

Why do *Ephemerella* nymphs scorpion posture: a “ghost of predation past”?

Barbara L. Peckarsky and Marjory A. Penton

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The behavior of intact *Ephemerella infrequens* (Ephemeroptera, Ephemerellidae) and *Ephemerella* with cerci amputated was observed in response to encounters with live predaceous stoneflies (*Megarcys signata*, Plecoptera: Perlodidae), tethered-live and tethered-model predators, freshly excised stonefly antennae, and thin wires. The incidences of defensive posturing (scorpion posture), movement (crawl, swim, drift) and freezing (no response, stop) behavior were video-taped in response to these predatory stimuli. Scorpion postures occurred with significantly higher frequency when *Ephemerella* was touched by live and model *Megarcys* than by *Megarcys* antennae and wires, with no differences between the two former or the two latter treatments. Frequency of posturing was not altered by prey orientation toward or away from predators or by direction of predator approach with respect to current (upstream, downstream, or beside prey). Thus, hydrodynamic cues associated with live and model *Megarcys* rather than simple tactile, chemical or visual cues are probably most important in stimulating *Ephemerella* to scorpion posture. Removal of *Ephemerella* cerci resulted in a decreased incidence of scorpion posturing, and modification of frequencies of movement and freezing behaviors with predator-prey orientation. These results suggest that cerciless mayflies may have impaired or altered sensory systems. However, cercal removal did not increase *Ephemerella*'s risk of predation, since numbers of intact and cerciless prey consumed during predation trials did not differ. Gut content analysis of *Megarcys* showed that they were size selective on smaller *Ephemerella*, which are known to scorpion posture with significantly lower frequency than large *Ephemerella*. We speculate that the posture is an evolutionary relict, a “ghost of predation past,” that is not as effective in smaller individuals, which are also softer-bodied and have smaller spines. Present-day preference for small *Ephemerella* or other mayfly species over large *Ephemerella* may be attributed to the historical effectiveness of the scorpion posture, long prey handling times, difficulty in prey capture, or absence of an appropriate behavioral attack stimulus. None of these factors was affected by removal of cerci.

B. L. Peckarsky, Dept of Entomology, Cornell Univ., Ithaca, NY 14853, USA, and Rocky Mountain Biological Laboratory, Crested Butte, Co 81224, USA. M. A. Penton, Rocky Mountain Biological Laboratory, Crested Butte, CO 81224, USA.

Introduction

Immature mayflies of the genus *Ephemerella* posture in response to presence of predatory stoneflies (Peckarsky 1980, 1987, Williams 1987). *Ephemerella* flex their caudal filaments and posterior abdominal segments vertically over their dorsum. The extent of the posture ranges through almost a 180° radius, from cerci slightly elevated above the substrate surface to cerci pointing

directly anteriorly (Peckarsky 1980). This posture is exhibited following approximately 40% of touch encounters with predaceous stoneflies (Peckarsky 1980, 1987). Mayflies that do not posture either remain or become motionless (freeze) or move (crawl, swim, or drift) in response to predators.

Defensive postures have been reported for many other insect and noninsect species (see Edmunds 1974 and Curio 1979 for reviews). Postures may function in a

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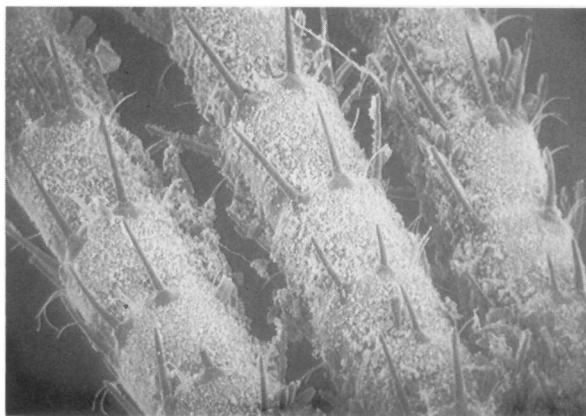


Fig. 1. Scanning electron micrograph of caudal filaments of *Ephemerella infrequens* (186x) (Martínez 1987).

variety of ways, blocking most stages of a successful predation event (Ender 1985). Postures may alter the apparent prey size and shape, thus disrupting detection or identification by predators using visual or, in aquatic habitats, hydrodynamic cues. Or they may serve as behavioral aposematism, warning predators of true or false (mimicry) punishing defenses, disrupting the subjugation (if true) or identification (if false) stages of a successful predation event. Alternatively, a posture can startle an approaching predator long enough to enable the prey individual to escape.

Previous work on the stimuli producing *Ephemerella* "scorpion" posture enables elimination of some of these alternative hypotheses for mode of effectiveness. Although the posture is exhibited primarily when mayflies are touched by a predaceous stonefly, occasionally (20% of all postures) mayflies "scorpion" in the absence of predator touches, especially when a stonefly is immediately upstream of the prey individual (Peckarsky 1987). Small individuals posture less frequently than larger members of the same population (Peckarsky 1980, 1987). There is some variation in the frequency of the scorpion posture with species of predaceous stonefly tested (Peckarsky 1980), consistent with relative risk of predation. Specific body parts of predators touching prey and particular prey body region touched also affect frequencies of posturing (Peckarsky 1987).

