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#2 PREDATOR-PREY INTERACTIONS BETWEEN STONEFLIES AND MAYFLIES: BEHAVIORAL OBSERVATIONS[1]

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Abstract. Field experiments were conducted at two streams to determine the mechanisms by which mayfly prey detect and avoid stonefly predators, and to quantify the effect of stonefly predators upon mayfly behavior, distribution, and activity levels. Direct observations of the interactions between stoneflies and mayflies were made at Otter Creek, Sauk County, Wisconsin, USA and the East River, Gunnison County, Colorado, USA using plexiglass boxes with screen ends and an artificial substrate. *Ephemerella subvaria* and *Stenonema fuscum*, Otter Creek, avoided the stonefly predator *Acroneuria lycorias* given only noncontact chemical stimuli. *Ephemerella infrequens* and *Baetis bicaudatus*, East River, responded to long-range chemical stimuli from *Megarcys signata* and *Kogotus modestus*, East River. *Baetis phoebus* and *Heptagenia hebe*, Otter Creek, and *Cinygmula* sp., East River, did not respond to stonefly predators given long-range chemical cues alone. Differences among responses of different mayflies may be due to differential predation pressure or effectiveness of predator evasion tactics. None of the species of mayflies tested responded to the presence of stonefly predators given only visual stimuli.

The *Ephemerella* species assumed a "scorpion"-like display posture upon encounter with the stoneflies. This posture may increase the apparent size of the mayflies which are then rejected by the tactile predators. The *Baetis* species characteristically swam or drifted in response to contact with the stonefly predators. Predator evasion could partially explain the high incidence of this genus of mayflies reported in stream drift. The remaining mayflies, of the family Heptageniidae, showed an effective crawling evasion upon contact with stonefly predators. *Ephemerella infrequens* and *B. bicaudatus* differentially responded to contact with three different stonefly predators in the East River. Both species of mayflies evaded contact with *Pteronarcella badia*, a large omnivorous stonefly which morphologically resembles *M. signata*, significantly less frequently than they evaded *M. signata* and *K. modestus* upon contact. The mechanism by which this differentiation occurs could be chemotactile. *Cinygmula* sp. avoided all stoneflies equally regardless of size or relative threat of consumption. Tactile stimuli are probably responsible for this behavior.

Key words: behavior; chemical; display; distribution; drift; mayflies; predator avoidance; stoneflies; streams; tactile; visual.

INTRODUCTION

Considerable experimental evidence exists of the effects of biological interactions such as predation and competition upon the distribution and abundance of aquatic invertebrates in the marine rocky intertidal (Paine 1969, Woodin 1974, Menge 1976), and in freshwater lakes and ponds (Brooks and Dodson 1965, Dodson 1974*a*, and Kerfoot 1977). Such evidence is rare for stream ecosystems (Peckarsky 1979*a*, *b*).

Experimental manipulations by Peckarsky and Dodson (1980) suggest that stonefly predators influence the distribution and abundance of benthic invertebrates in streams. This study was undertaken to determine the mechanisms by which mayfly prey detect and avoid stonefly predators, and to explore further the effects of stonefly predators upon prey distribution, behavior, and activity levels.

Several studies have examined the mechanisms by which primarily fish and molluscan prey detect fish predators (literature review by Stein 1979). The mechanisms by which aquatic invertebrate prey detect or avoid invertebrate predators have received considerably less attention. Zooplankton have been shown to detect and avoid predators and objects simulating predators creating mechanical waves in freshwater laboratory systems (Strickler 1975). Tissue extracts of starfish predators have been found to elicit defense responses in some marine gastropod prey (Bullock 1953, Feder 1963, Yarnall 1964). Phillips (1978) demonstrated that sea urchins can distinguish foraging and inactive starfish predators given only chemical cues. No such studies exist for freshwater insect predator-prey interactions.

The capacity for sensory perception in aquatic invertebrates is well documented. Kohn (1961) and Slifer (1970) review the older literature on the structure and existence of chemoreceptors in gastropods and insects. Recent scanning electron microscope studies have clarified the fine structure of invertebrate sensory organs. Mechanoreceptors and chemoreceptors have been observed on adult mayfly antennae (Schmidt 1974, Slifer 1977), on antennae of mayfly nymphs (Peckarsky 1979*b*), mechanoreceptors on adult stonefly antennae (Rupprecht and Gnatzy 1974), and auditory organs on the mesothorax of corixid Heteroptera

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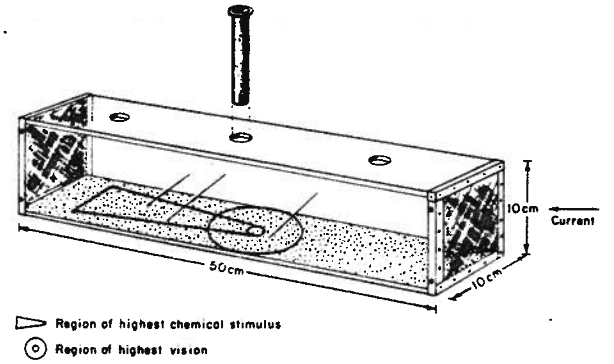

FIG. 1. The observation box with screen tube inserted in slot; schematic representation of proposed regions of highest chemical stimulus and highest vision.

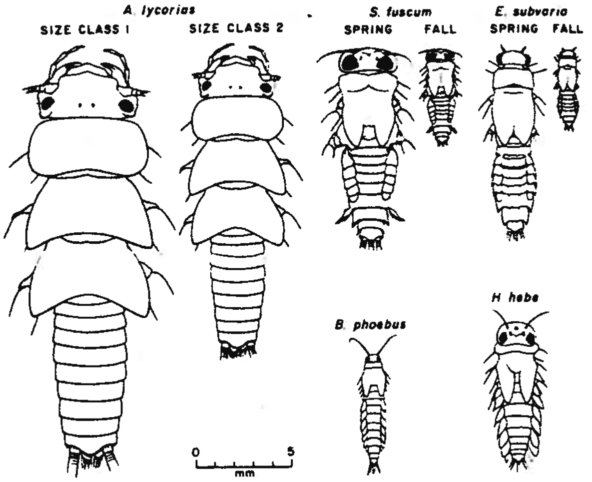

FIG. 2. Otter Creek stoneflies and mayflies. Size classes 1 and 2 of *A. lycorias* represent terminal and subterminal instars.

