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ALTERNATIVE PREDATOR AVOIDANCE SYNDROMES OF STREAM-DWELLING MAYFLY LARVAE¹

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Abstract. Experiments were conducted to compare the patterns, mechanisms, and costs of predator avoidance behavior among larvae of five species of mayflies that co-occur with the predatory stoneflies, *Megarcys signata* and *Kogotus modestus* in western Colorado streams. Mayfly drift dispersal behavior, use of high vs. low food (periphyton or detritus) patches, microhabitat use, positioning, and activity periodicity were observed in the presence and absence of predators in circular flow-through chambers using natural stream water. Also, distances from predators at which prey initiated escape responses were compared among prey and predator species. Costs of predator avoidance behavior were assessed by measuring short-term (24 h) feeding rates of mayflies in the presence or absence of predatory stoneflies whose mouthparts were immobilized (glued) to prevent feeding.

The intensity and associated costs of predator avoidance behavior of mayfly species were consistent with their relative rates of predation by stoneflies. *Megarcys* consumes overwintering generation *Baetis bicaudatus* > *Epeorus longimanus* > *Cinygmula* = *Ephemerella*; *Kogotus* consumes summer generation *Baetis* > *Epeorus deceptivus* = *Cinygmula*; *Megarcys* eats more mayflies than *Kogotus*. While *Megarcys* induced drift by *Baetis*, *Epeorus*, and *Cinygmula*, this disruptive predator avoidance behavior only reduced food intake by *Baetis* and *Epeorus*. The morphologically defended mayfly species, *Ephemerella*, neither showed escape behavior from *Megarcys*, nor any cost of its antipredatory posturing behavior. Only *Baetis* responded by drifting from *Kogotus*. No mayfly species shifted microhabitats or spent less time on high-food patches in the presence of foraging stoneflies. However, predators enhanced the nocturnal periodicity of *Baetis* drift, which was negligible in the absence of stoneflies as long as food was abundant. Lack of food also caused some microhabitat and periodicity shifts and increased the magnitude of both day and night drift of *Baetis*. Thus, *Baetis* took more risks of predation by visual, drift-feeding fish not only in the presence of predatory stoneflies, but also when food was low or they were hungry. All other mayflies were generally nocturnal in their use of rock surfaces, as long as food was abundant. Finally, the distances at which different mayfly species initiated acute escape responses were also consistent with relative rates of predation.

This study demonstrates alternative predator avoidance syndromes by mayfly species ranging from an initial investment in constitutive morphological defenses (e.g., *Ephemerella*) to induced, energetically costly predator avoidance behaviors (e.g., *Baetis*). Although the costs of *Ephemerella*'s constitutive defense are unknown, experiments show that prey dispersal is the mechanism underlying fecundity costs of induced responses by *Baetis* to predators, rather than microhabitat shifts to less favorable resources or temporal changes in foraging activity. A conceptual model suggests that contrasting resource acquisition modes may account for the evolution and maintenance of alternative predator avoidance syndromes along a continuum from *Baetis* (high mobility) to heptageniids (intermediate mobility) to *Ephemerella* (low mobility). Prey dispersal (swimming) to avoid capture results in reduction of otherwise high fecundity by *Baetis*, which trades off morphological defense for enhanced ability to acquire resources. Thus, improved foraging efficiency is the selection pressure maintaining the highly mobile life style in *Baetis*, which increases resource acquisition and fecundity, offsetting the high mortality costs associated with this behavior.

Key words: adaptive syndromes; drift; induced defenses; mayflies; periodicity; predator avoidance; prey vulnerability; resource acquisition; stoneflies; streams.

INTRODUCTION

Behaviors and use of microhabitats that increase food intake are often dangerous, increasing a forager's risk of predation. This causes animals to strike a bal-

ance between foraging behavior that maximizes reproductive output and predator avoidance behavior that minimizes mortality (Sih 1980, Gilliam 1982, Gilliam and Fraser 1987, Werner and Anholt 1993). An alternative view to this optimal behavioral solution is that foragers reduce the risk of failing to satisfy minimum requirements for survival and reproduction (Schmitz

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and Ritchie 1991). In either case, the optimum or minimum solution may be the evolution of fixed (constitutive) defenses, or flexible (induced) responses (Harvell 1990) that reflect the costs and benefits of continuing to forage under the threat of predation (Sih 1987).

Flexible predator avoidance behavior (i.e., "risk adjusting" and "risk balancing," Fraser and Huntingford 1986) requires prey to assess the threat posed by a predator, and adjust their behavior to reflect the magnitude of the threat (Helfmann 1989). However, if the cost of gathering information about predation threat is prohibitive (e.g., low probability of surviving encounters with predators), evolution should favor fixed predator avoidance responses that do not fluctuate with predation pressure (Dill 1987, Sih 1987), or indirect assessment of predation risk associated with some other aspect of a forager's environment. Further, fixed anti-predator responses will be favored under conditions where the cost of such defenses is low in terms of reduced food intake (Dixon and Baker 1988). Lima and Dill (1990) argue, however, that feeding continuously and ignoring all predators ("risk recklessness," Fraser and Huntingford 1986) or giving up all feeding opportunities in response to predators, even if they may be nonthreatening ("risk avoidance," Fraser and Huntingford 1986) are rarely reasonable solutions to the dilemma of balancing conflicting demands, since they usually result in reduced fitness. Thus, the "all-or-nothing" solutions (always or never avoiding predators) should be rare, and one should commonly observe threat-sensitive predator avoidance behavior.

Prey may adjust their behavior to the presence or activity of predators over the short or long term (Helfmann 1986). For example, many prey modify their behavior when faced with a series of acute predator threats that vary in intensity (e.g., Peckarsky 1980, 1987, Sih 1987: Table 2, Soluk and Collins 1988, Peckarsky and Penton 1988, 1989b, Feminella and Hawkins 1994, Hileman and Brodie 1994, McIntosh and Townsend 1994). Further, ontogenetic shifts in behavior or microhabitats by foragers often reflect changes in risk of predation with increasing prey size (e.g., Peckarsky 1987, Peckarsky and Penton 1988, Werner and Hall 1988, Crowl and Covich 1990, Kats et al. 1994, Scrimgeour et al. 1994, Tikkanen et al. 1994). Such longer term responses could be due to selection pressures resulting in survival of individuals with the best behaviors, or to learning by individuals as they get older (Helfmann 1986).

Similarly, prey species that differ in vulnerability to predation by the same predator should show responses reflecting relative risks of predation. However, vulnerability or predation risk cannot necessarily be inferred from predation rates alone. Prey species may provide different nutritional gain (profitability) or inherent vulnerability to predators; and prey can invest energy into some combination of physical and behavioral defenses

to reduce their inherent vulnerability. Relative predation rates among alternative prey species indicate the effectiveness of each predator avoidance syndrome that is a function of nutritional, morphological, and behavioral antipredator adaptations. Thus, prey species may evolve alternative strategies that trade off investment in constitutive morphological defenses for reduced energetic costs of induced behavioral defenses. This study compares the patterns, mechanisms, and costs of behavioral responses of prey species with variable rates of predator-induced mortality, and applies a conceptual model to explain alternative predator avoidance syndromes observed.

Predatory stoneflies (Perlidae, Perlodidae) feed selectively on swimming mayflies of the family Baetidae in high-altitude streams in western Colorado (Allan and Flecker 1988, Peckarsky and Penton 1989a, Peckarsky et al. 1994), and elsewhere (Malmqvist and Sjöström 1980, Molles and Pietruszka 1983, 1987, Walde and Davies 1987, Williams 1987, Fuller and DeSteffan 1988). Other families of mayflies (Heptageniidae, Ephemerellidae) that do not swim in response to encounters with stoneflies have lower predator-induced mortality (Peckarsky and Penton 1989a, Peckarsky and Wilcox 1989); but all mayflies have similar nutritional profitability (Peckarsky et al. 1994). The specific goals of this study were to: (1) observe the patterns of predator avoidance behavior of five mayfly prey species interacting with two predatory stoneflies, (2) measure the costs of observed predator avoidance behaviors in terms of reduced resource acquisition, and (3) determine the mechanisms underlying the costs of predator avoidance behavior. Potential alternative mechanisms include dispersal from food patches or temporary suspension of foraging during acute predation risk (Bellman and Krasne 1983, Angradi 1992), spatial displacement to unfavorable food patches (Dixon and Baker 1988, Holbrook and Schmitt 1988, Turner and Mittelbach 1990), and temporal changes in activity or feeding periodicity resulting in reduced consumption rates (Bertness 1981, Holomuzki and Short 1988, Sih et al. 1988). These mechanisms are not mutually exclusive, and in many cases, more than one mechanism has been observed in the same prey organism (Skelly and Werner 1990, Resetarits 1991). A fourth objective of this study was to interpret the antipredatory behaviors of different mayfly species in the context of alternative adaptive syndromes that minimize losses of fecundity and maximize survivorship.