Since stoneflies are crepuscular, many species foraging mainly at night (Walde and Davies 1985, Sjöström 1985, Martínez and Peckarsky, in prep.) and under stones effectively without as with eyes (Martínez et al., submitted), visual crypsis or masquerade is an improbable function of the scorpion posture. Stoneflies do, however, respond to swimming patterns of their prey (Peckarsky and Wilcox, submitted), which makes hydrodynamic crypsis or masquerade a possible mechanism. *Ephemerella* is a relatively spiny mayfly, possessing a high density of long spines on its cerci (Fig. 1), in addition to abdominal and femoral spines (Martínez 1987). Thus, foraging stoneflies, which probe the sub-

strate with their antennae in search of prey, may be discouraged from attacking such spiny prey.

It is also possible that the posture warns predators of bad taste, since stoneflies have been shown to distinguish prey using chemotactile cues (Martínez and Peckarsky, submitted). Predators are sometimes visibly repulsed after touching *Ephemerella* in scorpion posture. Thus, the mechanical or chemical defenses are possible modes of effectiveness. But stoneflies have been observed to attack readily *Ephemerella* whose regular pattern of behavior is artificially disrupted by programming these mayflies to "swim" like the preferred mayfly species, *Baetis bicaudatus* (Peckarsky and Wilcox, submitted); the observation of *Ephemerella* remains in the stomachs of stoneflies (Peckarsky 1985) indicates that they are at least palatable, invalidating the bad taste hypothesis. Finally, since mayflies do not escape (flee) soon after posturing, the scorpion posture probably does not startle stoneflies.

The objectives of this paper include distinction between the remaining hypothesis potentially explaining the effectiveness of the *Ephemerella* scorpion posture. Experiments were designed to enable rejection of the most probably hypotheses: (1) the apparent size and shape hypothesis and (2) the punishing defense hypothesis. In addition, data were obtained to (3) pinpoint the specific stimuli producing the scorpion response. Experiments isolated visual, chemical, hydrodynamic and tactile predator stimuli to assess their relative effects on the frequency of the scorpion response.

Methods

Behavioral experiments were conducted at Benthette Brook, a first order tributary of the East River at the site of the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. *Ephemerella infrequens* (Ephemeroptera, Ephemerellidae) were collected from the East River and placed in observation boxes constructed of plexiglass with nitex mesh (80 μ m) ends. Nitex was also glued to the floor of the boxes (20 \times 10 cm) as a "foothold" for insects and a grid on which measurements of size and distance could be made. Sides of the observation boxes were also nitex-covered and sloped at 45° to facilitate viewing from above. A vertical plexiglass "guard rail" was attached to each side to prevent insects from crawling out of the arena. Behavior was recorded on video tape using a DC-Battery operated system described by Peckarsky et al. (1984). The observation boxes and video arena are illustrated in Peckarsky and Penton (submitted A).

In July and early August 1984-5, six trials of an experiment were run in which the behavior of 15 *Ephemerella* with intact cerci was contrasted to that of 15 *Ephemerella* with amputated cerci. Fresh-caught mayflies were hand-held for a few seconds while cerci were excised with a surgical scissors. Individuals were then placed

Tab. 1. Means \pm 1 se (mm) head capsule widths of predators and prey used in experiments. There were no differences between sizes of cerciless vs intact *Ephemerella* tested within any season. Sample sizes given in parentheses (N).

	Trial	<i>Megarcys</i>	<i>Ephemerella</i>
1984	Behavior	3.51 \pm 0.18 (6)	1.63 \pm 0.01 (77)
1985	Behavior	3.28 \pm 0.14 (6)	1.18 \pm 0.01 (85)
1987	Predation	3.23 \pm 0.06 (35)	1.17 \pm 0.05 (29): not eaten 0.93 \pm 0.04 (37): eaten

immediately in the observation box and watched for 15–20 min before beginning the trials. No individuals were injured or apparently traumatized by this procedure. All trials were run between 9 A.M. and noon mountain daylight time. Each mayfly treatment was introduced into separate observation boxes, and mayflies were subjected for 10 min to pursuit by *Megarcys signata* (Plecoptera, Perlodidae), the predaceous stonefly whose habitat and life cycle most closely overlaps with that of *Ephemerella*. Sizes of predators and prey used in experiments are summarized in Tab. 1.

Four predator treatments were used in 1984: (1) intact, free-living stoneflies, (2) intact, tethered stoneflies (a thin wire was attached to the ventral abdomen with non-toxic glue), (3) stonefly models (preserved stoneflies were “petrified” by spraying them with clear acrylic paint, then glued to a wire as above), and (4) stonefly antennae (also glued to a wire). In 1985, the live-predator treatment (1) was omitted, since frequencies of prey responses to live and tethered stoneflies were statistically indistinguishable (see Results), and prey stimulus using tethered stoneflies could be controlled for more efficient data acquisition. A fifth treatment was added in 1985: (5) wire alone.