(Prager 1973). However, these structural analyses provide only suggestive evidence of the sensory capabilities of invertebrates. Behavioral observations are necessary to support hypotheses concerning the functional capacity of aquatic invertebrates to detect predators.

The experiments described in this study were designed to investigate the following alternative mechanisms by which several abundant species of mayfly prey detect and avoid stonefly predators in two streams: noncontact chemical stimuli, visual stimuli, and contact stimuli. Changes in mayfly distribution, activity levels, or behavior in response to the presence of one or more stonefly predators were measured to determine the relative importance of the alternative avoidance mechanisms for each mayfly species.

MATERIALS AND METHODS

Study areas

Experiments were conducted at Otter Creek, Sauk County, Wisconsin, and the East River, Gunnison County, Colorado. Both are second-order streams, high in dissolved oxygen, low in dissolved inorganic material, and have heterogeneous rock, cobble substrates. Otter Creek, a temperate woodland stream, receives considerably higher allochthonous input from a more extensive riparian vegetation than the East River, a high-altitude (3100 m), montane stream. Temperature in Otter Creek ranges from 0°–24°C, a wider range than in the East River (0°–18°); and the Wisconsin stream has a lower discharge. Both streams are described in more detail elsewhere (Peckarsky 1979*a*, *b*).

Apparatus

Plexiglass observation boxes (50 × 10 × 10 cm) were constructed with screen ends (mesh 800 μm) and a silicon sand substrate spray painted light brown (Fig. 1). The boxes contain three holes on the upper surface through which experimental animals can be introduced, or into which screen tubes or test tubes can be inserted. The boxes were placed in the stream immediately adjacent to the bank at water depth 4–8 cm. Careful choice of sites facilitated observation of activities within the boxes and ensured that the current velocity was relatively laminar, and slow enough that experimental animals could maintain their hold on the artificial substrate.

Experimental animals

Acroneuria lycorias (Perlidae), *Megarcys signata*, and *Kogotus modestus* (Perlodidae) are tactile, searching predators which consume primarily mayflies and chironomids (Richardson and Gaufin 1971, Cather and Gaufin 1975, Allan 1978, Peckarsky 1979*c*). *Pteronarcella badia* (Pteronarcidae) morphologically re-

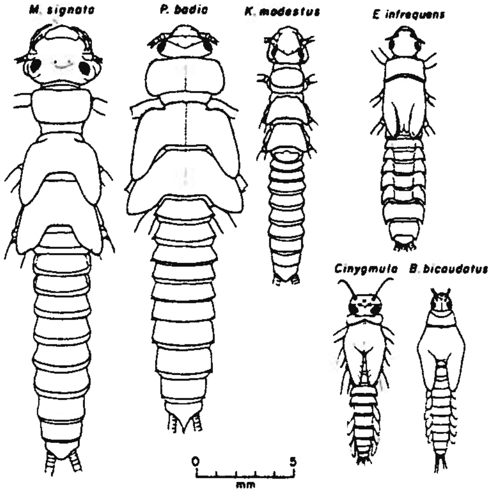

FIG. 3. East River stoneflies and mayflies.

sembles *M. signata*. Although previous stomach content analyses suggest that *P. badia* is a detritivore, late-instar nymphs have been shown to consume mayflies and chironomids in addition to their primarily detritivorous diet (Richardson and Gaufin 1971, Fuller and Stewart 1977). Observations made during this study confirm that *P. badia* nymphs are facultative search predators which consume some mayfly prey. However, the relative incidence of this occurrence is very low compared to that of the other stoneflies. Figs. 2 and 3 illustrate the average length and head capsule widths of each predator tested in Otter Creek and the East River. Head capsule widths of the predators indicate the mouth gape or maximum size of food that can be consumed (Devonport and Winterbourn 1976, Kliban 1976).

The prey species tested were of three types (Figs. 2 and 3). An Ephemerellidae species from each

TABLE 1. Preliminary gut content analysis of stoneflies. Relative abundances of mayflies within stonefly stomachs were calculated using the least abundant mayfly as a standard for each stonefly. Top: Otter Creek; bottom: East River.

Predator	Relative abundance of mayfly prey		Total stone-flies	Stone-flies with prey
A. lycorias	*B. phoebus*	5.4	780	438
	E. subvaria	4.9		
	S. fuscum	2.1		
	H. hebe	1.0		
M. signata	*B. bicaudatus*	5.0	67	25
	Cinygmula sp.	2.0		
	E. infrequens	1.0		
K. modestus	*B. bicaudatus*	21.3	154	127
	Cinygmula sp.	1.0		
P. badia	*B. bicaudatus*	1.0	144	27

TABLE 2. Summary of experiments.

A. *Technique*

Experiment	No. predators	Condition of predator(s)	No. mayflies	Time sequence of treatments for each replicate
(1) Noncontact chemical stimuli	1	in screen tube	15	mayflies introduced into box → at least 15 min acclimation → 15 min of distribution mapping on the minute → predator introduced → acclimation → mapping → predator removed → acclimation → mapping (screen tube in place through experiment)
(2) Visual stimuli	1	in test tube	15	mayflies introduced → acclimation → mapping → predator introduced → acclimation → mapping (test tube in place throughout)
(3) Contact stimuli	1	free	15	mayflies introduced → acclimation → predator introduced → acclimation → all encounters recorded for 15 min
(4) Activity change	3	free	6	mayflies introduced → acclimation → activity recorded for 15 min on the minute → predator introduced → acclimation → mayfly activity recorded