METHODS

Four experiments were designed to record predator avoidance behaviors and measure their associated resource acquisition costs for five mayfly species when exposed to the predatory stoneflies, *Megarcys signata* or *Kogotus modestus* (Perlodidae). The timing of experiments, choice of species pairs, and sizes of individuals tested reflected natural predator-prey combi-

TABLE 1. Summary of predation rates of *Megarcys signata* and *Kogotus modestus* on alternative mayfly prey species and attributes that affect prey vulnerability.

	Predation rate†	Response to predators‡	Prey density§
Prey species of <i>Megarcys signata</i>			
<i>Baetis bicaudatus</i> (overwintering generation)	1.872 ± .190	Swim, drift	352–2022
<i>Epeorus longimanus</i>	0.582 ± .176	Crawl	(no data)
<i>Cinygmula</i> sp.	0.275 ± .084	Crawl	19–296
<i>Ephemerella infrequens</i>	0.288 ± .065	Posture	94–752
Prey species of <i>Kogotus modestus</i>			
<i>Baetis bicaudatus</i> (summer generation)	0.167 ± .031	Swim, drift	638–1243
<i>Epeorus deceptivus</i>	0.148 ± .051	Crawl	65–909
<i>Cinygmula</i> sp.	0.057 ± .018	Crawl	19–296

Note: Data on *Epeorus longimanus* predation rates are reported in this paper. All other data are reported elsewhere (see footnotes for sources of other data). Units for predation rates are mean ± 1 SE instantaneous prey mortality rate (m) = prey eaten per prey per predator per day. Units of prey density are range of mean numbers per square metre in the East River.

† Peckarsky and Penton 1989a.

‡ Peckarsky 1980, Peckarsky and Penton 1988, 1989b.

§ Peckarsky 1991a.

nations that coexist in western Colorado streams, as in previous experiments (Peckarsky and Penton 1989a, Peckarsky et al. 1994). Two experiments measured predator effects on mayfly choice of food patches, selection of microhabitats, drift, and positioning periodicity. A third experiment compared escape-initiation distance of mayflies, and the fourth determined whether reduced resource acquisition by mayflies constituted a short-term (24 h) cost of predator avoidance.

Experiments were carried out in a streamside system of circular flow-through chambers (described and illustrated in Peckarsky and Cowan 1991) using natural stream water from the East River or a first order tributary (Benthette Brook) at the site of the Rocky Mountain Biological Laboratory in Gunnison County, Colorado. Water temperatures in the artificial streams were similar to those of the East River, because water was either pumped (and filtered) directly from the East River or delivered from the tributary to the chambers from a pipe submerged in the East River for ≈50 m before entering the system. Further, chambers were shaded by a white portable greenhouse (locally manufactured Weatherport) or a blue plastic awning that buffered them from the intense high-altitude solar radiation.

Ranking predation rates

To establish a context for interpretation of behavioral experiments, I first ranked stonefly predation rates on mayfly prey species. With the exception of one prey species, rankings were established from previous work (Table 1). In the East River and its tributaries *Megarcys* and *Kogotus* are the numerically dominant predatory stoneflies (Peckarsky 1991a). *Megarcys* attains about twice the mass of *Kogotus* (Peckarsky and Cowan 1991), and co-occurs with the overwintering generation of the highly abundant and mobile bivoltine mayfly *Baetis bicaudatus* (Baetidae). *Megarcys* consistently eats more *Baetis* than other mayfly species under a variety of conditions and measured by many different

approaches, such as: gut content analysis (Peckarsky 1985), single- and mixed-species predation trials with and without substrate refuges, and when hungry or starved (Peckarsky and Penton 1989a). Behavioral trials recording predator-prey encounter rates, attacks per encounter, and captures per unit time over the short (Peckarsky and Penton 1989a) and long term (Peckarsky et al. 1994) also show that *Baetis* suffers greater mortality to *Megarcys* than any other mayfly species. Heptageniid mayflies (*Cinygmula* sp., *Epeorus longimanus*), which are less abundant and less active than *Baetis* and avoid stoneflies by crawling rather than swimming or drifting (Peckarsky 1980) are eaten less often by *Megarcys* (Peckarsky et al. 1994). Ephemerellidae (*Ephemerella infrequens*), a sluggish, morphologically defended mayfly that freezes or postures in response to encounters with *Megarcys* (Peckarsky 1980, 1987, Peckarsky and Penton 1988) is invulnerable to stonefly predation, except when in postmort condition (Soluk 1990).

The smaller fast-growing species, *Kogotus*, exerts less predation pressure on the summer generation of *Baetis* (Peckarsky and Penton 1989a, Kerans et al. 1995), and is more variable in its preferences among mayfly species (Table 1). Although gut contents (Peckarsky 1985), behavioral measures such as attacks per encounter (Peckarsky and Penton 1989a), and long-term feeding rate experiments (Peckarsky et al. 1994) suggest that *Baetis* has the highest rate of predator-induced mortality, other tests show equal and sometimes higher susceptibility to predation for the heptageniids, especially *Epeorus deceptivus*, and to a lesser degree *Cinygmula* sp. (Peckarsky and Penton 1989a). Thus, the relative predation rates on different mayflies by *Kogotus* are less clear. If predator avoidance behavior of the different mayfly species is consistent with the threat-sensitivity hypothesis, I would expect all mayflies to be more responsive to *Megarcys* than to *Kogotus*.

Epeorus longimanus was added to the array of potential *Megarcys* prey items when it recolonized local streams in 1989 after having disappeared since the early 1980s (B. L. Peckarsky, unpublished data). Interestingly, this species shifted its seasonal phenology after recolonization, which reduced overlap with that of its congener, *E. deceptivus*, resulting in temporal overlap with *Megarcys*, instead of *Kogotus*. This phenological shift resulted in potential vulnerability to *Megarcys* rather than *Kogotus* predation, as in the early 1980s. A single-species predation trial, similar to those using all the other predator-prey combinations (Peckarsky and Penton 1989a) was conducted on 1–2 July 1992 to establish the predation rate of *Megarcys* on *E. longimanus*. Fifteen *Epeorus* were placed in replicate substrate-filled plexiglass flow-through circular streams (15 cm diameter) housed in the streamside Weatherport. Replicate chambers ($n =$ eight per treatment) were randomly allocated to one of three treatments: (1) one starved (held for 24 h in similar chambers without prey) female *Megarcys*, (2) one starved male *Megarcys*, or (3) controls without predators. Predators fed for 12 h overnight (the time of most active feeding, Peckarsky and Cowan 1995) after which chambers were destructively sampled and the number of mayflies killed was determined. Numbers killed were corrected by mean numbers of prey missing from controls (ranged from 0 to 1) to account for prey losses other than to predation. Instantaneous prey mortality rates (m) were calculated using the equation: $N_f = N_0 e^{-mt}$, where N_f = final prey density (corrected for losses from controls), N_0 = initial prey density, and t = duration of trial in days (Dodson 1975). Mortality rates were compared between chambers with male and female *Megarcys* by t tests on $\log(x + 1)$ transformed data. Predation rates on *Epeorus longimanus* were ranked qualitatively (Table 1), but not compared statistically to other species, because the latter were derived from different experiments (Peckarsky and Penton 1989a).

Experiment measuring costs of predator avoidance

Experiments were conducted in plexiglass circular streams to determine the impact of predator avoidance on the resource acquisition rates of: *Epeorus longimanus* with *Megarcys*, *Epeorus deceptivus* with *Kogotus*, *Cinygmula* sp. with *Megarcys* and *Kogotus*, and *Ephemerella infrequens* with *Megarcys*. (See legends for Figs. 1–6 for dates of each experiment.) Data on *Baetis* vs. *Megarcys* and *Kogotus* have been reported previously (Peckarsky et al. 1993). Since the heptageniids are periphyton grazers, like *Baetis*, algal resource levels were manipulated in the chambers as in Peckarsky et al. (1993). Five 24-h starved mayflies in developmental stage III (wingpads longer than wide) of each grazer species were placed in chambers containing one of three treatments: (1) high food: four slimy rocks from the East River with ambient periphyton, (2) high food + predator: four slimy rocks plus

one predator (either *Megarcys* or *Kogotus*) whose mouthparts were immobilized with Barge Cement, or (3) low food: four rocks that were boiled, then dried to remove algae. The low-food treatment served as a reference to determine the severity of predator effects on mayfly food intake. A drop of Barge Cement was placed on a small piece of gravel in the first and third treatments for control purposes. Behavior of glued predators was observed and compared to that of unglued predators (Peckarsky and Cowan 1995) demonstrating that this treatment of stoneflies did not affect their foraging behavior. For *Ephemerella* experiments all chambers received boiled rocks; and detritus and filamentous algae were used as the food source in treatments 1 and 2, as indicated by preliminary trials on the diet of this species (B. L. Peckarsky, unpublished data).

