

Mayfly cerci as defense against stonefly predation: deflection and detection

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In situ behavioral experiments were conducted in flow-through observation boxes in a Colorado and a New York stream to compare and contrast the cercal responses of Ephemerellidae and Baetidae mayflies to predaceous stoneflies. *Ephemerella infrequens* (Colorado) exhibited primarily a “scorpion” posture when touched by stoneflies. This posture was stimulated by the touch of any body part of an intact stonefly (antenna, mouthpart, leg, cercus), with some variation in frequency depending on the stonefly, and occurred more often when a mayfly was touched dorsally than on anterior, posterior or lateral body aspects. Scorpion posturing sometimes occurred without physical contact between predators and prey, usually when predators approached *Ephemerella* from upstream. With increasing size, both *E. infrequens* (Colorado) and *E. invaria* (New York) increased the frequency of scorpion posture responses to stoneflies. Very few *Ephemerella* were consumed by stoneflies during the experiments. Alternatively, the baetid mayfly, *Baetis bicaudatus* (Colorado) exhibited a “tail curl” posture during which cerci and posterior abdominal segments were flexed laterally in the direction of actively foraging predators. This response always occurred before touch by the stoneflies and usually when predators passed beside the mayflies rather than approached directly from upstream or downstream. Tail curl responses were followed by active swimming, drifting, or crawling by *Baetis* – behavior that prevented touch encounters between predators or prey. Thus, no *Baetis* were consumed after a tail curl response. I speculate that while the use of cerci by *Ephemerella* deflects stoneflies, cerci are used by *B. bicaudatus* to detect water wave disturbances produced by foraging stoneflies, enabling the prey to avoid predator encounters and thereby reduce the risk of predation.

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Introduction

Edmunds (1974) identified two major types of anti-predator defenses in animals. Primary defenses occur regardless of the vicinity of predator to decrease the chances of predator-prey encounters. Examples are cryptic or warning (aposematic) coloration. Secondary defenses operate during encounters with predators to increase the prey's chances of surviving such encounters. They may be passive, requiring no energy consumption on the part of the prey, such as the possession of spines or bad taste, or they may be active, as are behavioral defensive responses such as withdrawal or flight behavior and deimatic behavior.

Deimatic behavior is defined as a characteristic posture or display that startles or frightens the predator, warning that the prey is unpalatable or armed. Such behavior may also act as a “bluff” that deceives the predator (Batesian mimicry) long enough for the prey to escape being eaten. Deimatic behaviors have been reported to occur in terrestrial insects (Crane 1952), crustaceans (Stein and Magnuson 1976, Hayes 1977), molluscs (Townsend and McCarthy 1980), and aquatic insects (Peckarsky 1980).

The “scorpion” posture (Fig. 1) reported to occur for two species of *Ephemerella* (Peckarsky 1980) has now been observed by additional authors for other species of Ephemerellidae in response to interactions with pre-

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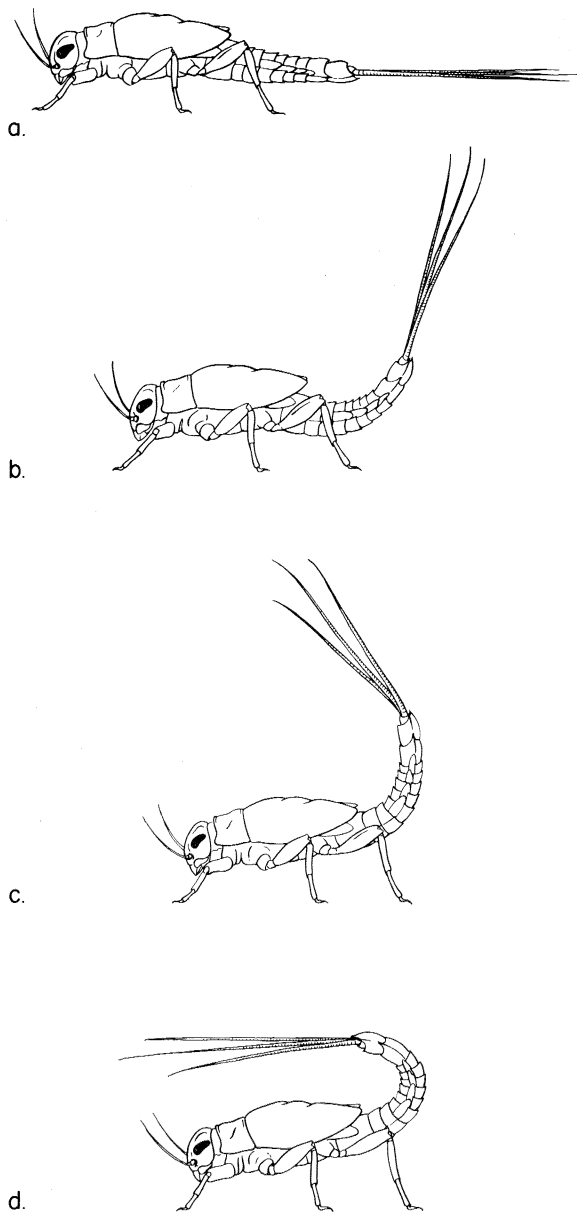


Fig. 1. *Ephemerella subvaria*. a. normal posture, b. low intensity, c. medium intensity and d. high intensity scorpion posture. (From Peckarsky 1980. The figure is published by courtesy of the Ecological Society of America.)

dators (Kratz 1983, Molles and Pietruszka 1983). A similar posture has also been observed in some stoneflies in response to disturbance by predators, competitors, or observers (Kondratieff and Kirchner 1982, Otto and Sjöström 1983, Peckarsky and Penton 1985). The mechanism by which the mayfly "scorpion" posture deters attackers has not been documented, but a hypothesis put forth by Peckarsky (1980) is that it alters the apparent size and shape of the mayfly prey species

to foil a tactile predator upon touch encounter. Further, the posture emphasizes the spiny, heavily sclerotized form of *Ephemerella* spp.