B. *Replicates*

Stonefly-mayfly pair	Location	Number of replicates: Noncontact chemical	Visual	Contact (encounters)	Activity change
	Otter Creek			Spring—156	
A. lycorias-				Fall—193	
E. subvaria		8	2	367	4
S. fuscum		4	2	225	4
B. phoebus		4	2	6 October—48	4
H. hebe		2	2	37	
M. signata-	East River				
E. infrequens		5	2	305	
Cinygmula sp.		4	2	217	
B. bicaudatus		4	2	282	
K. modestus-	East River				
E. infrequens		4	2	380	2
Cinygmula sp.		4	2	206	2
B. bicaudatus		4	2	284	2
P. badia-	East River				
E. infrequens		5	2	210	
Cinygmula sp.		4	2	198	
B. bicaudatus		4	2	386	

stream, *Ephemerella subvaria,* Otter Creek, *E. infrequens,* East River, represent a group of mayflies which attain a relatively large size and characteristically cling to rocks (Merritt and Cummins 1979). Three species of Heptageniidae, *Stenonema fuscum* and *Heptagenia hebe* from Otter Creek, and *Cinygmula* sp. from the East River are very dorsoventrally flattened crawlers. *Stenonema fuscum* becomes very large, but *H. hebe* and *Cinygmula* sp. emerge at smaller sizes than the ephemerellid species. Their head capsules, however, are disproportionately wider. *Baetis phoebus* (Baetidae) from Otter Creek and *B. bicaudatus,* East River, represent a family having many species which are very fast-swimming, cylindrical, streamlined mayflies. They were the smallest species tested and are common prey of many stonefly predators (Sheldon 1969, Siegfried and Knight 1976*a*, *b*, Fuller and Stewart 1977, Peckarsky 1979*c*, J. D. Allan, *personal communication*).

Table 1 represents preliminary data from gut content analysis of the predators tested. *Acroneuria lycorias* and *M. signata* consume all of the experimental mayflies in the relative abundances indicated. *Kogotus modestus* consumes only the two smaller species of mayflies, and only *B. bicaudatus* was recovered in the stomachs of *P. badia.*

The experiments

Four experiments were conducted in May, June, September, and October 1978 at Otter Creek, and in June, July, and August 1978 and 1979 at the East River. Table 2 summarizes the methods and numbers of replicates of each experiment.

For purposes of statistical analysis, a region of highest chemical stimulus was determined by introducing food coloring into the screen tube prior to each noncontact chemical experiment and observing its dispersal pattern. Dye was also used to standardize current velocity. Fig. 1 illustrates the region of the box which showed the highest concentration of food coloring and, presumably, other organic molecules emanating from the screen tube. A proposed region of highest vision was chosen conservatively since the reactive distance of mayflies is unknown (Fig. 1). Inspection of graphs of the number of mayflies within the region of highest chemical stimulus or vision over all 15 min of each treatment revealed that the distribution of mayflies stabilized after ≈10 min. Chi square statistical analysis (1 df) was applied to the data from the last 4 min of each treatment to make pairwise comparisons of the numbers in and out of the region of stimulus for each pair of treatments.

For the contact experiments, an encounter was defined as a physical contact between the stonefly and a mayfly (Evans 1976). The result of each encounter was scored as (a) attack or consumption, (b) locomotory evasion by the mayfly, and (c) freezing response by the prey. During fall at Otter Creek and summer 1979 at the East River, evasion responses were further classified as crawling, swimming, drifting (releasing hold of the substrate and passively floating downstream), and drift-swimming (briefly drifting, then actively swimming). A display posture observed in some mayflies upon encounters with stoneflies was also quantified. Mann-Whitney U tests were performed to compare the frequencies of different responses exhibited by different species of mayflies for the contact and activity change experiments.

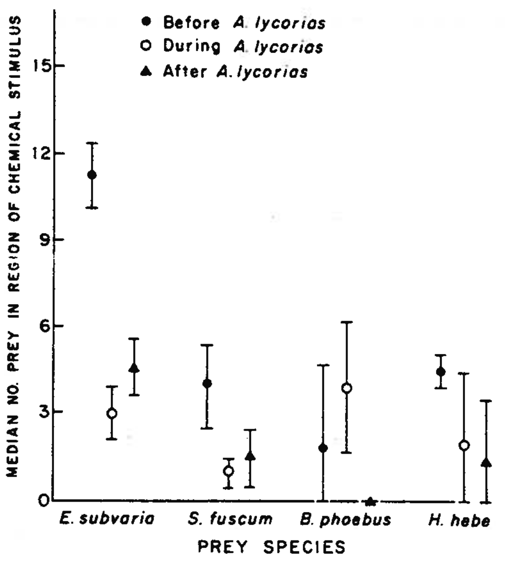

FIG. 4. Median and standard error of number of prey in region of chemical stimulus before, during, and after presence of *A. lycorias,* Otter Creek.

RESULTS AND DISCUSSION

The effect of noncontact chemical stimulus upon mayfly prey distribution

If mayflies can detect the presence of the stonefly given only noncontact chemical cues, the number of

TABLE 3. Summary of the statistically significant comparisons of the number of prey in the region of highest chemical stimulus. B = before predator, D = during predator, A = after predator. Asterisks indicate level of significance (chi square, 1 df). (* = .05, ** = .01, *** = .001)

Prey	Predator	Comparison	Significance level
E. subvaria	*A. lycorias*	B vs. D	***
		B vs. A	***
S. fuscum	*A. lycorias*	B vs. D	*
E. infrequens	*M. signata*	B vs. D	***
		D vs. A	**
B. bicaudatus	*M. signata*	B vs. D	***
		D vs. A	*
		B vs. A	*
	K. modestus	B vs. D	***
		D vs. A	**