Tab. 2 summarizes the information that could be obtained from contrasts between each prey \times predator treatment. Amputation of *Ephemerella* cerci could disrupt their sensory systems, causing them to respond to stoneflies differently. Or, loss of cerci could render

them more vulnerable to predation. In the latter case, increased rates of predation or attack on cerciless *Ephemerella* could be due to reduction of spininess, or to reduction of the ability to alter apparent size and shape (objectives 1 and 2). These two mechanisms need only be distinguished if predation and/or attack rates are affected by loss of cerci. Contrasts among the four predator treatments (assuming that there are no measurable artifacts associated with tethering stoneflies) enable distinctions to be made among the sensory cues that stimulate *Ephemerella* to scorpion or otherwise respond to stoneflies (objective 3).

In addition to these main effects, video recordings were used to obtain detailed information on the effects of touching mayflies with different parts of intact stoneflies (antennae vs legs), and of touching different regions of the mayflies’ bodies (anterior, posterior, dorsal, lateral). Direction of mayfly orientation and of predator approach were also recorded as another method of ascertaining the possible influence on prey responses of visual or chemical cues. These effects could be contrasted between intact and cerciless prey and among predator treatments.

Predation trials were conducted in the East River during summer 1987 to further test whether *Ephemerella* cerci were a deterrent to *Megarcys* predation. Fifteen intact or 15 cerciless *Ephemerella* were placed in 25 \times 10 \times 10 cm plexiglass boxes with 800 μ m mesh ends. Boxes contained standardized natural substrate materials (coarse cobble), and were placed in about 7–8 cm of water. Half the boxes of each *Ephemerella* treatment received one 24-h-starved *Megarcys*, and half served as controls with no predator. Boxes were left in the stream from 0500 P.M. (MDT) to 0700 A.M., the time of maximum stonefly feeding (Martínez and Peckarsky, unpubl.), after which they were destructively sampled. The remaining mayflies were counted and a random subsample was preserved for head capsule measurements. *Megarcys* were also preserved for size measurements and stomach content analysis (see Tab. 1).

Tab. 2.

Treatment comparison	Information obtained
Prey: Intact vs cerciless	1. Measures influence of cerci on frequency of posturing behavior. 2. Provides evidence of importance of cerci in effectiveness of posture.
Predators:	
Free-live vs tethered-live	Identifies experimental artifacts of tethering procedure.
Tethered-live vs model	Identifies importance of chemical cues in predation detection.
Tethered-live vs antenna	Identifies importance of visual and hydrodynamic cues associated with intact stoneflies.
Model vs wire	Enables distinction between visual plus hydrodynamic cues and purely tactile cues.
Antenna vs wire	Enables distinction between chemotactile and tactile cues.

Tab. 3. Observed (and expected) scorpion, movement and freeze responses of intact and cerciless *Ephemerella* to live-free and live-tethered *Megarcys*

	Intact <i>Ephemerella</i>		Cerciless <i>Ephemerella</i>	
	Live-free <i>Megarcys</i>	Live-tethered <i>Megarcys</i>	Live-free <i>Megarcys</i>	Live-tethered <i>Megarcys</i>
Scorpion	60 (58)	30 (32)	12 (14)	32 (30)
Move	72 (74)	43 (41)	19 (23)	57 (53)
Freeze	22 (19)	12 (12)	18 (12)	21 (27)

Results

Since the frequencies of scorpion postures, movement (crawl, swim, drift) and "freezing" responses (stop moving or no response) did not differ between intact and cerciless *Ephemerella* when touched by live-free *Megarcys* and live-tethered *Megarcys*, tethering predators caused no measurable change in prey behavior (Tab. 3, $\chi^2_{2df} = 0.819, 5.750$, intact and cerciless *Ephemerella* respectively). Thus, tethering *Megarcys* was considered a valid treatment by which to measure prey responses to live predators. Hereafter, all references to the live *Megarcys* treatment refer to tethered-live individuals.

Relative frequencies of the three prey response categories (scorpion, move and freeze) were arcsine transformed and compared by a Kruskal-Wallis test among four predator treatments (all but live-free *Megarcys*). If these tests were significant, pairwise Mann-Whitney U tests were performed with null hypotheses rejected at reduced alpha levels: $\alpha = 0.05/n$ where $n =$ the number of experimentwise comparisons (Bonferoni's Inequality, Snedecor and Cochran 1980). For both intact and cerciless *Ephemerella*, the frequency of scorpion posture was significantly higher when touched by live and model *Megarcys* than by *Megarcys* antennae or wires, with no difference between the two former and two latter predator treatments (Fig. 2, top). There were no significant differences among predator treatments for frequency of movement or freeze responses (Kruskal-Wallis tests, Fig. 2, center, bottom).