I have observed other softer-bodied mayflies use their cerci in response to the presence of stonefly predators. *Baetis bicaudatus* laterally flex their abdomens and point their cerci toward passing stoneflies (Fig. 2). Preliminary observations of this "tail curl" response suggested that it allowed *Baetis* to detect water wave disturbances generated by predators before encounter. Other investigators have shown that insect caudal cerci contain receptors effective in detecting air currents created by approaching predators (Camhi 1980).

The objective of this study was to compare and contrast the cercal responses of these two mayfly groups to test the hypothesis that the spiny, hard-bodied mayflies use cerci for deflection, whereas the smooth, softer-bodied mayfly uses cerci for detection of predaceous stoneflies. Specific questions addressed by experiments reported here are:

Deflection by scorpion posture (*Ephemerella*):

- 1) Does the response occur without touch by the predator?
- 2) Does the frequency of the response depend on the part of the predator's anatomy contacting the prey?
- 3) Does the frequency of the response depend on the part of the prey's anatomy touched?
- 4) Does the frequency of the response depend on the size of the prey individuals?
- 5) Are prey consumed less frequently when they posture?

Detection by tail curl (*Baetis*):

- 1) Is the response directed toward predators more often than in directions not related to the proximity of a stonefly?
- 2) Does the response occur without touch by the predator?
- 3) Does the frequency of response depend upon the direction of predator approach?
- 4) What prey responses follow the tail curl posture?
- 5) Are prey consumed less frequently when they tail curl?

Materials and methods

Apparatus and sites of experiments

Experiments were carried out in plexiglass flow-through observation boxes of a design illustrated in Peckarsky (1984). These boxes were placed in a shallow riffle section of the East River, Gunnison County, Colorado (described in Peckarsky 1979) at a water depth of 5 cm. Placement sites were chosen so that water flow through boxes was laminar and standardized at a speed allowing experimental insects to maintain hold of the substrate ($15\text{--}20\text{ cm s}^{-1}$, determined by timing the flow of a dye

through the boxes). All observations were made in the morning beginning at 0900 AM, Mountain Daylight Time), sometimes carrying over until early afternoon of summers 1980–1982. One experiment was also conducted in spring 1981 and 1982 at Six Mile Creek, Tompkins County, New York (see Bukantis 1983 for description of this stream).

Experimental species

The mayfly species tested were *Ephemerella infrequens* (East River), *E. invaria* (Six Mile Creek), and *Baetis bicaudatus* (East River). Both Ephemerellidae have relatively heavily sclerotized exoskeletons, lateral spines on posterior abdominal segments, and numerous long intersegmental spines on their cerci. They are characteris-

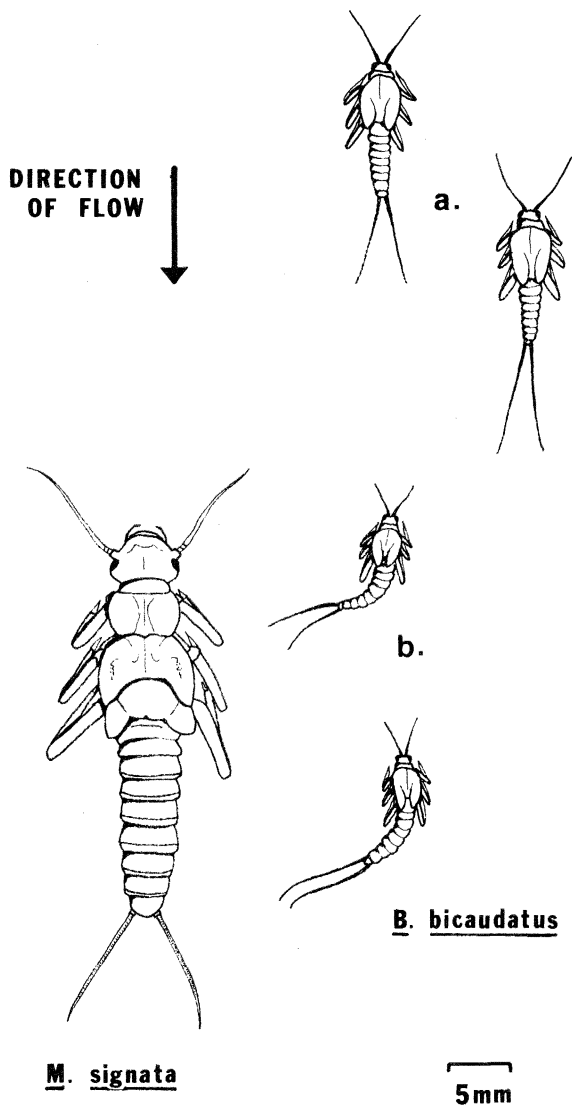


Fig. 2. *Baetis bicaudatus*. a. normal posture; b. tail curl posture, with *M. signata*.