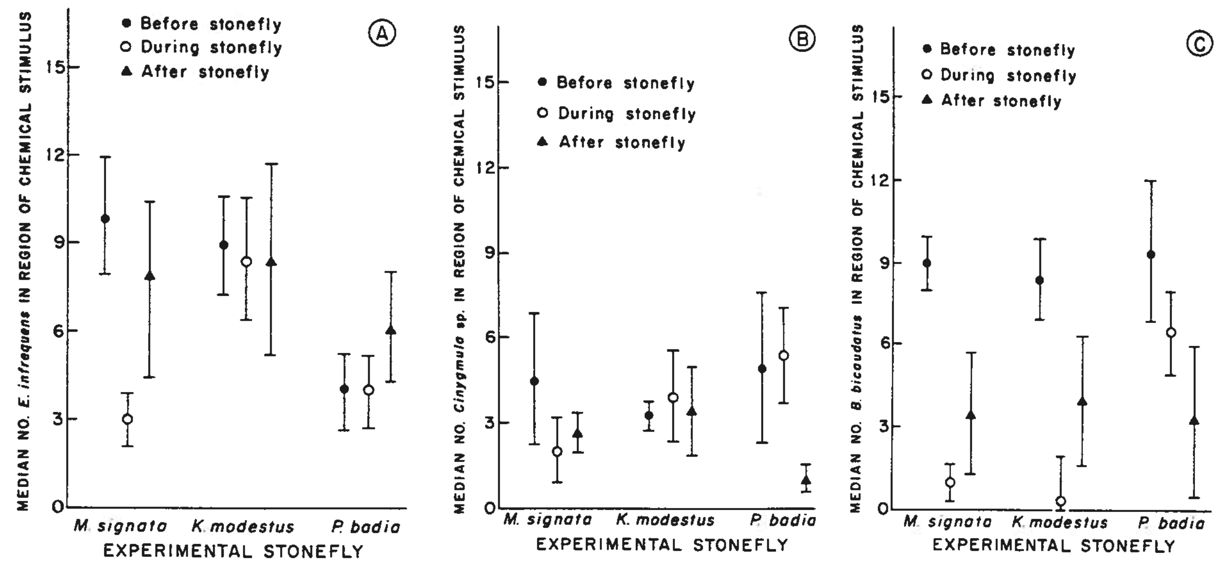

FIG. 5. Median and standard error of number of (A) *E. infrequens*, (B) *Cinygmula* sp., and (C) *B. bicaudatus* in region of chemical stimulus before, during, and after presence of each stonefly predator, East River.

mayflies in the region of highest chemical stimulus should decrease during the presence of a stonefly predator in the screen tube, and subsequently increase after removal of the predator. This trend was observed for *E. subvaria* and *S. fuscum* but not for *B. phoebus* and *H. hebe* at Otter Creek (Fig. 4). At the East River, *E. infrequens* and *Cinygmula* sp. responded as predicted to *M. signata* only (Figs. 5A, 5B); and *B. bicaudatus* showed the predicted response to *M. signata* and *K. modestus*, but not to *P. badia* (Fig. 5C).

The results of chi square statistical analysis of the differences between treatments are summarized in Table 3. A significant decrease in numbers of mayflies B vs. D indicates a systematic avoidance of the region downstream of a predator in the screen tube. *Ephemerella subvaria* and *S. fuscum* exhibited this response to *A. lycorias*, *E. infrequens* to *M. signata*, and *B. bicaudatus* to *M. signata* and *K. modestus*. A significant increase in numbers of mayflies D vs. A indicates a systematic recovery in numbers of mayflies within the proposed region of chemical stimulus after the removal of the predator. None of the Otter Creek mayflies showed this significant increase. However, a nonsignificant trend toward recovery by *E. subvaria* and *S. fuscum* suggests that given enough time, the original distribution may be resumed. At the East River, *E. infrequens* distributions showed significant recovery after the removal of *M. signata* and those of *B. bicaudatus* after the removal of *M. signata* and *K. modestus*. Longer acclimation time given during summer 1979 trials may explain this result.

No significant difference between the numbers of mayflies B vs. A the presence of the stonefly, following a significant decrease B vs. D, may also indicate recovery in numbers within the region of chemical stimulus. This result occurred with *S. fuscum* at Otter Creek, and for *E. infrequens* vs. *M. signata* and *B. bicaudatus* vs. *K. modestus* at the East River.

In summary, the predicted decrease in numbers of mayflies within the proposed region of chemical stimulus during the presence of the predator, and subsequent increase after removal of the predator were observed for two of four mayfly-stonefly pairs at Otter Creek, and three of nine pairs at the East River. Since the prey were screened from all other predator-related stimuli except noncontact chemical cues, this behavior suggests that the mayflies detect and avoid a chemical stimulus emanating from the predator.

Differences in responses by mayflies to noncontact

TABLE 4. Number of mayflies in proposed region of vision before and during the presence of the stonefly in a test tube.

Mayfly	Stonefly	Before	During
E. subvaria	*A. lycorias*	27	24
S. fuscum		5	8
B. phoebus		0	3
H. hebe		11	8
E. infrequens	*M. signata*	22	26
	K. modestus	44	35
	P. badia	31	26
Cinygmula sp.	*M. signata*	27	32
	K. modestus	18	11
	P. badia	23	14
B. bicaudatus	*M. signata*	16	19
	K. modestus	17	14
	P. badia	23	29

chemical stimuli from a stonefly predator may reflect the relative effectiveness at evading capture by stoneflies, or differential predator pressure. Since no feeding preference experiments have been performed on these stonefly nymphs, one must rely on gut content data for an estimate of the constituents of stonefly diets.

At Otter Creek. the two mayflies which avoided *A. lycorias* were the two largest species, *E. subvaria* and *S. fuscum*. Gut contents of some stoneflies suggest that larger prey may be preferred by larger predators (Sheldon 1969, J. D. Allan, *personal communication*). Stomachs of *A. lycorias* showed a high frequency of *E. subvaria* and a low incidence of *S. fuscum*. A proposed long-range chemical detection mechanism is not similarly reducing consumption of these two mayfly species; nor is the lack of such a response similarly increasing consumption of the smaller *H. hebe* and *B. phoebus*. Differences in predator preference, escape responses, or encounter probabilities may explain these differences.

At the East River the largest mayfly, *E. infrequens*, avoided noncontact chemical stimuli from only the largest predator, *M. signata*, which is also the only stonefly in whose stomachs it has been found. *Cinygmula* sp. did not avoid any of the stoneflies, although it is consumed by *M. signata* and *K. modestus*. Effective escape tactics, low preference, or low encounter probabilities may account for its low frequency in stonefly stomachs. *Baetis bicaudatus* avoided the large and small predators, but not the stonefly which only takes it occasionally. This very abundant mayfly is consumed in high relative frequency despite an avoidance response to noncontact chemical stimuli from two of the stoneflies.