Mann-Whitney U tests were used to compare the frequencies of responses between intact and cerciless mayflies within each predator treatment. Scorpion posturing occurred significantly more often in intact than cerciless *Ephemerella* but only with live predators. All other comparisons between responses of intact and cerciless mayflies were not significant (Fig. 2). Thus, the only measurable effect of excising *Ephemerella* cerci was a reduction in frequency of defensive posturing when encountered by a live predator.

No *Ephemerella* individuals were attacked or eaten during 10-min trials as in previous behavioral experiments (Peckarsky 1980, 1987). Thus, loss of cerci conferred no apparent increase in vulnerability to predation. Results of predation trials confirmed this hypothesis, since numbers eaten of intact and cerciless

Ephemerella did not differ significantly (Mann-Whitney U test), although the mean was slightly higher for cerciless mayflies (Fig. 3). However, an interesting finding of the gut content analysis was that the mean size of *Ephemerella* individuals consumed (in guts) was significantly smaller than the mean size of mayflies remaining in predation trial boxes (Tab. 1; Mann-Whitney U test,

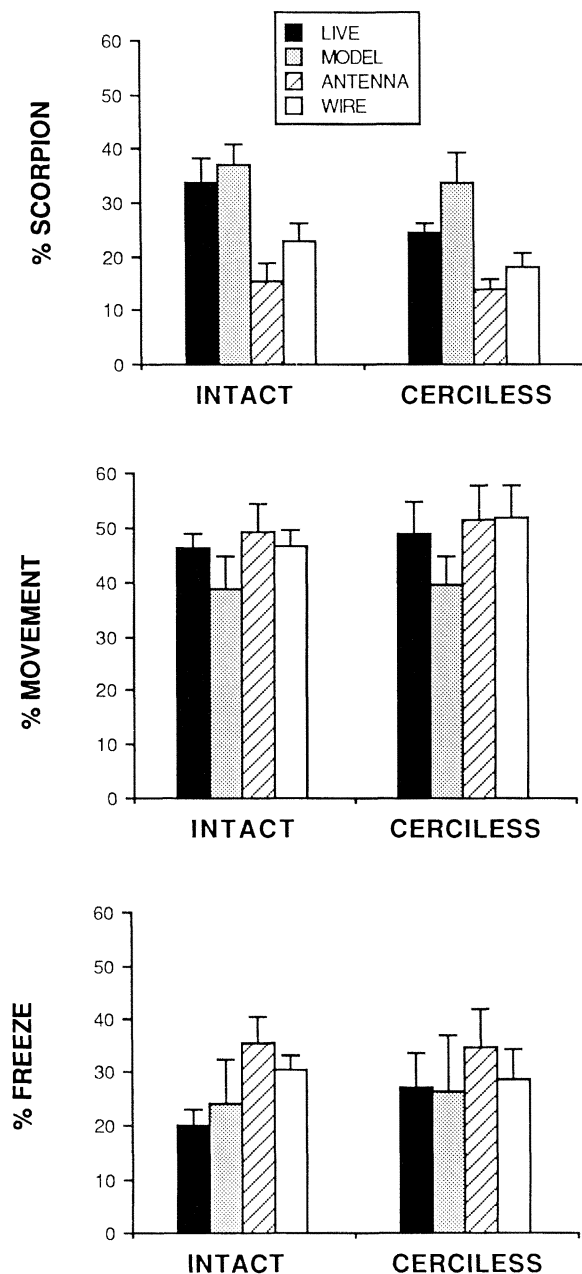


Fig. 2. Percent of encounters with each predator treatment resulting in scorpion posture (top), movement (crawl, swim or drift) (center), and freezing behavior (bottom). Means \pm 1 se of six 10-min observation periods. Differences in % scorpion postures among predator treatments were significant for both intact and cerciless *Ephemerella* (Kruskal-Wallis test, $p < 0.05$).

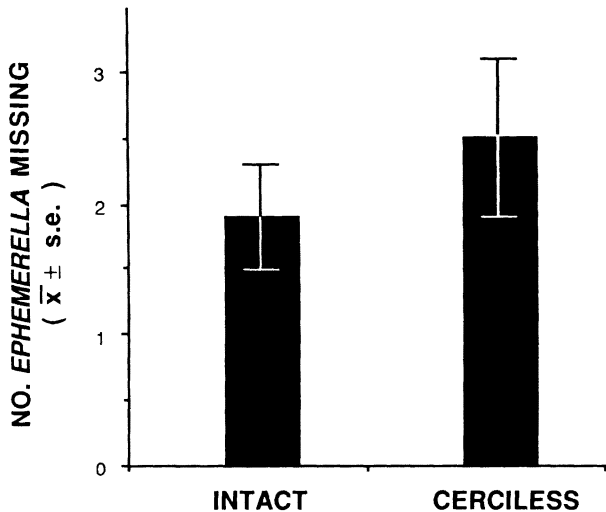


Fig. 3. Mean \pm 1 se intact and cerciless *Ephemera* missing from predation trial boxes with *Megarcys* present, corrected for average number missing from controls for each prey treatment (N = 18).