Tab. 1. Summary of recorded responses of mayflies to a foraging stonefly during a 10-min observation session.

A. *Ephemerella*

- 1) Responses to touch by a predaceous stonefly
 - a. Mayfly behavior [move (crawl, swim, drift), freeze (remain stationary), or scorpion (posture)]
 - b. Predator body part first touching mayfly [antennae, head (mouthparts), legs, or cerci]
 - c. Prey body part first touched [anterior, posterior, dorsal, or lateral]
- 2) Responses to close proximity without touch of a predaceous stonefly
 - a. Frequency of scorpion responses
 - b. Direction of predator approach with respect to current [upstream, downstream, or beside]
- 3) Attacks and consumption by predator

B. *Baetis*

- 1) Responses to touch by a predaceous stonefly
 - a. Mayfly behavior (move, freeze, tail curl)
- 2) Responses to close proximity of a predaceous stonefly without touch
 - a. Frequency of tail curl response [tail curl or no tail curl]
 - b. Direction of tail curl response with respect to predator [toward predator, away from predator, or spontaneous (predator not in close proximity)]
 - c. Direction of predator approach with respect to current [upstream, downstream, or beside]
 - d. Mayfly responses following tail curl behavior [crawl, swim, drift, or remain stationary]
- 3) Attacks and consumption by predator

tically slow crawlers and swimmers with slightly elongate, slightly dorsoventrally flattened body shapes (Edmunds et al. 1976). *Baetis bicaudatus*, on the other hand, has the typically cylindrical body form of the Baetidae, with weak sclerotization of the exoskeleton, and no spines or other body armor (Edmunds et al. 1976). Unlike *Ephemerella*, its cerci have numerous sensory receptors, morphologically similar to the receptors on their antennae (Martinez, unpubl., Peckarsky 1979). Baetids are very fast swimmers compared with ephemerellids.

Mayfly behavior was observed in response to predatory Perlodidae, *Megarcys signata*, and *Kogotus modestus*, and omnivorous Pteronarcidae, *Pteronarcella badia* in the East River; in Six Mile Creek mayfly responses to predatory Perlidae, *Acroneuria carolinensis*, and *Agnatina capitata* were observed. The hunting behavior of all of these stoneflies is similar (Peckarsky and Penton 1985). All stoneflies have been observed to consume *Baetis* predominantly, with occasional consumption of *Ephemerella* (Peckarsky 1985).

Responses of the largest individuals present of each mayfly prey species to subterminal instars of the stoneflies were observed. Sizes (head capsule width) of predators ranged from: *Megarcys*: 3.01 to 4.90 mm, $n = 22$; *Kogotus*: 1.96 to 3.12 mm, $n = 23$; *Pteronarcella*: 2.40 to 3.12 mm, $n = 27$; *Acroneuria*: 3.83 to 5.87 mm, $n = 12$; *Agnatina*: 2.84 to 5.08 mm, $n = 12$. Prey sizes (mean head capsule width \pm 1 s. d. of 15 per replicate) ranged from 1.31 ± 0.03 to 1.77 ± 0.08 (*E. infrequens*, $n =$

189), 0.97 ± 0.06 to 1.23 ± 0.09 mm (*Baetis*, $n = 189$), and 1.05 ± 0.20 to 1.83 ± 0.16 mm (*E. invaria*, $n = 60$).

Experimental design

For studies involving Ephemerellidae, 15 individuals of *Ephemerella* were collected from the stream and allowed to acclimate for at least 15 min in observation boxes, after which one stonefly, also collected from the stream, was added to the box. Once the stonefly began to crawl (generally from zero to 10 min), responses of the mayflies shown in Tab. 1A were recorded for 10 min. Since observers were not able to record all aspects of the prey responses in single 10-min observation periods, mayfly responses to stonefly touches by different predator parts, prey parts touched, direction of predator approach, and resultant scorpion responses to touch or no touch were each recorded during separate trials with the same individual predator.

Observations were made during 1980 to 1982 in the East River, Colorado during June and July between *Megarcyus* or *Pteronarcella* and *Ephemerella infrequens* and in late July between *Kogotus* and *E. infrequens*. Interactions between the Six Mile Creek, New York perils and *E. invaria* were observed in 1981 and 1982 during February through May. Only responses 1a and 3 (Tab. 1A) were recorded for these species.

Similarly, for studies involving Baetidae, 15 *Baetis bicaudatus* individuals collected in the East River were allowed to acclimate for at least 15 min in observation boxes. A stonefly was then added and information shown in Tab. 1B was recorded during 10-min trials.

Tab. 2. Mean frequency (%) \pm s.e. of the responses of *E. infrequens* to the East River stoneflies. Percentages underscored (–) indicate no significant differences between responses to different stoneflies (Mann-Whitney U Test). N = number of 10-min observation periods. Enc = number of stonefly-mayfly encounters.

	<i>Megarcyus</i>	<i>Kogotus</i>	<i>Pteronarcella</i>
Scorpion	<u>49 \pm 3</u>	<u>50 \pm 9</u>	44 \pm 2
Freeze	<u>28 \pm 3</u>	11 \pm 1	<u>22 \pm 2</u>
Move	20 \pm 3	<u>39 \pm 2</u>	<u>35 \pm 7</u>
N	25	28	28
Enc	1,518	1,607	1,678

Again, observers were limited to recording one or two aspects of the interactions per trial. Trials with *Megarcyus*, *Pteronarcella*, and *Kogotus* as predators were conducted during the same time periods as given above.