The experiments presented lend preliminary support to the hypothesis that some mayflies can detect the presence of stoneflies by long-range chemoreception. Detected chemically, the presence of a stonefly can significantly alter the distribution of some mayflies within observation boxes. Documentation of the existence and nature of chemical substances produced by stoneflies during different states of hunger, at different times of day or night, or as a response to stress would lend substantive support to these behavioral observations.

The lack of information regarding the importance of stonefly predation as a source of mortality in mayflies limits the interpretation of these results. Mortality of mayflies due to stonefly predation has not been measured, although Siegfried and Knight (1976*b*) reported that numbers of prey recovered in the gut contents of a western perlid stonefly nymph could account for fluctuations of prey observed in the benthos. Experimental manipulations presented here support direct cause-effect relationships between stonefly stimuli and mayfly responses, but one cannot extrapolate with certainty that variability in mayfly avoidance responses to different stoneflies is attributable to an evolutionary cause such as differential stonefly predation pressure.

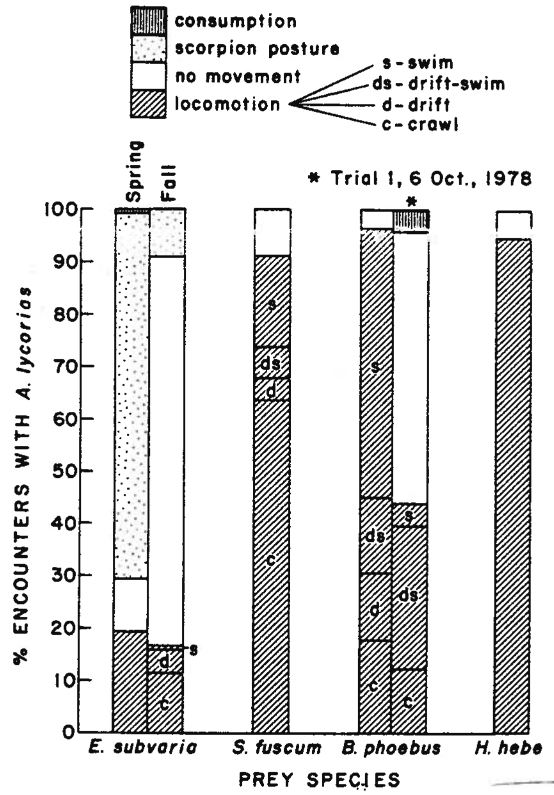

FIG. 6. Percent encounters of mayfly prey species with *A. lycorias* resulting in specific responses, Otter Creek.

The effect of visual stimulus upon mayfly prey distributions

If mayflies detect and avoid stonefly predators by visual cues, the number of mayflies occupying the proposed region of highest vision should decrease during the presence of a stonefly predator within the test tube. For 7 of the 13 mayfly-stonefly pairs this predicted trend was observed (Table 4). However, all comparisons were nonsignificant (chi square, 1 df). Any changes in numbers of mayflies occupying the region of highest vision were so small that directional trends should not be inferred. Given visual cues alone, mayflies did not avoid a region surrounding a stonefly predator.

Many benthic invertebrates live under stones in streams and are negatively phototactic (Bishop and Hynes 1969, Hughes 1969*a*, 1969*b*). This factor in addition to the probable nocturnal feeding habits of the stoneflies (Hynes 1970) lower the apparent adaptiveness of a visual sense as a mechanism of predator detection. It is not surprising that the experimental evidence suggests that mayflies do not avoid predators presented visually only. The uncertainty of a reactive

TABLE 5. Summary of statistical analysis of contact experiments. Asterisks refer to significance levels, Mann-Whitney U test. A species indicated in parentheses showed no significant difference from those on either side.

A. Otter Creek: Comparisons among prey. E = *E. subvaria*, S = *S. fuscum*, B = *B. phoebus*, H = *H. hebe*

Evasive behavior	All trials except 6 October 1978	6 October 1978
Total locomotion	*** *** E < S < B (H)	*** * E < B < S
Crawling	*** E B < S	*** E B < S
Drifting	*** S < B (E)	*** B < S (E)
Drift-swimming	E *** < B S *	E *** < B S *
Swimming	* *** E < S < B	no significant differences

B. East River: Comparisons among prey. E = *E. infrequens*, C = *Cinygmula* sp., B = *B. bicaudatus*, M = *M. signata*, K = *K. modestus*, P = *P. badia*.

Evasive behavior	Predator M	 K	 P
Total locomotion	*** C E < B	*** C E < B	*** *** E < B < C
Crawling	*** E B < C	*** E B < C	*** E B < C
Drifting	*** C < B (E)	** C < B (E)	*** * C < E < B
Drift-swimming	* E < C (B)	E *** < B C	no significant differences
Swimming	*** C < B (E)	*** B C < * E	C * < B E **

TABLE 5. Continued.

C. East River: Comparisons among responses to different predators.

Evasive behavior	Prey E	 C	 B
Total locomotion	* K M < P	no significant differences	*** M P < K
Crawling	no significant differences	* K < P (M)	no significant differences
Drifting	** K < P (M)	P *** < M K	* M K < P
Drift-swimming	no significant differences	* P K < M	M * < K P
Swimming	M * < K P ***	*** M < K (P)	no significant differences
Scorpion posture	*** K P < ** M		

distance and the possibility of the test tube creating an optical and hydrodynamic obstruction remain as problems in this analysis.