$p < 0.001$). This result suggests that smaller *Ephemera* individuals were more vulnerable to predation than large mayflies. Peckarsky (1987) reported that small *Ephemera* showed a significantly lower frequency of scorpion postures. These data are consistent with the hypothesis that relatively high posturing frequency decreased the risk of predation for large *Ephemera* when compared with small *Ephemera*. But other variables related to size cannot be ruled out as alternative hypotheses explaining predator preferences.

As in a previous study (Peckarsky 1987), most encounters between predators and prey occurred when *Megarcys*' antennae touched some part of *Ephemera*. Since these stoneflies search for and presumably identify prey with their antennae (Martínez et al., submitted), this type of encounter should confer the greatest potential risk of predation. Alternatively, stoneflies often touch prey with their legs, which may be a more accidental encounter. To determine whether *Ephemera* distinguishes between these two types of encounters, we tested for homogeneity of prey responses to touches by *Megarcys*' antennae and legs using chi-square analysis (3×2 contingency tables: scorpion, move, freeze responses \times antenna, leg stimuli) for each predator and prey treatment.

This analysis showed very few consistent patterns (Fig. 4). For model *Megarcys* the prey (both intact and cerciless) responded with similar frequencies of scorpion, movement and freeze behavior, regardless of whether they were touched by the predator's antenna or leg. These results are consistent with those of Peckarsky (1987) obtained by observing (without video recording) intact *Ephemera* vs live-free *Megarcys*. However, intact prey increased scorpion responses and decreased

"freeze" behavior when touched by legs of live *Megarcys* (significant cells test, Fagen and Mankovich 1980). In contrast, cerciless *Ephemera* showed decreased movement when touched by live *Megarcys* legs vs antennae. In general, although the frequencies of *Ephemera* responses to live *Megarcys* antennae vs legs were not always the same, behavioral modifications were not consistent with the prediction that encounters with predator antennae could produce heightened scorpion responses.

Since Peckarsky (1987) and Williams (1987) found that the frequency of scorpion posture was dependent on the specific prey body part touched, this hypothesis was further tested using the more accurate video recording method. Predators were observed to touch *Ephemera* in approximately equal frequencies on their anterior, dorsal, posterior body regions as in Peckarsky (1987). Thus, chi-square analysis was used to test for homogeneity of responses by intact and cerciless *Ephemera* to touches on each body part by each of four predator treatments (3×4 contingency tables: scorpion, move, freeze responses \times anterior, dorsal, lateral, posterior stimuli).

This analysis reveals a number of highly consistent patterns (Fig. 5). When touched anteriorly, intact and cerciless *Ephemera* rarely postured, regardless of the predator treatment. Instead, *Ephemera* tended to move or freeze with disproportionately high frequency. When touched dorsally, *Ephemera* consistently scorpioned with disproportionately high frequency. Variations in the frequencies of responses to posterior and lateral touches did not often provide substantial contributions to the significant chi-square values. In a few cases, however, "freeze" behavior was disproportionately low for *Ephemera* touched laterally and movement was more pronounced for *Ephemera* touched posteriorly or laterally; in one case scorpion responses

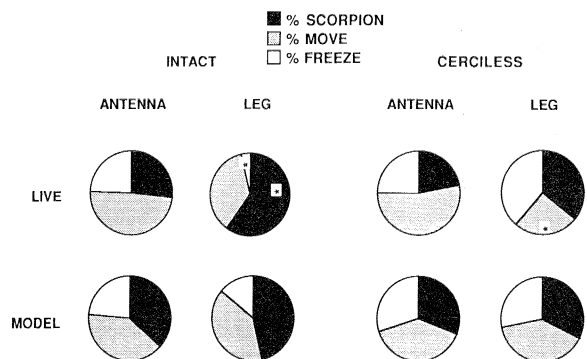


Fig. 4. Frequencies of scorpion, movement and freeze behavior of intact and cerciless *Ephemera* to stimulus by live or model *Megarcys* antennae and legs. Results of χ^2 analysis comparing observed with expected responses to touches by predator antennae vs legs are denoted with asterisks (*) inside each significant cell (3×2 contingency tables: scorpion, move, freeze response \times antennae, leg stimuli for each predator and prey treatment separately. Number of encounters ranged from 18–211).