After 24 h in chambers, individual mayflies were prepared for fluorometric analysis of the gut pigments (chlorophyll *a* and phaeopigments) by preserving them in amber bottles (to prevent interaction with light) containing 90% ethanol extract, and within 12 h of preservation, macerated to expose gut contents to the extract for a total of 24 h (Cowan and Peckarsky 1990). *Ephemerella* gut fullness was measured using the same technique, because preliminary fluorometric analysis picked up large quantities of phaeopigments associated with their largely detrital diet (Peckarsky and Cowan 1995). A one-way ANOVA was used to analyze the treatment effect on the total pigment per mayfly gut, which was a better index of gut fullness than chlorophyll *a*, because chlorophyll degraded rapidly into phaeopigments in mayfly guts (Cowan and Peckarsky 1990). Mean responses of the five individuals per chamber were used as replicates ($n =$ seven chambers per treatment). Due to problems with the fluorometer, a few of the chambers in the *Ephemerella* experiment had to be omitted (see df in Table 2). Analysis of residuals indicated that a log transformation was necessary to meet the assumptions of the ANOVA.

Experiments measuring predator avoidance behavior

1. *Predator-induced drift, microhabitat shifts, positioning and activity periodicity.*—During the 24-h resource acquisition cost experiments, periodic observations were made to determine whether avoidance of predatory stoneflies caused mayflies to disperse or affected their microhabitat selection, positioning, or activity periodicity. Many mayfly species are nocturnal in their use of rock tops, foraging on the rich periphyton resources during darkness to reduce the risk of predation by visually feeding fish (reviewed by Cowan and Peckarsky 1994, Peckarsky and Cowan 1995). This experiment was conducted using dim red light for nighttime observations, which did not affect the behavior of *Baetis* or *Epeorus*, but altered responses of *Cinygmula* (Peckarsky and Cowan 1995). Further, microhabitat use by *Ephemerella* could not be assessed

TABLE 2. Costs of predator avoidance: summary of one-way ANOVAs of effects of predator avoidance and low food on mayfly gut fullness ($y = \log$ total pigments per gut). HF = high food, M = high food + *Megarcys*, K = high food + *Kogotus*, LF = low food. A posteriori comparisons were made using Tukey's multiple comparisons tests.

Prey species	Predator	Source	ss	df	F	P	Paired comparisons
<i>Baetis bicaudatus</i> †	<i>Megarcys</i> and <i>Kogotus</i>	Treatment	15.76	3	17.19	.0001	HF > M = K > LF
		Error	7.33	24			
<i>Epeorus longimanus</i>		Treatment	27.68	2	117.66	.0001	HF > M > LF
		Error	2.12	18			
<i>Cinygmula</i> sp.	<i>Megarcys</i> and <i>Kogotus</i>	Treatment	2.58	3	6.01	.003	HF = M = K > LF
		Error	3.44	24			
<i>Ephemerella infrequens</i>		Treatment	5.20	2	14.99	.001	HF = M > LF
		Error	1.913	11			
<i>Epeorus deceptivus</i>	<i>Kogotus</i>	Treatment	11.31	2	76.11	.0001	HF = K > LF
		Error	1.34	18			

† Data from Peckarsky et al. (1993).

accurately due to the complex refuge afforded by their food source. Therefore, behavioral data are reported here only for *Baetis* and *Epeorus*.

Each chamber contained two slate and two granite rocks of ≈ 5 cm diameter from the East River situated randomly with respect to two water jets that directed the flow clockwise. The two rocks immediately downstream of the water jets had higher flows (15.6 ± 1.0 cm/s) than those upstream of water jets (6.3 ± 0.5 cm/s) measured with a Nixon micropropeller flowmeter (Charlton Kings Industrial Estate, Cheltenham, Gloucestershire, England). Therefore, each chamber provided two substrate types (slate and granite) and two flow microhabitats (high and low). These variables were manipulated for comparison to microhabitat preferences measured previously in the absence of predators (Peckarsky and Cowan 1995).

The five mayflies in each chamber were observed six times (instantaneous scan samples) over a complete diel cycle (1300, 1700, 2100, 0100, 0500, and 0900), recording which rock and rock surface was occupied and whether mayflies were drifting in the water column. The effects of treatment (high food, predator + high food, low food) on choices made by mayflies among rocks and periodicity of use of rock surfaces were analyzed with a one-way MANOVA on three interdependent response variables (arcsine-transformed): percent using granite rocks, percent using high-flow rocks and difference in percent using rock tops during night and day (nocturnicity). Percentages for choices among rocks were based on the total number of individuals actually observed on the rocks. Individual ANOVAs and Tukey's multiple comparison tests determined the precise differences responsible for significant MANOVAs. (In one case, overwintering generation *Baetis* vs. *Megarcys*, a posteriori tests were conducted even though the MANOVA was marginally insignificant, because the magnitude of differences in mean responses among treatments suggested biologically significant trends.) The effect of treatment on mayfly drift periodicity was analyzed using nonparametric (Kruskal-Wallis and pairwise Mann-Whitney *U*) tests on the percent of mayfly individuals drifting at night minus the

percent drifting during the day because a large number of zeros rendered transformations ineffective for normalizing data or stabilizing variances.

2. *Predator-induced shifts in food patch use.*—This experiment tested whether predatory stoneflies initiated mayfly dispersal from high- or low-food patches, and whether such dispersal behavior resulted in mayflies spending less time on high-food patches. Sixteen mayflies of each species (same seven predator-prey combinations as in previous experiments; see legends for Figs. 1–6 for dates of each trial) were placed in larger (30 cm diameter) plexiglass circular streams in a plexiglass tray elevated on an angle iron stand so that chambers could be observed from the underside and the top. In trials with grazers, a 10 cm diameter periphyton-covered granite rock from the East River, and a similar-sized granite rock that had been boiled and dried to reduce periphyton were placed on opposite sides of the arenas. Mayflies had to drift or swim in the water column to disperse from one rock to the other. For trials with *Ephemerella*, detritus and algal filaments were added to the food side of sterile (boiled) gravel-filled chambers, and nylon mesh provided nonfood refuges on the no-food side. After mayflies acclimated to the chambers (colonized a patch, began grazing, or remained on a patch for >10 min), observers noted the number of individuals on the high- and low-food rocks. Then for 10-min trials, we tape-recorded all dispersal events noting the location of takeoff and landing. I then calculated the number of mayfly-seconds (no. seconds \times no. mayflies) spent on the high- and low-food rocks, and the number of mayflies that dispersed from both rocks for each trial.

Nine replicates of each set of 16 mayflies (approximating a density of 300/m²) were observed between 0900 and 1200 (three replicates per day on consecutive days), a time of low natural mayfly drift rates (Allan 1987). The same mayflies were observed under two treatments: with and without a stonefly, randomizing the order of predator treatments. Any prey individuals that were captured and eaten by predators during trials (a rare occurrence) were immediately replaced to maintain initial prey densities in the chambers. Stoneflies

were starved for 24 h before trials, which increased their hunger levels and their motivation to forage within the observation arenas. First, one-tailed *t* tests were conducted to determine whether the percent time spent on the high-food patches differed from 50%, indicating whether mayflies discriminated between high- and low-food patches. Then paired *t* tests determined whether predators influenced mayfly use of food patches with percent total mayfly-seconds on the high-resource patch as the response variable. The influence of predators on mayfly dispersal rate was also tested with paired *t* tests. All tests were performed on untransformed data because analysis of residuals of response variables indicated that no transformations were necessary.

3. *Prey reactive distance to predators.*—Using grid-ded 20 cm long flow-through observation boxes placed directly in the stream as in earlier behavioral experiments (Peckarsky and Penton 1989a), 20 individuals of each mayfly species (predator–prey combinations as in Table 1) were exposed to a tethered *Megarcys* or *Kogotus* (as in Peckarsky and Penton 1988, 1989b) to determine the distance from the predator at which mayflies moved away (either by crawling, swimming, or drifting). Each mayfly was observed only once, and the direction of approach of the predator (upstream or downstream) was recorded. Data were analyzed using separate two-way ANOVAs for each predator species on the escape initiation distance as the response variable with treatment categories: prey (four species with *Megarcys* and three species with *Kogotus*) \times direction of predator approach (upstream or downstream). One-way ANOVAs were also conducted to compare the escape initiation distance of *Baetis*, *Cinygmula*, and *Epeorus* to the two different predators. These analyses determined whether prey species responded to approaching predators differently and consistent with the relative risk of predation.

RESULTS

Predation rate of *Megarcys* on *Epeorus longimanus*

Mean predator-induced mortality rates of *E. longimanus* did not differ significantly between male and female *Megarcys*, although females (0.746 ± 0.315 prey-predator⁻¹.d⁻¹) generally consumed more prey than males (0.417 ± 0.161 prey-predator⁻¹.d⁻¹), which is probably related to the larger size and metabolic demands of females (Peckarsky and Cowan 1991). The pooled mortality rate for both males and females ranks this species as having lower predation rates than *Baetis*, but higher than *Cinygmula* and *Ephemerella* (Table 1).

