sizes: means of ten body lengths of randomly selected daphnids from the fourteen experimental cultures ranged from 1.29 mm to 2.16 mm. But since cultures were assigned arbitrarily to particular treatments so that most replicates of a given experiment used different cultures, there is no reason to suspect that differences in daphnid size could have biased the results.

Simocephalus vetulus was cultured in plastic wading pools containing 80 l of filtered tap water, snails, and a few contaminant *D. pulex*. These pool cultures were fed on the same diet and schedule as the daphnids, though snail feces doubtless contributed a considerable bacterial flora. Only *Simocephalus* retained by a 0.6 mm mesh brass screen were used in the experiments; means of ten body lengths of randomly selected individuals from the eighteen samples used in experiments ranged from 1.21 mm to 1.49 mm. *Simocephalus* experimental densities were twice those for *Daphnia* to increase the encounter frequency of predators with these similar-sized but less active prey.

Ishnura verticalis nymphs used in these experiments were collected from several small ponds in and near Lexington in July through September, 1978. They were sorted to instar by measuring head widths and wing pad lengths. The nymphs were then placed in labeled vials containing filtered tap water and kept in a Percival I-35LL cycling incubator at 23°C and a 16:8 (light:dark) photoperiod. They were examined daily for exuvia and fed several daphnids three times per week.

Naiads newly molted into the final instar were set aside in the incubator for

use in experiments on the next day. These animals were either deprived of food during that 24 hr interval ("starved") or given about 75-150 daphnids to feed on *ad lib* ("fed"); earlier attempts to prepare "fed" animals with 50 or fewer daphnids yielded erratic results, as some nymphs had eaten or killed all of their prey overnight and were indistinguishable from their "starved" cohorts.

The experiments were carried out in 1.5 gal (5.7 l) glass aquaria containing 4 l of filtered tap water. A dense stand of rushes was simulated by about 320 eighth-inch (3.2 mm) wooden dowels inserted into a clear Plexiglas rectangle at 1 cm intervals in a hexagonally symmetric pattern. This density and stem diameter are representative of some extensive, well-established *Eleocharis* stands containing *I. verticalis* in Bays Mountain Lake, Sullivan Co., Tennessee (cf. JOHNSON & CROWLEY, 1979; personal observations). The dowel assembly fits snugly in the aquarium so that the free ends of the dowels are (almost) all flush with the bottom; the high dowel density restricts viewing to the top through the plexiglas rectangle and lighting to the bottom. The aquarium sides were covered by opaque black plastic to prevent interference from room light. "Light" experiments were illuminated by a 40W fluorescent fixture containing a straight cool-white tube, diffused by a rectangle of white translucent plexiglas. The intensity measured by a Weston Illumination Meter (Model 756) declined from 2400 lux at the aquarium bottom to 100-120 lux at the top; assuming an exponential reduction in intensity through the aquarium, this implies an average intensity of about 750 lux. "Dark" experiments were illuminated by a 20W fluorescent fixture containing a straight red tube, diffused by the white translucent plexiglas and by several sheets of bond typing paper. Intensities throughout the aquarium were well below 10 lux, the minimal sensitivity level of the meter. Behavioral observations were recorded using Rustrak Model 292-8 8-channel Event Recorders on chart paper moving at one inch per min. The experimental aquaria, dowel assemblies,

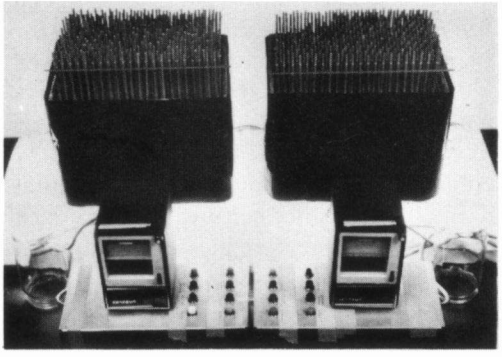

Fig. 1. Simulated weed beds and apparatus for recording the behavior of zygopteran nymphs. Two 1.5 gal (5.7 l) aquaria with dowel assemblies and two event recorders with switchboxes are shown. The 40W fluorescent fixture, translucent plexiglass plates, and aquaria are arranged as for the "light" experiments.

event recorders, switchboxes, and the 40W fluorescent fixture used in the "light" experiments are illustrated in Figure 1.