After each set of 10-min trials, all mayflies and stoneflies were preserved in 70% EtOH for size determination.

Nonparametric statistical tests were used to analyze the data on mayfly responses. Paired tests were used as noted in the results section where behavioral comparisons of the same group of mayflies were made. When multiple comparisons were made, null hypotheses were rejected at reduced alpha levels to correct for experiment-wise error ($\alpha = 0.05 n^{-1}$, where n = number of experiment-wise comparisons, Bonferroni's Inequality, Snedecor and Cochran 1980).

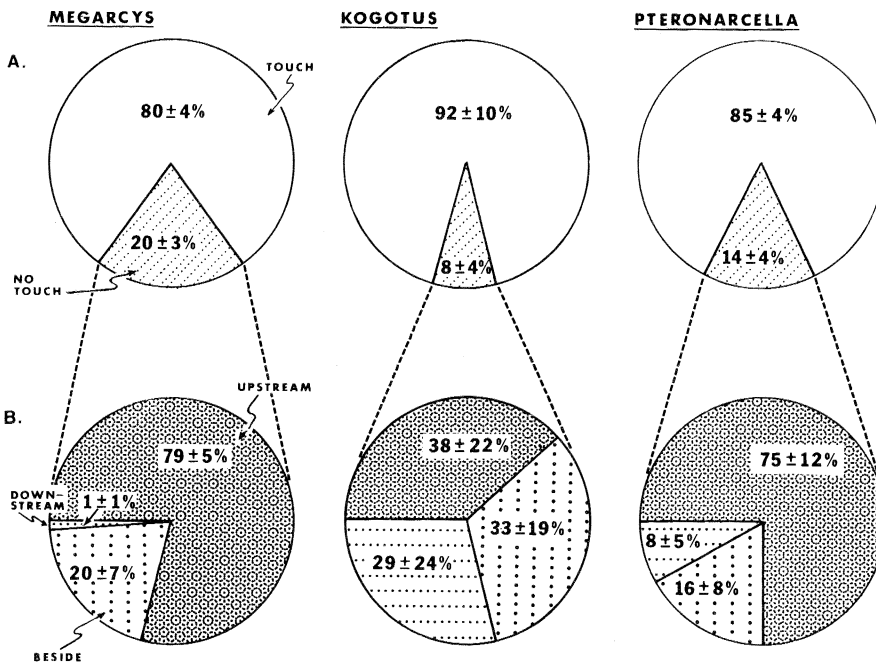


Fig. 3A: Percent of *E. infrequens* total scorpion responses ($\bar{X} \pm$ s.e.) that occurred with and without tactile contact by the predators. Means are based on 20, 13, and 14 replicate 10-min trials with 535, 266, and 239 total scorpion responses to *Megarcyus*, *Kogotus*, and *Pteronarcella*, respectively. B: Percent of scorpion postures ($\bar{X} \pm$ s.e.) that occurred without tactile contact by predators approaching from upstream, downstream, and beside *E. infrequens*. Means are based on 16, 4, and 8 replicate 10-min observation periods with 113, 15, and 38 total scorpion responses for *M. signata*, *K. modestus*, and *P. badia*, respectively.

Results

Ephemerella scorpion posture

Analysis of *Ephemerella* scorpion responses to touch by East River stoneflies showed that, as in Peckarsky (1980), the frequency of the posture was significantly higher during encounters with the predaceous perlodids than with the omnivore. The mayfly also "froze" more frequently in response to the larger stoneflies than to *Kogotus* and moved less frequently in response to encounters with *Megaracys* than with either *Kogotus* or *Pteronarcella* (Tab. 2, Mann-Whitney U-tests).

Scorpion postures occurred most often in response to touches by the stoneflies, but the behavior occasionally occurred when there was no touch by predators usually within one cm of *Ephemerella* (Fig. 3A), with a significantly greater response to *Megaracys* than to the other stoneflies (Mann-Whitney U test). For *Megaracys* and *Pteronarcella* the frequency of scorpion responses to no touch was significantly higher when the predators approached from upstream than from downstream or beside the prey (Fig. 3B). No such difference was observed for *Kogotus*. This result shows that noncontact responses to some predators by prey are greater when predators are upstream of prey.

Chi squared analysis was used to determine whether the frequency of the scorpion, movement, and stationary responses was independent of the predator body part touching *Ephemerella*. (Expected values were calculated as the product of the marginal totals divided by the total number of observations for all χ^2 tables.) Results showed that, for *Megaracys*, the frequency of scorpion, freezing and moving responses was independent of the part of the predator contacting *Ephemerella* ($\chi^2 = 7.20, 6$ df). However, touches by different body parts of *Kogotus* and *Pteronarcella* produced frequencies of the three measured responses that differed from random ($\chi^2 = 33.07, 14.08$ respectively, 6 df, $p < 0.05$, Tab. 3).