Costs of predator avoidance

Only *Baetis* (with *Megarcys* and *Kogotus*) and *Epeorus longimanus* (with *Megarcys*) ate less algae in chambers with stoneflies whose mouthparts were glued to prevent predation (Fig. 1). All other mayfly species

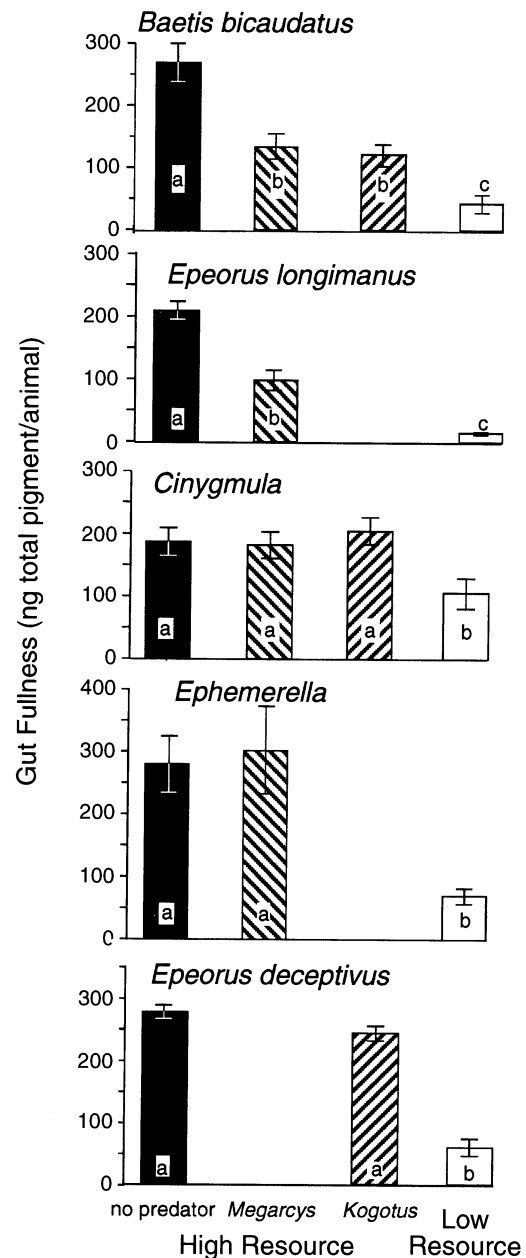


FIG. 1. Costs of predator avoidance: mean \pm 1 SE total pigment (chlorophyll *a* + phaeopigments) per mayfly gut in chambers with high food and no predators, high food + *Megarcys* or *Kogotus*, or low food ($n = 7$, except for *Ephemerella*, where $n = 5$). Means within axes having the same letters are not significantly different. Dates of experiments: *Baetis bicaudatus* (July 1990, from Peckarsky et al. 1993), *Epeorus longimanus* (5–6 July 1990), *Cinygmula* sp. (27–28 July 1991), *Ephemerella infrequens* (24–25 June 1993), and *Epeorus deceptivus* (8–9 August 1990).

only ate less food in the low-food treatment (Fig. 1, Table 2). Therefore, predator avoidance behaviors that occurred in the chambers over 24 h had no measurable costs on mayfly resource acquisition rates except for *Baetis* and *E. longimanus*.

TABLE 3. Predator-induced effects on microhabitat and positioning periodicity: results of one-way MANOVA on effect of treatments on use of granite rocks, high-flow rocks, and nocturnal use of rock tops (night-day). Treatments: HF = high food, M = high food + *Megarcys*, LF = low food ($n = 7$). A posteriori comparisons were made using Tukey's multiple comparisons tests.

Prey species	Predator	Variable	ss	df	F	P	Multiple comparisons
<i>Baetis bicaudatus</i> overwintering generation	<i>Megarcys</i>	MANOVA	.485†	6, 31	2.325	.056*	...
		Granite	.184	2	3.428	.055	LF > M
		Error	.483	18			
		High flow	.061	2	0.830	.452	...
		Error	.662	18			
		Night - Day	.239	2	0.119	.035	HF > LF
<i>E. longimanus</i>	<i>Megarcys</i>	Error	.529	18			
<i>Baetis bicaudatus</i> summer generation <i>E. deceptivus</i>	<i>Megarcys</i> <i>Kogotus</i> <i>Kogotus</i>	MANOVA	.714†	6, 32	0.978	.456	...
		MANOVA	.780†	6, 32	0.706	.647	...
		MANOVA	.777†	6, 32	0.718	.638	...

* A posteriori multiple comparisons were made since MANOVA was marginally insignificant.

† Wilks' lambda.

Mechanisms underlying costs of predator avoidance behavior

1. *Predator-induced drift, microhabitat shifts, positioning, and activity periodicity.*—Periodic observations made during the costs of predator avoidance trials showed that *Megarcys* and *Kogotus* had no significant effects on *Baetis* or *Epeorus* preferences for granite over slate rocks (Table 3), although overwintering *Baetis* tended to spend more time on granite rocks when food levels were low (Table 3, Fig. 2 upper left), and removal of periphyton tended to equalize time spent by both *Epeorus* species on granite and slate rocks (Fig. 2 lower left). Likewise, there were no significant treatment effects (predators or resource levels) on mayfly preferences for high- over low-flow rocks (Table 3, Fig. 2 right).

There was a significant treatment effect on the periodicity of overwintering *Baetis* use of rock tops (Fig. 3). However, increased nocturnicity occurred only in treatments with high-food levels (Table 3), and there were no predator-induced changes in mayfly positioning periodicity. Individuals of both the overwintering and summer generations of *Baetis* were nocturnal when food levels were high whether predators were present (*Megarcys*: $t = 2.84$, $P = 0.03$; *Kogotus*: $t = 2.93$, $P = 0.026$) or absent ($t = 4.53$, $P = 0.004$; $t = 6.87$, $P = 0.0005$), and aperiodic in the low-food treatment due to increased daytime use of rock tops ($t = 0.42$, $P = 0.692$; $t = 1.02$, $P = 0.346$) (Fig. 3 upper left). Both *Epeorus* species were generally nocturnal in their use of the top surfaces of rocks (*E. longimanus* high food: $t = 7.26$, $P = 0.0003$, low food: $t = 3.06$, $P = 0.022$; *E. deceptivus* high food: $t = 3.01$, $P = 0.03$, high food + *Kogotus*: $t = 3.76$, $P = 0.009$, low food: $t = 2.87$, $P = 0.029$), except *E. longimanus*, which was aperiodic in the presence of high food + *Megarcys* ($t = 1.82$, $P = 0.119$) (Fig. 3 lower left).

There were significant treatment effects of both predators and food levels on *Baetis* drift behavior (overwintering *Baetis* with *Megarcys*: Kruskal-Wallis sta-

tistic = 7.488, $P = 0.024$, 2df; summer *Baetis* with *Kogotus*: Kruskal-Wallis = 5.815, $P = 0.055$, 2 df) (Fig. 3 upper right). Interestingly, *Baetis* drift rates were negligible in chambers with abundant food and no predators, increased sharply in the presence of *Megarcys* (Mann-Whitney $U = 8.000$, $P = 0.03$), but only slightly in the presence of *Kogotus* (Mann-Whitney $U = 30.5$, $P = 0.404$). Both generations of *Baetis* drifted more when food levels were low than when they were high (overwintering: Mann-Whitney $U = 39.5$, $P = 0.046$; summer: Mann-Whitney $U = 40.5$, $P = 0.035$). Predators and food also affected the periodicity of *Baetis* drift. While overwintering *Baetis* were strongly nocturnal in the presence of *Megarcys* ($t = 3.03$, $P = 0.023$), they became aperiodic when food was reduced ($t = -0.81$, $P = 0.449$) (Fig. 3 upper right). Thus, enhancement of nocturnal drift probably results from direct interactions with predators, while increased day and night drift behavior are a function of *Baetis* hunger levels. In contrast, summer *Baetis* were nocturnal in both *Kogotus* ($t = 3.30$, $P = 0.017$) and low-food treatments ($t = 4.22$, $P = 0.006$). Both *Epeorus* species rarely drifted (mean drift rate of <3%, Fig. 3 lower right), and drift periodicity was not affected by presence of predators or resource levels (Kruskal-Wallis statistic = 2.566, $P = 0.277$, 2 df; Kruskal-Wallis = 0.364, $P = 0.833$, 2 df for *E. longimanus* and *E. deceptivus*, respectively).

In summary, although these data do not rule out the potential for subtle predator-induced or food-level associated effects on *Epeorus* microhabitat use, positioning periodicity, and drift behavior, the effects on *Baetis* were clearly more pronounced. Further, the data suggest that observed reductions in resource acquisition in the presence of stoneflies (Fig. 1) were caused by predator-induced dispersal (drift) (Fig. 3 right) rather than predator-induced shifts in microhabitat (Fig. 2) or positioning periodicity (Fig. 3 left).