Each experiment and the recording of behavioral observations began with the introduction of the nymph to an aquarium under the experimental illumination with prey (if used) already present. The following behaviors (and the durations of the first four) were recorded: climbing (walking along a dowel), sitting on the bottom, walking on the bottom, swimming, striking at prey, capturing prey, discarding prey (estimated in quarters of prey rejected), and ignoring prey (prey contacting the nymph's antennae or mouthparts, but not eliciting a strike). Observations were recorded for about 75 min; the first 10 min from each data tape was ignored as an "adjustment period", and the next 60 min provided the data used in all analyses presented below.

RESULTS

Table I compares the mean time spent moving (climbing, walking, or swimming) in the twelve different treatment combinations. An analysis of variance of these data (Table II) indicates that all three main effects (hunger, illumination, prey) are significant, particularly hunger and prey, and that

Table I

The time in minutes that nymphs spent climbing, walking, or swimming during sixty minutes of observation: means (±1SE) of seven replicates

Nymph condition	No prey		Daphnia		Simocephalus	
	Dark	*Light*	*Dark*	*Light*	*Dark*	*Light*
Starved	2.77±0.45	6.23±1.11	1.13±0.12	1.70±0.47	2.20±0.68	1.50±0.42
Fed	0.38±0.14	1.25±0.32	0.62±0.12	0.71±0.22	0.63±0.22	0.38±0.10

Table II

Analysis of Variance for movement, the time spent climbing, walking, or swimming

Source	df	SS	F	
Hunger (starved, fed)	1	77.88	52.03	$P < 0.001$
Illumination (light, dark)	1	9.49	6.34	$P < 0.05$
Prey (0 l^{-1}, 25 *Daphnia* l^{-1}, 50 *Simocephalus* l^{-1})	2	44.98	15.03	$P < 0.001$
Hunger x illumination	1	4.07	2.72	n.s
Hunger x prey	2	33.70	11.26	$P < 0.001$
Illumination x Prey	2	25.61	8.56	$P < 0.001$
Hunger x Illumination x Prey	2	8.46	2.83	n.s

both two-way interactions involving prey are highly significant. The orthogonal contrasts of Table III focus on particular treatment combinations to clarify these results: Contrasts 1-4 and 7-10 show that more nymph movement with prey than without accounts for the prey effect, rather than any difference between *Daphnia* and *Simocephalus* treatments. Contrasts 5 and 6 indicate that hunger increases nymph movement both in the dark and in the light. And contrast 11 seems to contradict the analysis of variance by finding no increase in movement in the light, though an increase was almost significant at the 5% level ($0.05 < P < 0.06$). Non-orthogonal and post-data contrasts proved insufficiently powerful to extend the results of Table III, but a careful inspection of Table I accounts for the significant two-way interactions: both hunger and light have synergistic effects with the absence of prey on nymph movement. In other words, the lack of prey increases movement in the light or of hungry nymphs disproportionately.

Table III

Orthogonal contrasts for movement, the time spent climbing, walking, or swimming. The contrasts were evaluated using one-tailed t-tests. Treatments and their abbreviations are: Hunger: starved (ST), fed (FD); — Illumination: light (LT), dark (DK); — Prey: none (NP), *Daphnia* (DA), *Simocephalus* (SI).