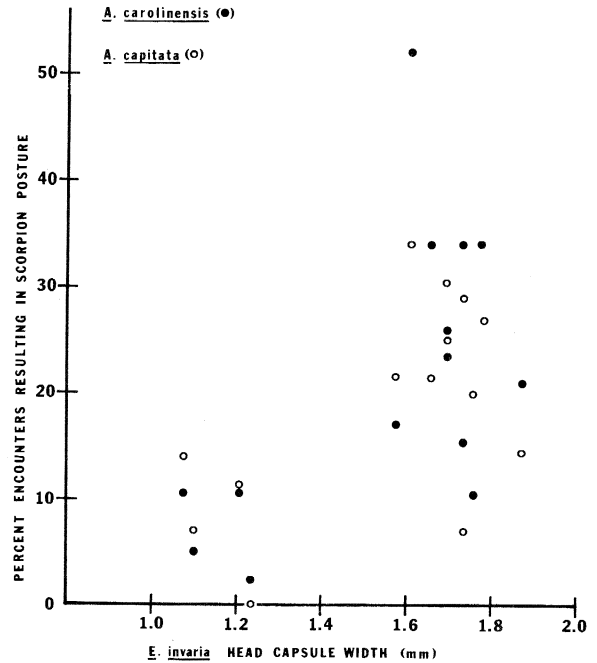


Fig. 4. Percent scorpion postures by different sizes of *Ephemerella invaria* in response to encounters with *Acroneuria carolinensis* and *Agetina capitata* (Six Mile Creek).

Ephemerella scorpioned more often than expected in response to touches by *Kogotus* mouthparts (head), and less often than expected when touched by *Kogotus* or *Pteronarcella* cerci. All stoneflies touched *Ephemerella* most often with their antennae, then legs, with only occasional touches with heads (mouthparts) and cerci (Mann-Whitney U test, Tab. 3).

Similar analysis of the responses of *E. infrequens* to touches by the predators of its particular body parts showed that the frequency of scorpion responses was

Tab. 3. Observed (and expected) total number of scorpion (Ø), stationary (O), and movement (M) responses to touches by predator antennae (A), legs (L), heads or mouthparts (H), or cerci (C). N = number of encounters between *E. infrequens* and each body part of the three East River stoneflies. Numbers underscored (–) indicate no significant difference between frequencies of prey encounters by different predator body parts [Mann-Whitney U test on 13 (*Megaracys*, *Pteronarcella*) and 14 (*Kogotus*) predators during 10-min observation periods].

	<i>Megaracys</i>				<i>Kogotus</i>				<i>Pteronarcella</i>			
	A	L	H	C	A	L	H	C	A	L	H	C
Ø	148 (148)	96 (99)	22 (19)	31 (31)	209 (210)	72 (72)	30 (22)	6 (13)	214 (204)	47 (51)	13 (14)	11 (16)
O	69 (78)	61 (52)	11 (10)	15 (16)	46 (61)	35 (21)	4 (6)	7 (4)	95 (110)	36 (27)	7 (7)	16 (9)
M	77 (68)	39 (46)	5 (9)	16 (14)	163 (146)	35 (50)	10 (15)	12 (9)	190 (184)	41 (46)	13 (12)	13 (15)
N	294	196	<u>38</u>	<u>62</u>	418	142	<u>44</u>	<u>25</u>	499	124	<u>33</u>	<u>13</u>
	$\chi^2 = 7.20, 6$ df n.s.				$\chi^2 = 33.07, 6$ df ($p < 0.05$)				$\chi^2 = 14.08, 6$ df ($p < 0.05$)			

Tab. 4. Observed (and expected) total number of scorpion (Ø), stationary (O), and movement (M) responses to touches by the three East River stoneflies to *E. infrequens* posterior (P), anterior (A), dorsal (D), and lateral (L) body aspects. N = total number of encounters. Numbers underscored (–) indicate no significant difference between frequencies of predator encounters of different prey body parts [Mann-Whitney U Test on 13 (*Megarcys* and *Kogotus*) and 16 (*Pteronarcella*) predators during 10-min observation periods].

	<i>Megarcys</i>				<i>Kogotus</i>				<i>Pteronarcella</i>			
	P	A	D	L	P	A	D	L	P	A	D	L
Ø	100 (87)	79 (74)	104 (108)	42 (47)	93 (106)	47 (52)	108 (82)	56 (64)	102 (112)	64 (65)	82 (66)	46 (52)
O	27 (44)	43 (38)	66 (55)	25 (24)	16 (26)	17 (12)	16 (20)	24 (15)	45 (54)	37 (32)	37 (32)	24 (25)
M	43 (59)	31 (33)	41 (48)	25 (21)	91 (68)	33 (33)	31 (53)	41 (41)	112 (93)	49 (54)	33 (55)	51 (44)
N	170	144	211	92	200	97	155	121	249	150	152	121

$\chi^2 = 15.01, 6 \text{ df}$ ($p < 0.05$)	$\chi^2 = 38.50, 6 \text{ df}$ ($p < 0.05$)	$\chi^2 = 23.34, 6 \text{ df}$ ($p < 0.05$)
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significantly dependent on the mayfly body part contacted by each of the stoneflies ($\chi^2 = 15.01$, *Megarcys*; $\chi^2 = 38.50$, *Kogotus*, and $\chi^2 = 23.34$, *Pteronarcella*; 6 df, $p < 0.05$, Tab. 4). Deviations of observed from expected frequencies of responses to the predators showed that *Ephemerella* was more likely to move and less likely to scorpion or freeze when touched posteriorly (except by *Megarcys*) and more likely to scorpion (except with *Megarcys*) and less likely to move when touched dorsally. *Megarcys* touched the mayflies' anterior, posterior, and dorsal aspects more often than lateral. *Kogotus* and *Pteronarcella*, on the other hand, touched *E.*

infrequens posteriorly more often than the other three body aspects (Mann-Whitney U test, Tab. 4).