Avoidance behavior of mayflies upon contact-encounter with stoneflies

Mayflies which do not show noncontact chemical avoidance of predators should show more intensified locomotory responses to contact by the predators. *Baetis phoebus*, *H. hebe*, and *S. fuscum* reacted to contact with *A. lycorias* by locomotory evasion >90% of the time. *Ephemerella subvaria* moved away from the predator after <20% of the encounters (Fig. 6). The primary locomotory responses of *E. subvaria* nymphs were crawling and drifting, of *S. fuscum*, crawling, and of *B. phoebus*, entering the water column by swimming, drift-swimming, and drifting. The results of Mann-Whitney U tests on the differences between the responses by mayfly species to encounters with *A. lycorias* are summarized in Table 5A. *Stenonema fuscum* showed greater total locomotion than *E. subvaria* but less total locomotion than *B. phoebus*. There was no statistical difference between the frequencies of evasion by locomotion for *H. hebe* and *S. fuscum* or *B. phoebus*.

On 6 October 1978, two *B. phoebus* individuals were consumed by *A. lycorias* during the experiment. The effect of this event upon the behavior of the remaining *B. phoebus* nymphs is illustrated in Fig. 6 and Table 5A. The percentage of total locomotory responses significantly dropped, especially the swimming and drifting behaviors. The percentage of drift-swim responses to stonefly encounters significantly increased.

Ephemerella subvaria responded most frequently to encounters with *A. lycorias* by freezing and extending its caudal filaments and posterior abdominal segments vertically and anteriorly through a 180° radius. I have termed this behavior "scorpion" display. Fig. 7a–d illustrates the various intensities of this posture observed before or during encounters with *A. lycorias*. The frequency of this response markedly dropped from spring when the nymphs of *E. subvaria* were mature to fall when early instars primarily responded to encounters with *A. lycorias* by freezing in normal posture (Fig. 7a).

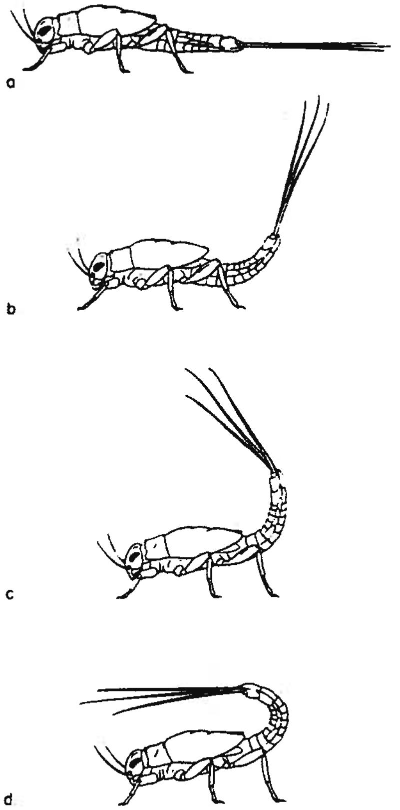

FIG. 7. *E. subvaria*: a. normal resting posture, b. low-intensity scorpion posture, c. moderate-intensity scorpion posture, d. high-intensity scorpion posture.

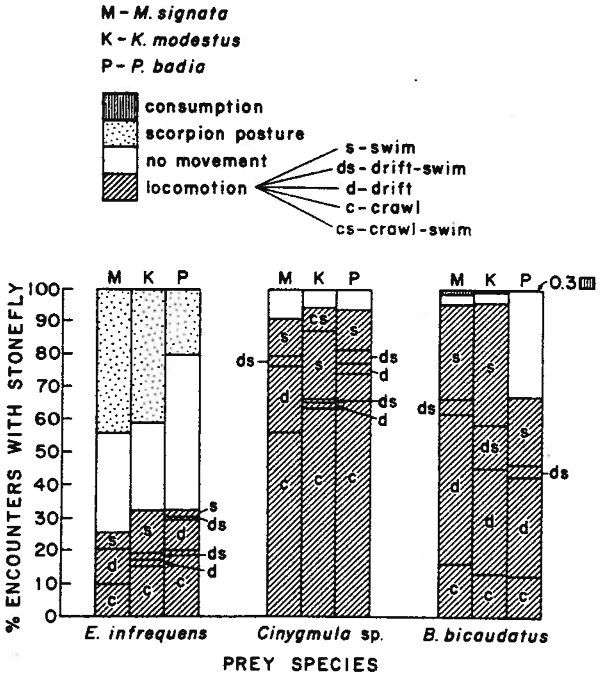

FIG. 8. Percent encounters of mayfly species with three stonefly predators resulting in locomotory responses, East River.

Responses of the East River mayflies to encounters with the stonefly predators are shown in Fig. 8. In general, *E. infrequens*, which also froze and displayed a scorpion posture before and during contact by stoneflies, showed a low frequency of locomotory evasion of all three predators. *Baetis bicaudatus* and *Cinygmula* sp. demonstrated a significantly higher percentage of total locomotion in response to encounters with all stoneflies. The results of Mann-Whitney U tests comparing the responses of the mayflies are summarized in Table 5B.

The most frequent types of locomotory responses of *E. infrequens*, like *E. subvaria*, were crawling and drifting. *Cinygmula* sp. primarily crawled, and *B. bicaudatus* entered the water column, for the most part, by drifting, drift-swimming, or swimming in response to contact with the stoneflies.

Differences in mayfly behavior were observed in response to encounters with the different predators (Table 5C). *Ephemerella infrequens* froze or scorpioned more frequently in response to *M. signata* and *K. modestus* than to *P. badia*. Its total locomotory evasion of *M. signata* was less frequent than that of the other two stoneflies. *Cinygmula* sp. showed no differences in the frequency of total locomotion responses to encounters with any of the stoneflies. Individuals of this species exhibited a crawl-swim sequence of responses to *K. modestus* encounters. *Baetis bicaudatus* showed more frequent locomotion in response to *M. signata* and *K. modestus* than to *P. badia*. Differences within specific behavior patterns in response to the three stoneflies occurred for some mayflies, and appear in Table 5B and C.

To summarize, in response to contact-encounters with stonefly predators, the *Ephemerella* species from both streams primarily clung to the substrate or postured, *Baetis* species entered the water column, and heptageniid species crawled.