Contrast	Hunger: / Illumination: / Prey:	ST DK NP	ST LT NP	FD DK NP	FD LT NP	ST DK DA	ST LT DA	FD DK DA	FD LT DA	ST DK SI	ST LT SI	FD DK SI	FD LT SI	
(1) NP>DA,SI (ST,DK)		+2				−1				−1				$P < 0.05$
(2) NP>DA,SI (ST,LT)			+2				−1				−1			$P < 0.001$
(3) NP>DA,SI (FD,DK)				+2				−1				−1		$P < 0.05$
(4) NP>DA,SI (FD,LT)					+2				−1				−1	$P < 0.01$
(5) ST>FD (DK)		+1		−1		+1		−1		+1		−1		$P < 0.001$
(6) ST>FD (LT)			+1		−1		+1		−1		+1		−1	$P < 0.001$
(7) SI>DA (ST,DK)						+1				−1				n.s
(8) SI>DA (ST,LT)							+1				−1			n.s
(9) SI>DA (FD,DK)								+1				−1		n.s
(10) SI>DA (FD,LT)									+1				−1	n.s
(11) LT>DK		+1	−1	+1	−1	+1	−1	+1	−1	+1	−1	+1	−1	n.s

Table IV shows that, except in one replicate, nymphs only swam when starved and with *Simocephalus* or no prey present. An analysis of variance found only the hunger effect to be significant ($P < 0.05$), probably because the relatively high variance in the frequency and duration of swimming masked the prey effect. There is no overall indication that nymphs swim more in the dark (as if to avoid fish); the apparently higher swimming time (if real) in the starved-dark-*Simocephalus* treatment combination may be triggered by the very low encounter frequencies and ingestion rates (see below).

Table V presents analysis of variance tables for strikes, captures, and ingestion of prey by nymphs. (Another table could have been included for prey encountered — strikes + ignores — but so few prey were ignored that this is virtually indistinguishable from the strikes table shown). The main

Table IV

The time in minutes that nymphs spent swimming during sixty minutes of observation: means of seven replicates (± 1 SE for non-zero means), with the number that swam at all indicated in parentheses

Nymph condition	No prey		Daphnia		Simocephalus	
	Dark	*Light*	*Dark*	*Light*	*Dark*	*Light*
Starved	0.09 (5) ± 0.04	0.14 (4) ± 0.10	0 (0)	0 (0)	0.23 (3) ± 0.15	0.01 (2) ± 0.01
Fed	0 (0)	0 (0)	0.00 (1)	0 (0)	0 (0)	0 (0)

Table V

Analyses of variance for total numbers of prey stuck, captured, and ingested in experiments with prey present

	Strikes				Captures				Ingestion			
Source	df	SS	F		df	SS	F		df	SS	F	
Hunger	1	833.14	15.14	P<0.001	1	138.29	7.55	P<0.01	1	111.45	12.84	P<0.01
Illumination	1	787.50	14.31	P<0.001	1	330.29	18.03	P<0.001	1	70.88	8.17	P<0.01
Prey	1	848.64	15.42	P<0.001	1	178.57	9.75	P<0.01	1	39.45	4.54	P<0.05
Hunger x Illumination	1	8.64	0.16	n.s.	1	16.07	0.88	n.s.	1	9.04	1.04	n.s.
Hunger x Prey	1	77.79	1.41	n.s.	1	12.07	0.66	n.s.	1	6.11	0.70	n.s.
Illumination x Prey	1	412.57	7.50	P<0.01	1	120.07	6.55	P<0.05	1	16.61	1.91	n.s.
Hunger x Illumination x Prey	1	2.57	0.05	n.s.	1	1.14	0.06	n.s.	1	0.07	0.01	n.s.

effects are all significant and the interactions non-significant, except the illumination-prey interaction for strikes and captures. Notice that, in contrast to its marginal influence on movement, illumination strongly affects these predation parameters; the unusually high F-value for captures suggests that vision may play an important role in prey capture. Table VI, containing the corresponding orthogonal contrasts, accounts for the significant interaction and restricts this light effect largely to daphnid prey (contrasts 3 and 6). This

Table VI

Orthogonal contrasts for total number of prey struck, captures, and ingested in experiments with prey present. The contrasts were evaluated using one-tailed t-tests. Treatments and abbreviations are: Hunger: starved (ST), fed (FD); — Illumination: light (LT), dark (DK); — Prey: *Daphnia* (DA), *Simocephalus*, (SI).