2. *Predator-induced dispersal and shifts in food patch use.*—Results of the food patch experiment

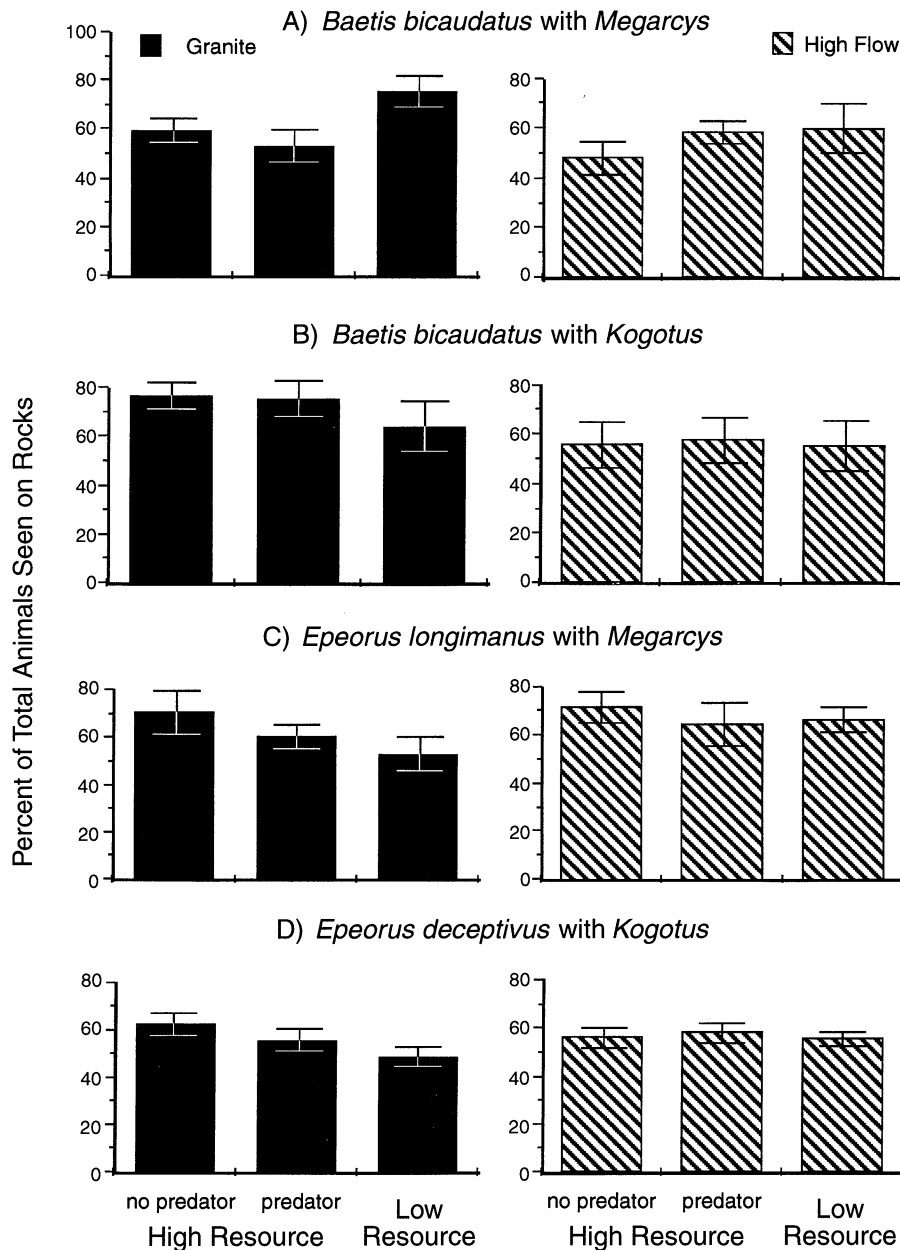


FIG. 2. Predator-induced shifts in prey microhabitat: mean \pm 1 SE percent of (A) overwintering generation *Baetis bicaudatus* (17–18 June 1991), (B) summer generation *B. bicaudatus* (17–18 July 1991), (C) *Epeorus longimanus* (5–6 July 1990), and (D) *E. deceptivus* (8–9 August 1990) visible on granite (vs. slate) rocks (left) and on high-flow (vs. low-flow) rocks (right) in treatments with high periphyton, high periphyton + *Megarcys* or *Kogotus*, and low periphyton ($n = 7$).

showed that *Baetis*, *Cinygmula*, and *Epeorus deceptivus* generally spent >50% of the time during trials on the high-food patch in each chamber (Fig. 4, see Table 4 for exceptions). Interestingly, neither *E. longimanus* nor *Ephemerella* discriminated between high- and low-food patches during trials. Further, presence of predators had no significant effects on the time spent by any mayflies on the high- vs. low-resource patches (Fig. 4, Table 5). However, *Megarcys* caused an increase in drift of *Baetis*, *Epeorus longimanus*, and *Cinygmula*

from high- or low-food patches (Fig. 5, Table 6). *Megarcys* had no effect on *Ephemerella* drift rates; and *Kogotus* significantly affected drift rates of only *Baetis*, with no effects on *E. deceptivus* or *Cinygmula* (Fig. 5, Table 6). Thus, while neither predator caused mayflies to spend less time on high-food patches, *Megarcys*, the more threatening predator, increased the drift rate of *Baetis* and the heptageniids from substrates on which they were foraging, and *Kogotus* only induced *Baetis* to drift. These data further support the hypothesis that

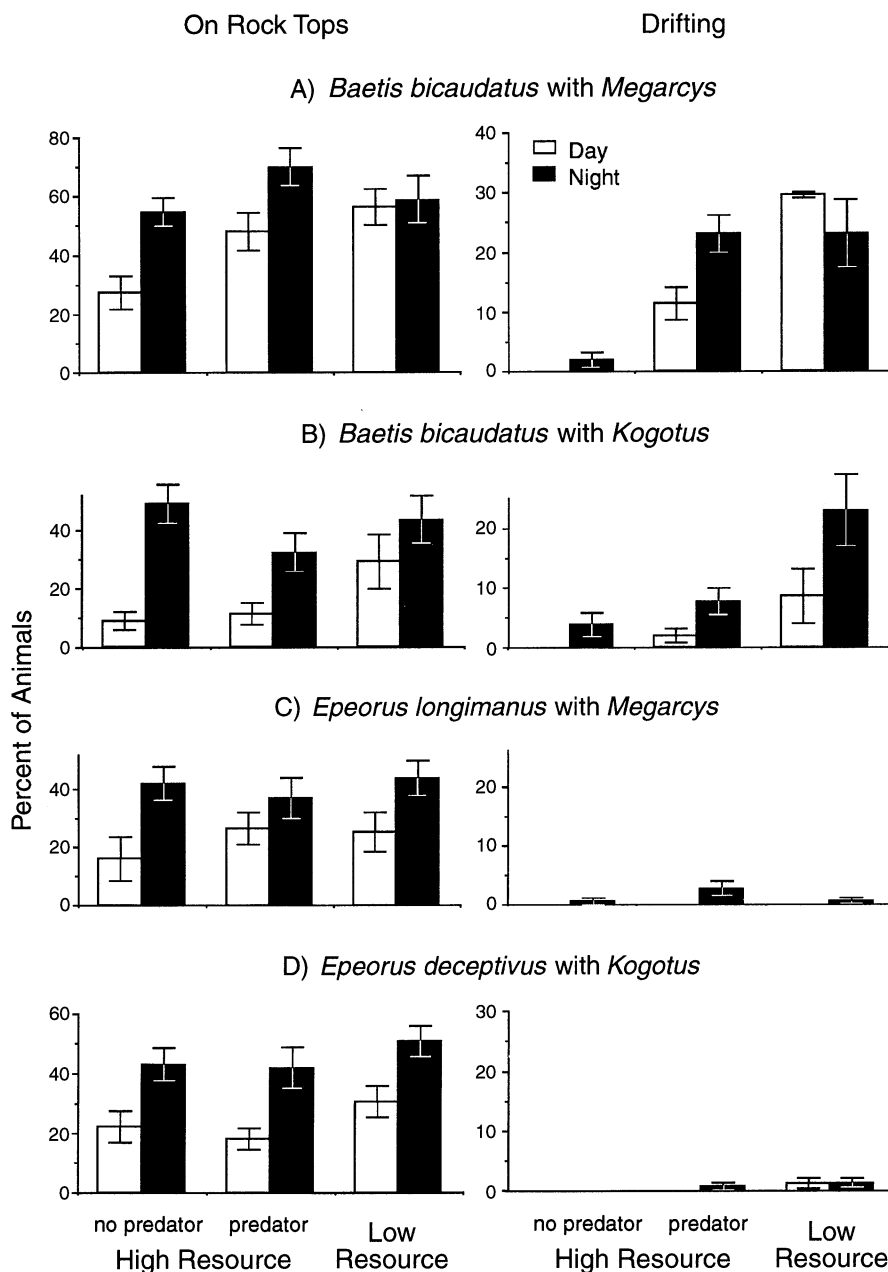


FIG. 3. Predator-induced shifts in prey positioning and drift periodicity: mean \pm 1 SE percent of (A) overwintering generation *Baetis bicaudatus* (17–18 June 1991), (B) summer generation *B. bicaudatus* (17–18 July 1991), (C) *Epeorus longimanus* (5–6 July 1990), and (D) *E. deceptivus* (8–9 August 1990) visible on the top surfaces of rocks (left) and drifting (right) during day or night in treatments with high periphyton, high periphyton and *Megarcys* or *Kogotus*, and low periphyton ($n = 7$).

predator-induced dispersal (Fig. 5), and not a micro-habitat shift (Fig. 4) is responsible for reductions in mayfly resource acquisition observed in the presence of foraging stoneflies (Fig. 1).