Large *E. invaria* (Six Mile Creek) showed higher frequencies of scorpion responses than small ones to both predators tested (Fig. 4; significant Spearman Rank Correlation Coefficients: $R_s = 0.584, 0.577, N = 14$ for *E. invaria* vs. *A. carolinensis* and *A. capitata*, respectively). A heightened scorpion behavior with increasing size of individuals of *E. infrequens* was significant in response to only *M. signata* in the East River observation boxes ($R_s = 0.552, 0.399, -0.113, N = 24$ vs. *M. signata*, *P. badia*, and *K. modestus*, respectively).

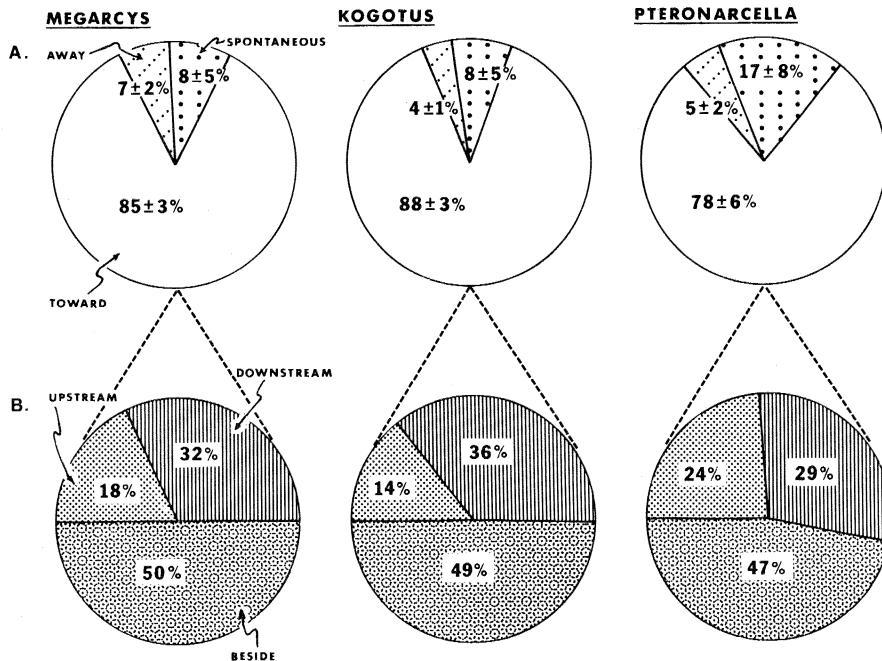


Fig. 5. A: Percent of total *Baetis bicaudatus* tail curl responses directed toward, away from passing predators, and spontaneously (without proximity to predators) ($\bar{X} \pm \text{s.e.}$). Data based on 386, 291, and 302 total responses to *Megarcys*, *Kogotus*, and *Pteronarcella*, respectively. B: Percent of total tail curl responses occurring toward a predator passing upstream, downstream, or beside *B. bicaudatus*. Data based on 491, 344, and 466 total tail curls toward *Megarcys*, *Kogotus*, and *Pteronarcella*, respectively.

Tab. 5. Frequency of tail curl and no tail curl responses when predators passed within 2 cm of *B. bicaudatus* from upstream, downstream, or beside.

	Upstream		Downstream		Beside	
	tail curl	no tail curl	tail curl	no tail curl	tail curl	no tail curl
<i>Megarcys</i>	22	23	57	30	80	61
<i>Kogotus</i>	26	23	60	11	83	34
<i>Pteronarcella</i>	34	34	62	33	75	64
	$\chi^2 = 0.18, 2 \text{ df}$ n.s.		$\chi^2 = 9.03, 2 \text{ df}$ ($p < 0.05$)		$\chi^2 = 8.57, 2 \text{ df}$ ($p < 0.05$)	

Although remains of *Ephemerella* have been found occasionally in stonefly stomachs, in 1,110 min of observations over three summers with 4,803 recorded encounters between *E. infrequens* and three East River stoneflies, only three attacks were observed (two by *Megarcys* and one by *Kogotus*). In each of these encounters the mayfly assumed a scorpion posture, which immediately caused the stoneflies to give up attempted consumption. Similarly, only one *E. invaria* was attacked and eaten by *A. capitata* in Six Mile Creek trials during 140 min of observation among 838 encounters. Four others were attacked and not eaten by the same predator, and one unsuccessful attack by *A. carolinensis* was also observed. The mayfly that was consumed did not scorpion in response to encounter by the predator. In contrast, of the five individuals not consumed after attack, three scorpioned, one crawled, and one drifted from encounters with the stoneflies.