Contrast	Hunger:	ST	ST	FD	FD	ST	ST	FD	FD	Strikes	Captures	Ingestion
	Illumination:	DK	LT	DK	LT	DK	LT	DK	LT			
	Prey:	DA	DA	DA	DA	SI	SI	SI	SI			
(1) ST>FD (DK,DA)		+1		−1						P<0.01	P<0.01	P<0.01
(2) ST>FD (LT,DA)			+1		−1					n.s.	n.s.	n.s.
(3) LT>DK (DA)		+1	−1	+1	−1					P<0.001	P<0.001	P<0.05
(4) ST>FD (DK,SI)						+1		−1		P<0.05	P<0.01	P<0.01
(5) ST>FD (LT,SI)							+1		−1	P<0.05	n.s.	n.s.
(6) LT>DK (SI)						+1	−1	+1	−1	n.s.	n.s.	n.s.
(7) DA>SI		+1	+1	+1	+1	−1	−1	−1	−1	P<0.01	P<0.01	P<0.05

table also shows that starved nymphs strike, capture, and ingest more prey than fed nymphs, but this result is mainly confined to the dark experiments (contrasts 1, 2, 4 and 5). Finally, *Daphnia* are significantly more vulnerable to nymphs than *Simocephalus*, despite the daphnids' lower density.

Encounter frequencies, handling efficiencies, and prey ingested are listed in Table VII. Note that encounter frequency multiplied by strike efficiency is strike frequency — multiplied by capture efficiency is capture frequency — multiplied by ingestion efficiency is prey ingested. Each multiplicative component appears to vary somewhat across treatment combinations, though the ingestion pattern is already virtually determined by the encounter frequencies: daphnid prey, light, and hunger yield more frequent prey encounters than do the alternatives. Strike efficiencies were all 1.00 (i.e. all prey encountered by nymphs were struck at) except for the two treatment combinations with the highest ingestion rates; in these cases, nymphs may

Table VII

Mean prey encounter frequencies; strike, capture, and ingestion efficiencies; and prey ingested; in experiments with prey present. Treatments and their abbreviations are: Hunger: starved (ST), fed (FD); — Illumination: light (LT), dark (DK); — and Prey: 25 *Daphnia* l^{-1} (DA), 50 *Simocephalus* l^{-1} (SI). Treatment combinations were replicated seven times each.

	Hunger: ST Illumination: DK	ST LT	FD DK	FD LT	Prey
Encounter frequency (prey nymph^{-1} hr^{-1})	9.9	26.7	0.4	13.6	DA
	5.0	7.4	0.0	1.7	SI
Strike Efficiency: strikes/(strikes + ignores)	0.94	0.88	1.00*	1.00	DA
	1.00	1.00	—	1.00	SI
Capture Efficiency: captures/strikes	0.29	0.51	0.00*	0.53	DA
	0.29	0.56	—	0.67	SI
Ingestion Efficiency: (captures - discards)/captures	0.96	0.58	—	0.37	DA
	1.00	0.80	—	0.38	SI
Prey Ingested (prey nymph^{-1} hr^{-1})	2.6	6.8	0.0	2.5	SI
	1.4	3.3	0.0	0.4	SI

have become temporarily satiated, an effect even more apparent in the pattern of ingestion efficiencies. For starved nymphs, ingestion efficiency is inversely related to total ingestion, whereas for fed nymphs, ingestion efficiency is relatively low and apparently independent of total ingestion (cf. JOHNSON et al., 1975 on "wasteful killing" by damselflies). In the light, the capture efficiencies range from 0.51 to 0.67, possibly being slightly higher for fed nymphs and with *Simocephalus* prey; in the dark, capture efficiencies are about half the light values, again suggesting the possible importance of vision in prey capture.