3. *Distance from predators at which prey avoidance response was initiated.*—During the experiment measuring prey reactive distances, all mayfly species except *Ephemerella* responded to stoneflies from a mean

distance of ≈ 1 –2 cm (Fig. 6). Responses included drift or swim behavior (predominantly with *Baetis*), and crawling behavior (predominating in the heptageniids). *Baetis* and the heptageniids often wagged their caudal filaments when predators approached from downstream before initiating crawling behavior that moved them out of the predator's path. Direction of predator approach had no effect on prey response distance (*Me-*

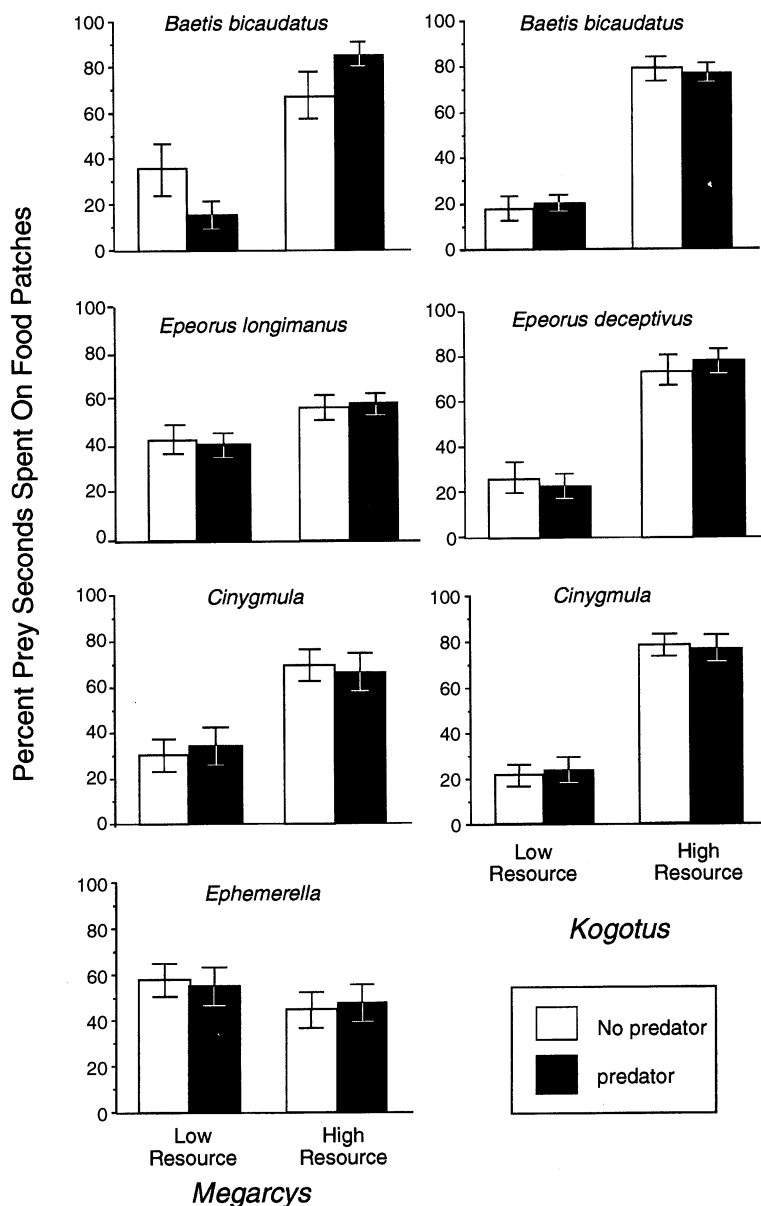


FIG. 4. Predator-induced shifts in food patch choice: mean \pm 1 SE percent time spent by mayflies on low- and high-food patches with and without predators. Left: overwintering generation *Baetis bicaudatus* (2–6 July 1990), *Epeorus longimanus* (9–11 July 1991), *Cinygmula* sp. (15–17 July 1992), and *Ephemerella infrequens* (9–16 July 1992) with *Megarcys*. Right: summer generation *Baetis* (30 July–1 August 1990), *E. deceptivus* (25–30 July 1991), and *Cinygmula* sp. (28–31 July 1992) with *Kogotus* ($n = 9$).

garcys: $F = 3.251$, 1, 152 df, $P = 0.073$, *Kogotus*: $F = 1.636$, 1, 114 df, $P = 0.203$), although there was a trend for mayflies to respond from farther away when *Megarcys* approached from upstream. In general, mayflies reacted to stoneflies from similar distances whether the predators were upstream or downstream from the mayflies, implicating the potential importance of hydrodynamic rather than visual or chemical cues generated by foraging stoneflies (Peckarsky 1987, Peckarsky and Penton 1988, 1989b). There was also no significant interaction between prey species and *Me-*

garcys ($F = 1.139$, 3, 152 df, $P = 0.335$) or *Kogotus* direction of approach ($F = 0.241$, 2, 114 df, $P = 0.785$).

Results of the two-way ANOVA (prey species \times predator direction) on prey responses to *Megarcys* demonstrated a highly significant prey effect ($F = 35.599$, 3, 152 df, $P = 0.0001$), with overwintering generation *Baetis* and *Cinygmula* responding to predators from the longest distance followed by *Epeorus longimanus*, then *Ephemerella* (Fig. 6). Summer generation *Baetis*, *Cinygmula*, and *Epeorus deceptivus* responded to *Kogotus* from similar distances (Fig. 6, $F = 0.125$, 2, 114 df,

TABLE 4. Food patch use experiment: Summary of *t* tests on percent mayfly time spent on high-food patches during 10-min trials vs. 50% as a null hypothesis (*n* = 9).

Prey species	Predator treatment	<i>t</i>	<i>P</i>
<i>Baetis bicaudatus</i> overwintering generation	<i>Megarcys</i>	5.76	<.001
	no <i>Megarcys</i>	1.47	.179
<i>Epeorus longimanus</i>	<i>Megarcys</i>	1.10	.305
	no <i>Megarcys</i>	0.83	.430
<i>Cinygmula</i> sp.	<i>Megarcys</i>	1.89	.095
	no <i>Megarcys</i>	2.78	.024
<i>Ephemerella infrequens</i>	<i>Megarcys</i>	-0.478	.645
	no <i>Megarcys</i>	-0.861	.415
<i>Baetis bicaudatus</i> summer generation	<i>Kogotus</i>	6.70	<.001
	no <i>Kogotus</i>	6.50	<.001
<i>Epeorus deceptivus</i>	<i>Kogotus</i>	4.99	.001
	no <i>Kogotus</i>	3.52	.008
<i>Cinygmula</i> sp.	<i>Kogotus</i>	4.17	.003
	no <i>Kogotus</i>	6.08	<.0001

P = 0.882). Although *Megarcys* constitutes a greater threat of predation to mayflies than does *Kogotus* (Peckarsky and Penton 1989a), neither *Baetis* (*F* = 2.279, 1, 78 df, *P* = 0.135) nor *Cinygmula* (*F* = 0.292, 1, 78 df, *P* = 0.591) discriminated between *Megarcys* and *Kogotus*, initiating avoidance responses at only slightly farther distances from the more dangerous predator. In contrast, *Epeorus deceptivus* responded to *Kogotus* from longer distances than *E. longimanus* did to *Megarcys* (*F* = 5.997, 1, 78 df, *P* = 0.017).

DISCUSSION

Behavioral data reported in this study show that the most vulnerable mayfly species (*Baetis*) showed strong, induced, and costly predator avoidance behaviors. The least vulnerable mayflies (*Ephemerella*) were unresponsive to foraging stoneflies, and mayflies with intermediate risks of predation (heptageniids) exhibited weaker and less consistent, but potentially costly antipredator behavior. These data are consistent with the prediction that induced predator avoidance behaviors should predominate in species where such behaviors have a high cost in fitness (Dill 1987). Thus, while dispersal to avoid capture by stoneflies reduces *Baetis* mortality, it has an associated cost in reduced resource acquisition rates, growth rates, and fecundity (Peck-

arsky et al. 1993). *Epeorus longimanus* was the only other mayfly in this system that showed reduced resource acquisition rates as a cost of predator avoidance. The untimely disappearance of *E. longimanus* has prevented a test of whether the short-term cost of predator avoidance has a long-term consequence on growth rates and fecundity, similar to those observed in *Baetis* (Peckarsky et al. 1993). This is the only mayfly species for which lower reproductive success (reduced number of matings) has been measured for small males (Flecker et al. 1988). Thus, if lower resource acquisition rates result in smaller male size (as in *Baetis*), a strong, less speculative connection could be made between fitness and reduction in male size as a consequence of predator avoidance.