Baetis tail curl

Baetis bicaudatus (East River) showed a significant tendency to turn their cerci toward all three stonefly species rather than away from them or in a direction not related to the location of a predator (predators not within 2–3 cm) (Fig. 5A, Wilcoxon Sign Rank Test). This result suggests that the tail curl is oriented toward an approaching predator and is not merely a response to current or other abiotic factors. In contrast to *Ephemerella* scorpion posturing, *Baetis* tail curl behavior never

occurred after touches by predators, but always before the predator physically encountered the prey. The frequency of total tail curl behaviors was highest when predators passed longitudinally (with respect to current) beside the mayfly rather than perpendicularly upstream or downstream of *Baetis* (beside > downstream > upstream for all three predators, Wilcoxon Sign Rank Test, Fig. 5B). The probability of a predator stimulating a tail curl response in *Baetis* was also dependent upon the direction of predator approach. *Baetis* was more likely than not to respond by tail curl when a stonefly passed downstream or beside ($\chi^2 = 9.03, 8.57$, respectively, 2 df, $p < 0.05$), but responded about 50% of the time when predators approached from upstream ($\chi^2 = 0.18, 2 \text{ df}$, distribution not differing from random (Tab. 5).

Following a tail curl response, the mayflies most often moved (crawled, swam, or drifted) from the vicinity of the predator, with swim and drift behavior most prominent (Fig. 6, Wilcoxon Sign Rank Test). Note that crawling behavior, the slowest, and least effective means of escape from stoneflies, was practically non-existent in response to *K. modestus*.

Finally, the frequency of movement responses (crawl, swim or drift) by *B. bicaudatus* to the presence of the predator was similar regardless of whether *Megarcys* actually touched the mayflies; *Baetis* moved more often than expected when touched by *Pteronarcella* and more often when not touched by *Kogotus* ($\chi^2 = 26.25, 2 \text{ df}$ $p < 0.05$, Tab. 6)

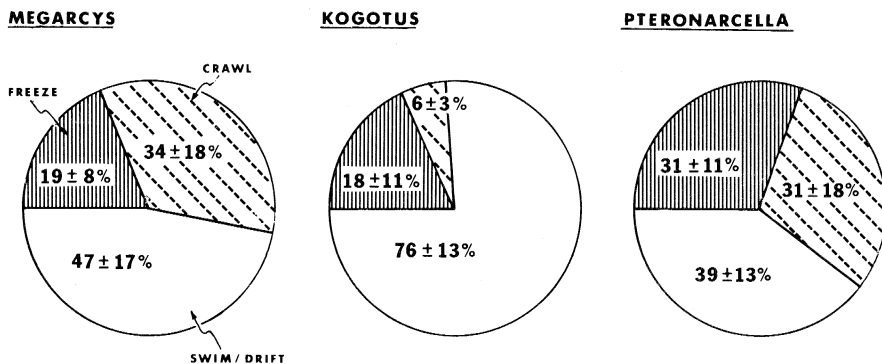


Fig. 6. Percent freeze, crawl, and swim-drifting behavior following tail curl by *B. bicaudatus* toward the three predators. Data based on 67, 123, and 93 tail curls toward *Megarcys*, *Kogotus*, and *Pteronarcella*, respectively.

Tab. 6. Frequency of movement responses (crawl, swim, or drift) by *B. bicaudatus* after touch or no touch by the stoneflies.

	Touch	No touch
<i>Megarcys</i>	76	81
<i>Kogotus</i>	31	71
<i>Pteronarcella</i>	75	40

$\chi^2 = 26.25, 2 \text{ df}$
($p < 0.05$)

In contrast to *Ephemerella*, 29 *Baetis* were attacked by *Megarcys*, and 12 individuals were consumed partially or entirely during 290 min of observation. *Pteronarcella* attacked 9 *Baetis* with 7 complete or partial consumptions in 260 min of observation. *Kogotus* attacked 20 *Baetis*, consuming 13 in 260 min. All of these attacks and consumptions followed touch encounters not preceded by tail curl responses. Thus, tail curl responses followed by swimming, drifting, or crawling from predators without touch encounter significantly reduced the risk of predation by stoneflies.

Discussion

The results of these experiments suggest that one use of cerci by these two species of mayflies was as defense against predation from stoneflies. However, the mechanisms for their effectiveness were entirely different. I speculate that the scorpion response exhibited by Ephemerellidae exposes the tip of the abdomen plus the cerci as a warning behavior against predaceous stoneflies; whereas the baetid tested appeared to use cerci as sensory structures to detect passing predators and thereby avoid physical encounters.

Casual observation may suggest that the scorpion posture is a generalized stress response in Ephemerellidae. In fact, many naturalists probably notice that ephemerellids scorpion in response to touch by forceps or human fingers. However, the frequency of scorpion responses was variable with touches by different predator parts and body part of prey touched (Tab 3, 4). *Ephemerella infrequens* tended to scorpion more often when touched by predator mouthparts or dorsally, and less often when touched by predator cerci. They also tended to move more often when touched posteriorly.

The frequency of these responses was also variable to different stonefly species. *Megarcys*, the largest predator, representing the greatest risk of predation, stimulated more scorpion responses than the large omnivore, and caused *Ephemerella* to scorpion without touch more often than either of the other two stoneflies. The frequency of scorpion responses to *Megarcys* was also independent of the body part of the predator touching the prey, and significantly increased with *Ephemerella* size. *Kogotus*, the smaller predator, also elicited more

scorpion responses than the omnivore, with a heightened mayfly reaction to touches by stone fly mouthparts. *Pteronarcella*, representing the lowest predation risk, produced the least scorpion responses by *Ephemerella*.