DISCUSSION

These experiments yield a consistent picture of last instar *Ischnura verticalis* nymphs in weed beds as sit-and-wait or ambush predators: Starved naiads in the light with no prey available spent an average of only 10.4% of the observation period moving, mostly creeping very slowly up or down a dowel; other treatment combinations produced even less movement on average. It has been suggested that remaining motionless (and thus being an ambush predator) is an adaptation by zygopterans to the presence of visual predators, primarily fish (CORBET, 1962; JOHNSON & CROWLEY, 1979). If this interpretation is correct, then one might expect zygopteran nymphs characteristic of fishless lakes and ponds (e.g. *Enallagma aspersum*, some lestid species) to be more active, providing them better access to sessile cladocerans like *Simocephalus* and *Sida*. True ambush predators such as *I. verticalis* may appear to be selecting the more active prey like chironomids and chydorids, though few data bearing on this possibility are currently available.

Superimposed on this predominately motionless life-style of *I. verticalis* nymphs is the increase in movement documented here with hunger, absence of prey, and increased illumination. These results are qualitatively consistent with the shift in search mode with prey density hypothesized by AKRE & JOHNSON (1979) for the closely related *Anomalagrion hastatum*. The present experiments of course cannot distinguish between a smoothly continuous increase in nymph movement with declining prey density and the distinct shift implied by discrete search modes. But the relatively small absolute mean difference in minutes spent moving per hour by starved nymphs in the dark with *Daphnia*, *Simocephalus*, and no prey (1.13, 2.20, and 2.77 in Table I, or 1.9%, 3.7%, and 4.6% of the observation time), the conditions most similar to those in Akre and Johnson's experiments, suggests an alternative explanation for their results: Hunger or few prey may trigger dispersal of the nymphs, stimulating a relocation of the ambush site (or "fishing site" of MACAN, 1964). If *Daphnia* and *Simocephalus* tended to be distributed somewhat differently in the containers in Akre and Johnson's experiments, as they did in mine (*Simocephalus* were more nearly confined to the bottom), then trial-and-error relocations by the nymphs should produce the switching they observed. (This kind of density-dependent relocation by an ambush predator has been documented for an orb-weaving spider by TURNBULL, 1964; MURDOCH et al., 1974 have demonstrated switching by fish predators for two prey distributed differently in an aquarium). The swimming data of Table IV further support this dispersal interpretation.

Despite the prevailing view that non-lestid zygopterans are primarily "tactile" (CORBET, 1962; JOHNSON & CROWLEY, 1979), illumination clearly influenced the behavior of *I. verticalis* in the experiments reported

here. Nymphs spent more time moving in the light (Tab. I), at least with no prey present, even though this should increase their vulnerability to visual predators; this light response is direct, rather than a circadian activity pattern entrained by the photoperiod, since all experiments were performed near the middle of the nymphs' sixteen light hours. It seems possible that a lack of visual stimuli from moving prey in the light may provide further impetus for nymph dispersal. The higher capture efficiencies in the light (Tab. VII) have also suggested that vision may be important in prey capture — either in coordinating labial seizure or in locating regions in the aquarium where more strikes could be successful.

Since Table VII suggests that encounter frequency is both the first and the most significant of several components influencing ingestion rate, in the experiments it is useful to briefly consider the factors that determine encounter frequency:

(1) Predator position relative to prey. — Zygopteran nymphs apparently find prey either by successive relocations until a satisfactory encounter or ingestion frequency is achieved, or by inversely varying the proportion of time spent moving with encounter or ingestion frequency. Fed nymphs with *Simocephalus* present often did not move enough during the hour of observation to discover the prey concentrated near the bottom, curtailing their encounter frequencies. Of course movement in turn depends on hunger, illumination, and prey, among other factors.