Many other studies have reported that costs of predator avoidance vary consistently with relative prey vulnerability to predation. Cook and Streams (1984) observed that the *Notonecta* (backswimmer) species most vulnerable to fish predation remained motionless and stayed in vegetation more often when predators were present, which reduced their risk of predation, but also their foraging time. Behavioral changes to avoid predation resulted in reduced feeding (Pierce 1988, Jeffries 1990, McPeck 1990) and growth rates of the more susceptible classes of odonates (Dixon and Baker 1988). Lawler (1989) reported graded responses of larval anurans to fish predation that resulted in significant differences in development rates of different tadpole species. Kohler and McPeck (1989) argued that graded responses of different grazer species (*Baetis* and a grazing caddisfly, *Glossosoma*) to avoid predatory sculpins could indirectly affect the outcome of competitive interactions between these two grazers favoring the species less vulnerable to predation. This hypothesis has been tested in other systems (e.g., Persson 1991), but remains to be tested directly in the East River system.

Similar gradations in the intensity and associated cost of acute predator-escape responses have been demonstrated in freshwater snails (Alexander and Covich

TABLE 5. Predator-induced shifts in food patch use. Summary of paired *t* tests of effects of predators on percent prey time spent on high-food patches during 10-min trials (*n* = 9).

Prey species	Predator	<i>t</i>	<i>P</i>
<i>Baetis bicaudatus</i> overwintering generation	<i>Megarcys</i>	-1.424	.192
<i>Epeorus longimanus</i>	<i>Megarcys</i>	1.146	.285
<i>Cinygmula</i> sp.	<i>Megarcys</i>	-0.642	.539
<i>Ephemerella infrequens</i>	<i>Megarcys</i>	0.500	.631
<i>Baetis bicaudatus</i> summer generation	<i>Kogotus</i>	0.699	.504
<i>Epeorus deceptivus</i>	<i>Kogotus</i>	1.710	.126
<i>Cinygmula</i> sp.	<i>Kogotus</i>	-0.657	.530

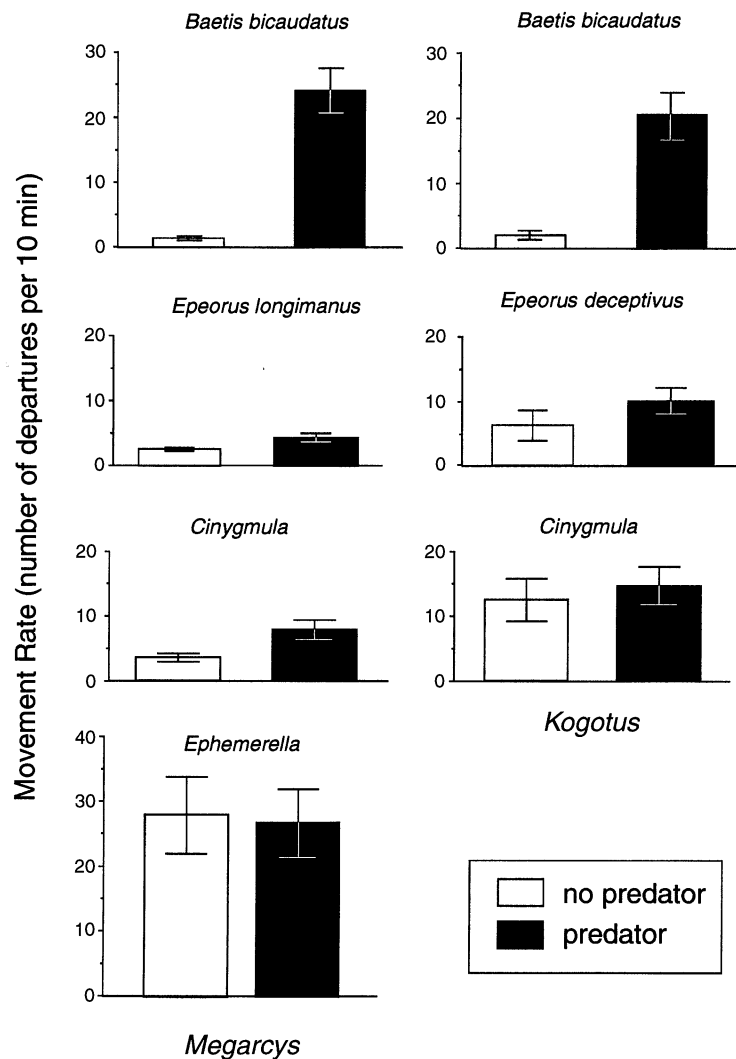


FIG. 5. Predator-induced dispersal from food patches: mean ± 1 SE number of times mayflies drifted per 10-min trial with and without predators. Left: overwintering generation *Baetis bicaudatus* (2–6 July 1990), *Epeorus longimanus* (9–11 July 1991), *Cinygmula* sp. (15–17 July 1992), and *Ephemerella infrequens* (9–16 July 1992) with *Megarcys*; Right: summer generation *Baetis* (30 July–1 August 1990), *E. deceptivus* (25–30 July 1991), and *Cinygmula* sp. (28–31 July 1992) with *Kogotus* ($n = 9$).

TABLE 6. Predator-induced dispersal. Summary of paired t tests of effects of predators on prey dispersal from food patches (number of drift events per 10-min trial, $n = 9$). In all cases where effects were significant, predators increased rates of prey dispersal.

Prey species	Predator	t	P
<i>Baetis bicaudatus</i> overwintering generation	<i>Megarcys</i>	†	.008
<i>Epeorus longimanus</i>	<i>Megarcys</i>	2.462	.039
<i>Cinygmula</i> sp.	<i>Megarcys</i>	2.623	.031
<i>Ephemerella infrequens</i>	<i>Megarcys</i>	-0.310	.765
<i>Baetis bicaudatus</i> summer generation	<i>Kogotus</i>	†	.008
<i>Epeorus deceptivus</i>	<i>Kogotus</i>	1.357	.212
<i>Cinygmula</i> sp.	<i>Kogotus</i>	0.678	.517

† Wilcoxon signed-ranks tests were performed because too many zero drift values caused transformations to be ineffective in normalizing data and stabilizing variance.

1991), marine snails (Schmitt 1981, 1982), sticklebacks (McLean and Godin 1989, Bishop and Brown 1992), and damselfly larvae (McPeck 1990). The snail and stickleback prey systems were similar to the East River mayflies in that the least vulnerable prey species that lacked behavioral responses to predators were also morphologically defended, like *Ephemerella*. As in the mayflies, the reactive distance of sticklebacks was shorter than that of banded killifish, which have less armor and tended to compensate behaviorally (McLean and Godin 1989).

In contrast to predator-induced graded drift responses by these mayfly species to the species posing the most serious threat (*Megarcys*), spatial shifts in mayfly habitat use were not induced by predatory stoneflies on any of the mayfly species observed in this

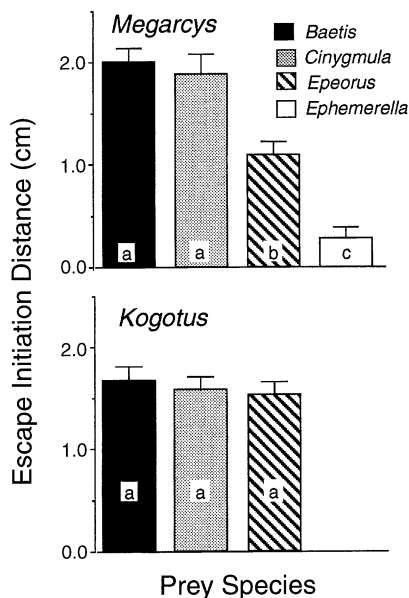


FIG. 6. Reactive (escape) distances of mayflies (mean \pm 1 SE) when approached by tethered stoneflies. Upper panel: overwintering generation *Baetis bicaudatus*, *Epeorus longimanus*, *Cinygmula* sp. and *Ephemerella infrequens* with *Megarcys* (26–30 June 1989). Lower panel: summer generation *B. bicaudatus*, *E. deceptivus*, and *Cinygmula* sp. with *Kogotus* (15 August 1989). Means having the same letters are not significantly different ($n = 20$). Values were pooled for responses of mayflies to stoneflies approaching from upstream and downstream because there were no significant effects of this variable.

study. All mayfly species had fixed responses to microhabitat and food patch quality that were not responsive to presence of stoneflies. Even though stoneflies caused prey dispersal off food patches, mayflies generally returned to patches of similar quality, resulting in no associated reduction in time spent on good food patches. Unlike this study, others have shown that stream-dwelling fish often occupy inferior food patches in the presence of piscivores (Cerri and Fraser 1983, Power 1984, 1987, Schlosser 1987, Harvey and Stewart 1991, Persson 1991), and that larval notonectids are relegated to foraging in lower quality food patches to avoid predation by adult cannibals (Sih 1982).