Although most scorpion postures occurred after a stonefly touched *Ephemerella*, as high as 20% occurrence of the behavior without predator touch is noteworthy (Fig. 3). For *Megarcys* and *Pteronarcella*, postures were assumed as the predator approached from upstream, which implicates the use of chemical cues by *Ephemerella* to detect the stoneflies. However, these experiments do not rule out the use of vision by mayflies as a cue stimulating the response. Peckarsky (1980) showed that *E. infrequens* responded by avoidance only to *M. signata* (not to *P. badia* or *K. modestus*) in experiments providing only chemical cues (i.e., preventing visual interaction between predators and prey). Whatever the cues used, assuming a scorpion posture before touch encounter with stoneflies should improve its effectiveness in deflecting or intimidating predators. In fact, most noncontact scorpion postures occurred in the vicinity of the largest predator (*Megarcys*) where the risk of being consumed was highest.

The observation that larger *Ephemerella* scorpion more often than smaller to encounters with stoneflies suggests that the posture increased the apparent size of the mayflies, and that posturing by small *Ephemerella* nymphs had less influence on their vulnerability to predation. Other studies have shown that threatening behavior increased in larger lepidopteran and decapod prey individuals (Iwao and Wellington 1970, Robinson et al. 1970).

The behavior of stoneflies during encounters with *Ephemerella* is both interesting and puzzling. When these mayflies posture, stoneflies appear repulsed by the encounter. They either back off, go around, or continue to crawl over the dorsum of the mayflies. The vertically extended spiny cerci act as a mechanical or "punishing" defense, making capture by the stoneflies very difficult. The posture also enhances the efficacy of the abdominal spines of *Ephemerella*. Thus, the mechanism proposed here for the effectiveness of this posture is similar to that of stonefly cerci exhibited in response to yearling brown trout predators (Otto and Sjöström 1983).

The puzzling aspect of stonefly behavior is that they do not readily attack even *Ephemerella* that do not scorpion. Although they are not visibly repulsed by encounters with *Ephemerella* in normal posture, the stoneflies usually show no interest in these mayflies, in contrast to their behavior with *Baetis*. This behavior suggests that *Ephemerella* has other mechanisms of defense in addition to the scorpion posture, but does not necessarily negate the effectiveness of the cerci in preventing attacks by stoneflies. Possible alternative defenses are exoskeletons difficult to penetrate or that *Ephemerella* was distasteful to stoneflies. In fact, the exoskeleton of

E. infrequens is covered with a thick coating of organic debris and microbial growth (Martínez, unpublished scanning electron micrographs) that may contain substances distasteful to predators. However, *Ephemerella* does appear in the stomachs of these predators (though rarely), and others have reported high rates of consumption of *Ephemerella altana* by predaceous stoneflies after long periods of starvation (6 d) (Molles and Pietruszka 1983).

In contrast to *Ephemerella* cerci, the cerci of *Baetis bicaudatus* are clearly not defensive weapons. Instead, behavioral and morphological evidence suggest that one of their functions is predator detection probably by water wave disturbances since the response is least common when predators approach *Baetis* from upstream and most common to predators crawling beside *Baetis*. Since *Baetis* usually orient facing upstream (Fig. 2), the cerci would be most effective in detecting predator-generated water waves as predators crawl past *Baetis* starting from downstream or beside prey. Others have reported similar sensory capacity in aquatic invertebrates. *Chaoborus* (the phantom midge larva), *Notonecta* (the backswimmer), *Plectrocnemia* (a net-spinning predatory caddisfly), and planktonic copepods locate prey with receptors sensitive to wave disturbances (Murphey and Mendenhall 1973, Strickler 1975, Tachet 1977, Giguère and Dill 1979, Lang 1980, Winner and Greber 1980). Moreover, Eastham (1936) reported that mayfly gills have receptors capable of detecting vibrations. Other aquatic invertebrates sensitive to water-borne vibrations include crayfish (Tautz and Sandeman 1980) and polychaetes (Townsend 1939).

The tail curl posture in *Baetis* occurred as a similar response to all three species of stoneflies despite the fact that *Pteronarcella* consumes fewer prey than do the perlotids. The behavior allowed the mayfly to avoid encounters with stoneflies, thereby significantly decreasing their risk of predation. In the present study, mayflies predominantly swam or drifted from the predators, although the frequency of their remaining stationary was generally higher following a tail curl (Fig. 6) than following a touch encounter with stoneflies (Peckarsky 1980). Also, the frequency of crawling, a behavior that resulted in a relatively slight readjustment of position as compared with transport by swimming or drifting, was higher following tail curl responses to *Megarcys* and *Pteronarcella* (Fig. 6) than following touch encounters (Peckarsky 1980). This more conservative movement pattern should minimize the risk of *Baetis* exposure to visual (fish) predators or being transported from a favorable feeding patch without increasing the risk of consumption by stoneflies.

Corkum and Clifford (1981) concluded that mayfly caudal filaments were not effective in deterring stonefly predators. However, their laboratory experiments showed that in daylight a perlotid predator consumed significantly more *Baetis* with excised caudal filaments than intact *Baetis*. Also, they found no difference be-

tween consumption by a predaceous perlotid of *Baetis bicaudatus* and *B. tricaudatus* in field experiments. Since both mayfly species had intact caudal filaments, two and three respectively, this result does not rule out the possibility of sensory rather than deflective use of cerci in predator avoidance.

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