Baetis and *Ephemerella* species are commonly reported in the drift of streams (Lehmkuhl and Anderson 1972, Hildebrand 1974, Ciborowski et al. 1977, and Corkum 1978). These authors attribute the high frequency of these mayflies in the drift to their morphology, and to the interaction of their activity patterns with physical factors which tend to dislodge them from the substrate. Waters (1972), Müller (1974), and Keller (1975) summarize the occurrence of mayfly nymphs in the drift. Although differing opinions exist, the most prevalent explanation for invertebrate drift is that negative phototaxis causes the benthos to appear on the surface of the substrate to feed during periods of low light intensity. Their vulnerability to the current and physical disturbance from other foragers accounts for the high incidence of drift during these active periods. No previous information has been presented to document the importance of drift as an active predator avoidance mechanism. The behavior of *Ephemerella* and *Baetis* species shown here in response to foraging stonefly predators could in part explain the high incidence and diel periodicity of these mayflies in the drift.

The *Baetis* species showed the most frequent evasive responses to stoneflies. However, upon a successful attack by *A. lycorias* of *B. phoebus,* a severe reduction in swimming and drifting behavior occurred. The remaining mayflies aggregated in corners and ends of the observation box. As an aggregate, they did not respond as frequently upon encounters with the predator. Charnov et al. (1976) report similar evasion of fish predators by a *Baetis* species which responded by aggregating in corners of an aquarium. The stimulus causing this change in behavior is unknown.

The scorpion display of the *Ephemerella* species is the first of its kind to be reported for aquatic insect larvae or nymphs, although an early reference to this behavior exists (Needham et al. 1935). This type of response is not unique to invertebrates, however. Crane (1952) published an inclusive study of the defense postures of Trinidad mantids. The studies of Bullock (1953), Feder (1963), and Yarnall (1964) describe displays of various marine invertebrates in response to starfish and gastropod predators. Stein and Magnuson (1976) and Hayes (1977) report defensive postures of crayfish as a response to simulated and real fish predators in freshwater.

The adaptive significance of the scorpion posture has not been experimentally documented. One possible explanation is that the posture alters the apparent size and shape of the mayfly, which foils a tactile predator. Stoneflies merely walked over or around *Ephemerella* nymphs in scorpion posture. Perhaps the display creates a seemingly large spiny creature in the perception of a stonefly. Small *E. subvaria* instars assumed a scorpion posture significantly less frequently in response to encounters with *A. lycorias*. The results are consistent with the interpretation that an increase in the apparent size of a small *Ephemerella* might cause it to appear as a preferred size for stonefly consumption. Iwao and Wellington (1970) describe a similar change in defensive behavior of the tent caterpillar from the fourth to the fifth instar upon predation by a pentatomid bug. As prey become larger and more conspicuous, they intensify their defensive behavior when attacked by a predator.

The effectiveness of altering apparent size to reduce predation by invertebrate tactile predators has been suggested by Dodson (1974*b*), Zaret (1975), O'Brien and Vinyard (1978), and O'Brien et al. (1979), for cyclomorphotic cladocerans, and Gilbert (1967, 1973) for cyclomorphotic rotifers. O'Brien et al. (1976) propose that vertebrate predators select prey by their apparent size rather than their real size.

The results of the contact experiments demonstrate differences among escape behaviors of the mayflies tested, which may clarify results of the noncontact chemical experiments. Since the *Ephemerella* species are not active escapers but display in response to stonefly predators, long-range chemoreception would be advantageous for these species. In many instances, the scorpion posture was observed to occur prior to physical contact with the predator. The stimulus producing this response could be chemical. The combination of chemical forewarning and display posture is not fail-safe, however, since predators may capture smaller nymphs which do not display. Also, predators approaching from downstream of the mayflies should have higher capture success than those approaching from upstream. This has interesting implications for successful search strategies of stream predators; one would expect predators to hunt upstream. High incidence of *E. subvaria* in *A. lycorias* stomachs may reflect predator preference and the fallibility of the scorpion display. Low frequency of consumption of *E. infrequens* may be due to lack of predator preference; or *M. signata* nymphs may only consume smaller *E. infrequens* nymphs (J. D. Allan, *personal communication*).

The high frequency of escape responses in addition to smaller size of the heptageniids, *H. hebe,* Otter Creek, and *Cinygmula* sp., East River, may be related to their lack of a long-range chemical avoidance response to stonefly predators, and their low frequencies in stonefly stomachs. However, the larger, more common, heptageniid, *S. fuscum* also appeared in relatively low numbers in *A. lycorias* stomachs. This may be due to long-range chemical detection of the predator which compensates for a lower frequency of locomotion response to contact. In late-instar *S. fuscum* nymphs, their very large size could create a prohibitive energetic cost of handling after capture. *Acroneuria lycorias* nymphs were observed to spend over 2 min consuming a *S. fuscum* as opposed to almost instantaneous consumption of *B. phoebus*.

In addition to being the smallest mayflies tested, the *Baetis* species were extremely fast swimmers. Upon contact with stoneflies both species showed the highest frequencies of evasion by locomotion. The only captures occurred when the predator cornered the prey rather than out-pursued it. The lack of experimental evidence for chemoreception in *B. phoebus* in Otter Creek may reflect the effectiveness of its evasion response upon close-range contact detection, or a lower predation pressure by *A. lycorias* due to its small size. *Baetis bicaudatus,* on the other hand, is more heavily preyed upon than any other mayfly species by all three stoneflies in the East River. The high probability that a stonefly might encounter this extremely common mayfly could explain its high incidence in stonefly stomachs, despite a high evasion frequency and response to noncontact chemical stimuli from stoneflies.

The differential responses by the East River mayflies to the three stoneflies provides additional information regarding the predator detection mechanisms used by each mayfly. If the mayflies can differentiate predators by chemoreception, their responses should differ consistently with the threat of consumption, regardless of the size differential among predators. If a tactile sense is used, the mayflies may avoid stoneflies differentially by size; or prey might react to all stoneflies of sizes greater than a certain threshold size which poses a threat of consumption.

Ephemerella infrequens showed an intensified display posture to *M. signata* and *K. modestus*, and the highest combination of freeze and display behavior to *M. signata*, the only stonefly which consumes it. These responses, consistent with the interpretation of the results of the noncontact chemical experiments, suggest that a contact-chemical or chemotactile mechanism is used by the mayflies to differentiate stoneflies.