(2) Strike volume. — This is the volume of water within which the probability of a prey eliciting a strike equals or exceeds some set value, say 0.5. The strike volume probably also varies with hunger, illumination, and prey characteristics, though its influence on ingestion could be reduced or entirely negated by compensatory changes in capture efficiency (i.e. a nymph striking at more distant prey may catch fewer of them).

(3) Prey behavior and morphology. — Swimming speed, visibility and body size are some obvious examples. These could all vary with prey density and illumination. See below.

(4) Physical structure of the habitat. — The density and pattern of obstacles, supports, and hiding places can certainly affect encounter frequencies, interacting with all of the major treatment effects considered here. Encounter frequencies might have been quite different in these experiments if a different dowel density had been used.

That strikes, captures, and ingestion of *Simocephalus* are consistently lower than for *Daphnia* — despite the density bias in favor of *Simocephalus* — underscores the significance of prey behavior in littoral predator-prey interactions. Without thorough documentation of the distribution and behavior of predators and prey within the context of the appropriate habitat structure, little can be determined about the potential influence of one

population on another in the "real world".

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REFERENCES

AKRE, B.G. & D.M. JOHNSON, 1979. Switching and sigmoid functional response curves by damselfly naiads with alternate prey available. *J. Anim. Ecol.* (In press).

BENKE, A.C., 1976. Dragonfly production and prey turnover. *Ecology* 57: 915-927.

BENKE, A.C., 1978. Interactions among coexisting predators — a field experiment with dragonfly larvae. *J. Anim. Ecol.* 47: 335-350.

CORBET, P., 1962. *A biology of dragonflies.* Witherby, London.

CROWLEY, P.H., 1975. *Spatial heterogeneity and the stability of a predator-prey link.* Ph.D. thesis, Michigan St. Univ.

FISCHER, Z., 1966. Food selection and energy transformation in larvae of Lestes sponsa (Odonata) in astatic waters. *Verh. int. Ver. theor. angew. Limnol.* 16: 600-603.

GERKING, S.D., 1962. Production and food utilization in a population of bluegill sunfish. *Ecol. Monogr.* 32: 31-78.

JOHNSON, D.M., B.G. AKRE, & P.H. CROWLEY, 1975. Modeling arthropod predation: Wasteful killing by damselfly naiads. *Ecology* 56: 1081-1093.

JOHNSON, D.M. & P.H. CROWLEY, 1979. Odonate "hide-and-seek": Habitat-specific rules? *Amer. Soc. Limnol. Oceanogr. Special Symp.* 3. (In press).

LAWTON, J.H., 1970. Feeding and assimilation in larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). *J. Anim. Ecol.* 39: 669-689.

LAWTON, J.H., J.R. BEDDINGTON, & R. BONSER, 1974. Switching in invertebrate predators. *In*: M.B. Usher and M.H. Williamson [Eds.], Ecological stability, pp. 141-158.

MACAN, T.T., 1964. The Odonata of a moorland fishpond. *Int. Revue ges. Hydrobiol.* 49: 325-360.

MURDOCH, W.W., 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39: 335-354.

MURDOCH, W.W., S.L. AVERY & M.E.B. SMYTH, 1974. Switching in predatory fish. *Ecology* 56: 1094-1105.

PEARLSTONE, P., 1971. Observations of a population of damselfly larvae in Marion Lake. *In*: I.E. Efford [Ed.], Marion Lake project. IBP Canada, Report 1970-1971.

TURNBULL, A.L., 1964. The search for prey by a web-building spider Achaearanea tepidariorum (C.L. Koch) (Araneae, Theridiidae). *Can. Entomol.* 96: 568-579.

WALKER, E.M., 1953. *The Odonata of Canada and Alaska, Vol. 1.* Univ. Toronto Press, Toronto.