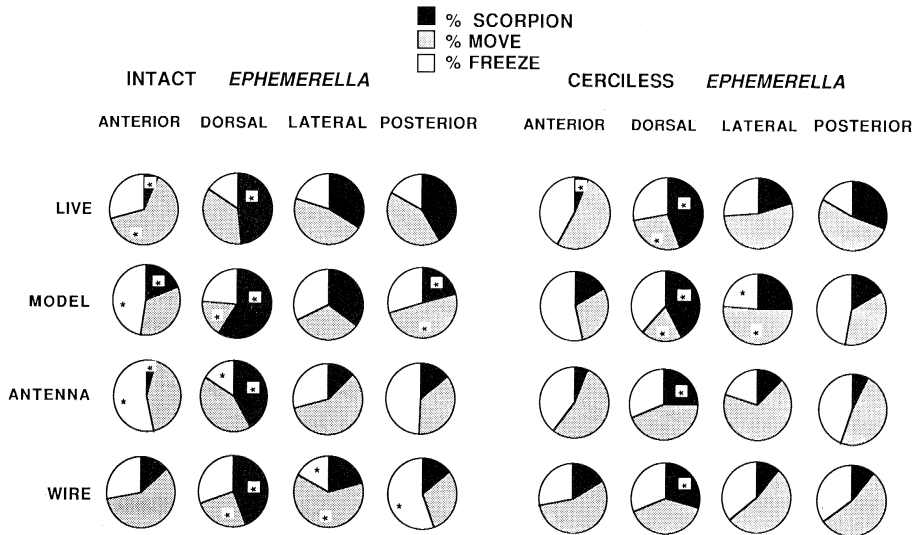


Fig. 5. Frequencies of scorpion, movement, and freeze behavior of intact and cerciless *Ephemerella* to stimulus by live *Megaracys*, model *Megaracys*, antenna or a wire when touched on anterior, dorsal posterior or lateral body areas. Results of χ^2 analysis comparing observed with expected responses to touches on different *Ephemerella* body parts are given for each predator and prey treatment. Significant cells are indicated as in Fig. 4 (3×4 contingency tables: scorpion, move, freeze responses \times anterior, dorsal, lateral, posterior stimuli for each predator and prey treatment separately. Number of encounters ranged from 53–91).

were reduced when *Ephemerella* was touched posteriorly. But these trends were not as consistent as were those for anterior and dorsal stimuli.

Responses of intact and cerciless *Ephemerella* oriented toward and away from live or model *Megaracys* were also compared by chi-square analysis (Tab. 4). Intact *Ephemerella* showed the same frequency of responses toward live or model *Megaracys* regardless of whether they faced toward or away from the predators ($\chi^2 = 3.19$, 2 df). Although cerciless *Ephemerella* did not alter their behavior with respect to orientation toward model *Megaracys*, they moved more often and froze less often than expected when facing toward live *Megaracys* ($\chi^2 = 8.73$, 2 df). The frequency of scorpion postures, however, was consistently unaffected by prey orientation.

Direction of predator approach likewise did not affect response frequencies of intact *Ephemerella* ($\chi^2_{4df} = 3.26$, 8.45, live and model *Megaracys*, respectively) but did have a significant effect on responses by cerciless mayflies (Tab. 5, $\chi^2_{4df} = 37.10$, 11.07, live and model *Megaracys*, respectively). Again, deviation from expected fre-

quencies of scorpion postures did not contribute substantially to the significant chi-square. When live *Megaracys* approached cerciless *Ephemerella* from upstream, movement responses increased and freezing behavior decreased compared with predator approaches from downstream. Cerciless *Ephemerella* moved more than expected, however, when model *Megaracys* approached from downstream (Tab. 5).

Discussion

Excising the cerci of *Ephemerella infrequens* did not increase the vulnerability of this mayfly to predation or attack by *Megaracys* under the experimental conditions. This result suggests that the increase in spininess and in the alteration of apparent size and shape provided by the cerci had minimal impact on the defense against predation by stoneflies. *Megaracys* did not attack nor eat *Ephemerella* during behavioral trials, and ate very few individuals during predation trials regardless of the presence of cerci. Smaller *Ephemerella* were selectively consumed by *Megaracys* during these trials, with no dif-

Tab. 4. Observed (and expected) scorpion, movement and freezing responses of intact and cerciless *Ephemerella* facing toward or away from live *Megaracys* and model *Megaracys*. * = significant cell (Fagen and Mankovich 1980).

		Prey orientation			
		Intact <i>Ephemerella</i>		Cerciless <i>Ephemerella</i>	
		Toward	Away	Toward	Away
Live <i>Megaracys</i>	Scorpion	22 (28)	64 (58)	18 (21)	49 (46)
	Move	42 (39)	76 (79)	44 (34)*	62 (72)
	Freeze	17 (14)	27 (30)	12 (19)*	48 (41)
Model <i>Megaracys</i>	Scorpion	22 (25)	48 (45)	22 (18)	44 (48)
	Move	36 (31)	52 (57)	24 (23)	58 (59)
	Freeze	13 (10)	26 (23)	15 (10)	45 (40)

Tab. 5. Observed (and expected) scorpion, movement and freezing responses of intact and cerciless *Ephemerella* to live *Megaracys* and model *Megaracys* approaching from upstream, downstream, or beside prey. * = significant cell (Fagen and Mankovich 1980).