Baetis bicaudatus, which avoided *M. signata* and the smaller *K. modestus* given noncontact chemical stimuli, also showed a significantly reduced response to contact with *P. badia* despite its larger size. A chemotactile differentiation of these three stoneflies is consistent with results of the noncontact chemical experiments. *Cinygmula* nymphs, which did not avoid the stoneflies without contact, avoided all three stoneflies upon contact regardless of size or threat of consumption. Since *Cinygmula* has been recovered in *M. signata* and *K. modestus* stomachs only, *K. modestus* could represent the threshold size for predator avoidance by *Cinygmula* nymphs using a tactile detection mechanism.

Change in activity of mayflies in the presence of stoneflies

If mayflies can detect the presence of stonefly predators given all available cues, their activity levels should change as a reflection of avoidance behavior. *Ephemerella subvaria* nymphs, usually active mayflies, reduced their level of activity in the presence of *A. lycorias* (Fig. 9), especially the frequency of crawling behavior. They also increased the frequency of scorpion postures in the presence of the predators. *Stenonema fuscum* and *B. phoebus*, relatively inactive species, increased their activity levels in the presence of *A. lycorias*. *Stenonema fuscum* crawled, and *B. phoebus* crawled and swam more frequently. Table 6 summarizes the statistical comparisons between mayfly activity levels before and during the presence of the stoneflies.

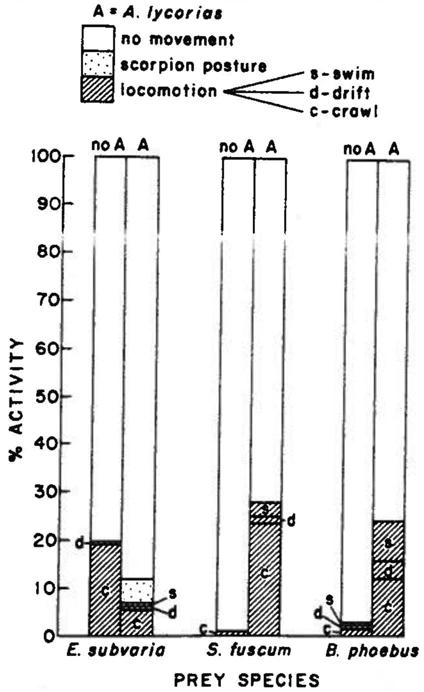

FIG. 9. Change in percent activity by mayflies before and during the presence of *A. lycorias*, Otter Creek.

In the presence of *K. modestus*, *E. infrequens*, like *E. subvaria*, became less active, reducing its frequency of crawling. It similarly increased the number of scorpion displays (Fig. 10). *Cinygmula* sp., like *S. fuscum* became more active, increasing the frequency of crawling behavior in the presence of *K. modestus*. *Baetis bicaudatus* did not alter its behavior pattern in the presence of *K. modestus*.

This experiment was originally suggested by a qualitative observation early in July, 1978, that given only

TABLE 6. Summary of statistical significance of change of activity of mayflies in the presence of stoneflies, Mann-Whitney U test. Asterisks refer to levels of significance. Blank squares indicate no significant difference. (+) = increase, (−) = decrease.

Predator	Prey	Total locomotion	Crawling	Swimming	Drifting	Scorpion
A. lycorias	*E. subvaria*	** (−)	** (−)			* (+)
	S. fuscum	*** (+)	*** (+)			
	B. phoebus	*** (+)	* (+)	* (+)		
K. modestus	*E. infrequens*	** (−)	* (−)			** (+)
	Cinygmula sp.	* (+)	* (+)			
	B. bicaudatus					

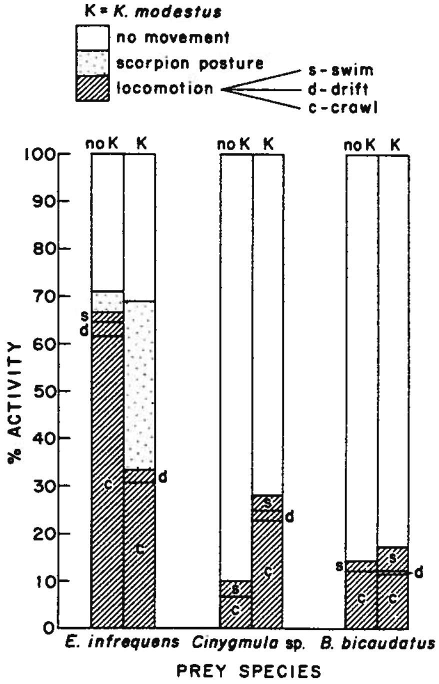

FIG. 10. Change in percent activity of mayflies before and during the presence of *K. modestus*, East River.

long-range chemical cues, *Baetis* nymphs became relatively inactive in the presence of *K. modestus*. However, the quantitative observations reported here were made during an emergence period of *B. bicaudatus* indicated by blackened wing pads and direct observations of emergences. Thus, the pattern recorded may not be indicative of behavior characteristic of this species during other phases of its development.

In summary, two of three pairs of species representing three families of mayflies in two streams, showed analogous behavioral alterations in the presence of free stonefly predators. Both *Ephemerella* species reduced their activity levels clinging to the substrate more often, and both Heptageniidae increased their crawling behavior. These activity changes have interesting implications regarding the energetic costs of predator avoidance.

CONCLUSIONS

The presence of a stonefly predator within an observation box in streams has considerable influence upon the distribution, behavior, and activity levels of mayfly prey. Mechanisms of mayflies used for detection of stonefly predators probably include noncontact chemoreception, close-range contact chemoreception, and mechanoreception. Later instars of some mayflies respond to predator detection by freezing and assuming a posture which may increase their apparent size and cause them to be rejected by stonefly predators. Other mayflies evade capture by stoneflies by the locomotory behaviors of crawling, swimming, drift-swimming, or drifting away from the predator. This behavior may be part of the complex set of interactions involved in the diel periodicity and relative abundances of invertebrates in the drift.

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