		Predator approach					
		upstream	downstream	beside	upstream	downstream	beside
Live <i>Megaracys</i>	Scorpion	36 (41)	30 (25)	28 (27)	29 (30)	70 (74)	28 (23)
	Move	60 (59)	34 (37)	41 (39)	63 (40)*	79 (96)*	24 (30)
	Freeze	27 (23)	12 (14)	13 (15)	23 (45)*	131 (110)*	45 (34)*
		upstream	downstream	beside	upstream	downstream	beside
Model <i>Megaracys</i>	Scorpion	43 (42)	15 (17)	19 (18)	60 (54)	4 (8)	4 (7)
	Move	53 (50)	24 (20)	15 (22)	60 (67)	16 (10)*	9 (9)
	Freeze	18 (21)	6 (8)	15 (9)	49 (49)	4 (7)	9 (6)

ference in the mean size of intact and cerciless mayflies eaten. These data further support the conclusion that *Ephemerella* cerci provided no measurable predatory defense, even for small individuals. This finding is consistent with the results of stonefly predation trials on *Ephemerella* and *Baetis* reported by Williams (1987) and on *Baetis* reported by Corkum and Clifford (1981), which showed no difference in stonefly feeding on intact and cerciless mayflies, but inconsistent with results of experiments measuring rates of predation by brown trout on stoneflies with excised cerci (Otto and Sjöström 1983). The latter study showed that trout preferred to attack intact stoneflies from the anterior, and switched preferences to attack one species of stonefly from the posterior when its cerci were removed. Presence of prey cerci increased the handling time and prey ejection rate by predators.

Removal of cerci did, however, alter *Ephemerella* behavior pattern. Cerciless mayflies responded to encounters with live stoneflies with a lower frequency of scorpion postures. This result could be due to the loss of sensory capability to detect oncoming predators, or to the observers' inability to distinguish subtle posturing in nymphs without their cerci. Cerciless mayflies also tended to move more often than expected when oriented toward live predators and when live predators approached from upstream regardless of the prey orientation. Since hydrodynamic cues would be available from all directions and regardless of prey orientation, these responses may indicate the reliance on other sensory cues (vision and chemical stimuli) for recognition of predator presence by mayflies without cerci.

Comparison of posturing frequency in response to the various predator stimuli further enables identification of the sensory cues detected by *Ephemerella*, thus leading to heightened defensive behavior. Referring to the comparisons in Tab. 2, mayflies postured as frequently to live as to model stoneflies and likewise with equal frequencies to a freshly excised stonefly antennae as to a wire. These results suggest that chemotactile cues asso-

ciated with the stoneflies or their antennae are of little importance in stimulating responses. The heightened responses of mayflies to live and model stoneflies compared with antennae or wire stimuli, respectively, support the importance of either visual or hydrodynamic cues associated with a whole stonefly rather than simply a tactile cue from a stonefly antenna or a pointed object. Williams (1987) likewise reported reduction of scorpion responses by *Ephemerella* toward non-stonefly stimuli.

As discussed above, the equal frequencies of responses by intact *Ephemerella* facing toward and away from live or model *Megaracys* tentatively support the hydrodynamic rather than the visual hypothesis. However, the specific visual field of *Ephemerella* and the hydrodynamic wave patterns of live and model stoneflies need to be measured to distinguish these two potential mechanisms of predator detection. Thus, contrary to previous suggestions that the scorpion posture is a generalized defensive behavior resulting from tactile stimuli (Peckarsky 1987), data reported here support the hypothesis that this posture is a more precise anti-predator response (Sih 1986) probably to hydrodynamic disturbances or visual stimuli associated with intact, but not necessarily live, stoneflies.

The characteristics of wave patterns created by crawling *Megaracys* are very distinctive and relatively intense (Peckarsky and Wilcox, unpubl.). Presence of predators may be detectable from substantial distances (30 cm), alerting prey to enter a defensive behavior pattern. Reduced scorpion behavior of cerciless *Ephemerella* may, likewise, be related to loss of sensitivity to hydrodynamic stimuli. Defensive behavior of zooplankton has been elicited by hydrodynamic wave stimuli (Strickler 1975), and the escape system of some terrestrial insects, such as the cockroach, is triggered by wind puffs made by approaching predators (Camhi 1980).

It remains a puzzle that from these and other published data, essentially all of the proposed alternative hypotheses can be ruled out regarding the function of

the scorpion posture. Although the posture obviously alters the apparent size and shape of *Ephemerella*, if the assumption is true that removal of cerci disrupted this function, such a disruption did not lead to higher attack rates nor increase the risk of predation. The same can be concluded regarding reduction in the potentially "punishing" or noxious spininess associated with *Ephemerella* cerci. Thus, we conclude that removal of cerci did not disrupt this mayfly's defensive system.

The apparent size and shape hypothesis was proposed originally to explain the observation that larger *Ephemerella* postured with higher frequency than smaller individuals of the same species (Peckarsky 1980). The strength of this hypothesis was dependent on the validity of the assumption that the change in apparent size and shape of early instar *Ephemerella* would be a less effective deterrent to stonefly predation. This reduction of effect could be due either to small size alone, or to some other variable associated with small size, such as a reduction in exoskeletal hardness or spininess. The data reported here from predation trials and those of enclosure experiments (Peckarsky 1985) support small prey size-selectively by *Megarcys*. In predation trials, the mean size of both intact and cerciless *Ephemerella* from stonefly stomachs was smaller than the mean size of those recovered (uneaten) from predation trial boxes. Thus, as with large *Ephemerella*, removal of cerci of small *Ephemerella* had no measurable effect on their vulnerability to stonefly predation.

The question remains, then, why does the posturing behavior persist, and why is there ontogenetic variability in its frequency given that the posture does not affect the vulnerability of large or small *Ephemerella*? We can only speculate on an evolutionary scenario that might explain this anomaly: if scorpion posturing behavior evolved originally as a defensive response to stonefly predation, it must have been a more effective predator-deterrent for large than for small *Ephemerella* for reasons discussed earlier. Thus, natural selection would have favored a heightened frequency of posturing through ontogenetic development, a phenomenon that has been shown to occur in other insects as well (Iwao and Wellington 1970). If the defense became so effective in deflecting predation on large instar *Ephemerella*, perhaps by advertising capture difficulty and long handling times, selection on stoneflies would have favored individuals that attacked alternative prey species, leading to the evolution of avoidance of attempted predation on *Ephemerella*. Thus, the scorpion posture is no longer a necessary deterrent to stonefly predation, i.e., it is a "ghost of predation past" (cf. Connell 1980). Alternatively, the posture might have evolved in response to selection pressure from fish predation, which it has been shown to deter (Kratz 1983).

Stoneflies attack preferentially another mayfly, *Baetis*, presumably due to its conspicuous swimming pattern (Peckarsky and Penton, submitted A). In contrast to *Baetis*, *Ephemerella* responds to encounters with stone-

flies by general lack of movement in or out of posture. Thus, the attack behavior of *Megarcys* is triggered by a specific stimulus not usually produced by *Ephemerella*. Martínez (1987) also suggests that the prevalence of an extensive layer of fungi, bacteria, diatoms and amorphous material growing on the surface of *E. infrequens* may mask attractive cues that might otherwise be associated with their cuticle; that is, this species may be mimicking the substrate, thereby disrupting their identification as prey. Further, *Megarcys* can be stimulated to attack *Ephemerella* artificially programmed to swim instead of freeze or posture (Peckarsky and Wilcox, submitted). These data suggest that the observed low incidence of swimming in response to encounters by predators is an effective defense in itself. Lack of motion has been shown to reduce attack rates of fish on *Daphnia* (Wright and O'Brien 1982) and on *Notonecta* (backswimmers) (Cook and Streams 1984). Mort (1986) also suggests that the effect of tail spines on hydromechanical patterns of swimming *Daphnia* may be an effective defense against *Chaoborus* (phantom midge larvae) predation.

Molles and Pietruszka (1983) observed predatory behavior of *Megarcys* on another species of *Ephemerella*. They observed much greater incidence of attacks by stoneflies starved for six days prior to experiments than by predators well-fed before experiments. Although *Ephemerella* was easier to catch than *Baetis*, its spiny and relatively tough exoskeleton made it more difficult to handle. In a follow-up study, Molles and Pietruszka (1987) tested the effect of prey size and hunger levels of another stonefly species on its attack rates on a wide range of prey species. *Ephemerella* was the only prey species tested that combined small size (relative to the other prey species) with long handling times. It also did not fit the general relationship between prey body size and attack rates shown for all other prey species. The authors attributed an unusually low attack rate on *Ephemerella* to the effectiveness of its deceptive behavior, that is, the behavioral increase in its apparent size by posturing. If our evolutionary scenario is correct, the disproportionately long *Ephemerella* handling time may be advertised by the scorpion posture, but perhaps not altered by it, i.e., prey profitability is low regardless of posture behavior. These results suggest further that stonefly attack behavior has evolved to favor the prey species easiest to consume once captured (Peckarsky and Penton, submitted A).

In conclusion, although the incidence of scorpion postures declined when *Ephemerella* cerci were removed, attack and consumption rates by *Megarcys* on cerciless mayflies did not increase. Thus, cerci did not reduce the risk of stonefly predation, nor was frequency of posturing related to attack rate. We hypothesize, then, that scorpion posture behavior is an evolutionary relict, a "ghost of predation past", no longer necessary to reduce predation rates on *Ephemerella*. Posture frequency was not affected by plasticizing stoneflies, but declined in

response to excised fresh stonefly antennae or to wires. Thus, presence of the stonefly, live or model, was the precise cue eliciting significantly higher incidence of scorpion behavior in mayflies either facing toward or away from *Megarcys* approaching from upstream or downstream.

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