Similarly, data reported in this study provide little evidence of stonefly-induced temporal changes in mayfly activity or feeding periodicity. Neither *Baetis* nor the less vulnerable mayfly species responded to the presence of predatory stoneflies by temporal changes in activity or positioning periodicity that could have resulted in reduced resource acquisition. Presence on upper rock surfaces and nocturnal drift have been associated with mayfly food search behavior, especially in *Baetis* (Kohler 1985). All mayflies in this system were generally fixed in their nocturnal use of rock surfaces and their nocturnal drift periodicity, as long as food was abundant. Apparently, this is an adaptive for-

aging strategy in which flexible responses to predatory stoneflies do not play a role. These results are in strong contrast to previous reports of shifts in diel drift or positioning periodicity induced by drift-feeding fishes (Cowan and Peckarsky 1994, McIntosh and Peckarsky 1996). These observations suggest that fish may exert a greater selection pressure than stoneflies for flexible antipredator shifts in feeding periodicity by mayflies, especially if the costs of changing diel feeding periodicity are high (Dixon and Baker 1988).

Although *Baetis* did not shift its drift periodicity in the presence of stoneflies, they did show stonefly-induced increases in drift magnitude, especially nocturnal drift. This observation is consistent with the hypothesis that encounters with predatory stoneflies are in part responsible for the periodicity of mayfly drift observed in natural systems (Peckarsky 1980). Interestingly, *Baetis* was often observed drifting in chambers with foraging stoneflies even without actual encounters or after other mayflies in their vicinity had drifted in response to predator encounters. This behavior suggests that elevated mayfly drift rates in the presence of foraging stoneflies may reflect both direct and indirect responses to predators, and are not a simple function of predator and prey densities and rates of movement. While encounter frequencies between *Baetis* and stoneflies are too low to account for the magnitude of nocturnal drift (Peckarsky et al. 1994), non-contact drift responses by mayflies could further enhance naturally occurring increases in nocturnal drift in the presence of predators. Other investigators have observed increases in the magnitude of mayfly drift in the presence of predatory stoneflies (Corkum and Pointing 1979, Walton 1980, Malmqvist and Sjöström 1987, Malmqvist 1988, Lancaster 1990) or benthic feeding fish (Culp et al. 1991).

Baetis did change their drift and activity periodicity in response to food reduction, increasing their daytime drift rates and daytime use of upper rock surfaces for foraging. Daytime foraging behavior is rarely reported in mayflies because of the increased vulnerability to predation by visually feeding fish (Allan 1978, Flecker 1992, Cowan and Peckarsky 1994). Nocturnal drift or feeding periodicity by *Baetis* in many streams has been associated with the presence of drift-feeding fish (Allan 1978, Flecker 1992, Culp and Scrimgeour 1993, Cowan and Peckarsky 1994). Thus, while visually feeding fish constrain *Baetis* foraging to nighttime, encounters with nocturnal stoneflies may be a proximal mechanism that actually induces higher rates of nocturnal drift. Further, presence of predatory stoneflies increases the use of upper rock surfaces by *Baetis* during the day in fishless streams (B. L. Peckarsky and A. R. McIntosh, unpublished data). These complex, interacting effects often cause subtle, but recognizable patterns of substrate surface use in streams with high-fish and low-stonefly populations (little daytime drift or use of rock surfaces) vs. low-fish and high-stonefly populations (more day-

time drift or use of substrate surfaces), even though the overall pattern of drift and activity periodicity may be nocturnal (Cowan and Peckarsky 1994, McIntosh and Peckarsky 1996).

Other studies have shown that the willingness of foragers to take risks, such as foraging on upper rock surfaces during the day may be influenced by hunger levels. Kohler and McPeck (1989) demonstrated that *Baetis tricaudatus* made "adaptive compromises" between feeding and avoidance of predatory sculpins, taking more risks (feeding on tops of substrates) when starved and food levels were high. This same mayfly species decreased its reactive distance to stoneflies and benthic fish predators when food levels were reduced fourfold (Scrimgeour and Culp 1994). Only the most vulnerable mayfly in this study (*Baetis*) took more risks by foraging on rock tops during daylight when food levels were low. All other mayfly species showed fixed diel foraging periodicity unresponsive to predators or to reduction in food resources.

The behavioral responses of mayflies observed in this study illustrate alternative predator avoidance syndromes, or different solutions to the evolutionary problem of foraging under risk of predation. These adaptive syndromes can be interpreted using a conceptual model comparing the effects of alternative strategies of foraging and predator avoidance behavior on resource acquisition, fecundity, and mortality for each species along an axis of increasing prey mobility (Fig. 7). The model illustrates the hypothetical optimal predator avoidance syndrome for each species where the difference (d) between fecundity and mortality due to predation (fitness) is maximized. Resource acquisition for mayflies, which do not eat as adults, should vary directly with fecundity, because all resources necessary to grow and produce eggs are acquired during the larval phase. Therefore, behaviors that increase resource acquisition also increase fecundity. Mortality curves are based on previous data on predator-prey encounter, and attack and capture rates (Peckarsky and Penton 1989a, Peckarsky et al. 1994). Some resource acquisition data are reported in this paper, but curves are more speculative forming the bases for testable hypotheses. Although this conceptual model was developed to interpret data from the stonefly-mayfly system, it is generally applicable to any predator-prey system in which predators induce an array of avoidance behaviors among alternative prey species.

Mortality curves for all mayflies have the same shape (Fig. 7) because the potential mortality costs and benefits of increasing mobility are the same for all prey. Curves rise sharply along the mobility axis from crawl to swim avoidance behaviors because swimming stimulates stoneflies to attack prey. In fact, stoneflies may not recognize prey items until they swim (Peckarsky and Penton 1989a). This attack behavior is stereotyped and does not change when stoneflies are reared on diets of prey that don't swim (Peckarsky et al. 1994). How-

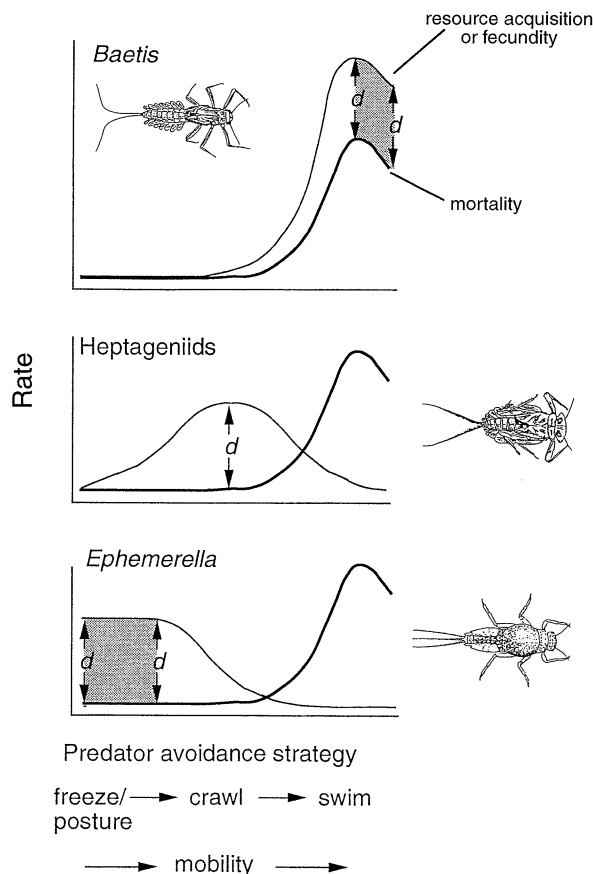


FIG. 7. Conceptual model contrasting changes in rates of mortality, resource acquisition, and fecundity of different mayfly species along an axis of increased prey mobility to avoid predation by stoneflies. Alternative predator avoidance syndromes of *Baetis* (upper), heptageniids (center), and *Ephemerella* (lower) illustrate different solutions to the evolutionary problem of foraging under risk of predation. Each predator avoidance syndrome maximizes fitness, represented as the difference (d) between rates of resource acquisition (and consequent fecundity) and mortality due to predation. See Discussion for more detailed explanation.

ever, the actual mortality costs due to stonefly predation of the three mayflies differ, depending on how often they swim (Fig. 7, see arrows along the mobility axis). *Baetis* mortality is high (primarily swims), heptageniids have lower mortality rates (occasionally swims), and *Ephemerella* has the lowest mortality since it normally freezes, postures, or crawls away from stoneflies (Peckarsky 1980, 1987, Peckarsky and Penton 1988, 1989a). However, stoneflies attacked *Ephemerella* at rates similar to *Baetis* when we experimentally forced them to swim (Peckarsky and Wilcox 1989). Finally, swimming behavior may increase or decrease mayfly mortality depending on its timing. While swimming after encounters is risky (conspicuous to predators) for any mayfly (rising limb of the mortality curve), swimming after attacks enables mayflies to reduce capture rates (descending limb of mortality curves). The ob-

servation that all mayflies have similar probabilities of capture per attack (Peckarsky and Penton 1989a) indicates that the survival benefits of escape swimming behavior are probably the same for all mayfly species.

It is intriguing that *Baetis* is the most abundant mayfly species in the system (Peckarsky 1991a), while incurring the highest mortality due to stonefly predation and predation by trout, which feed primarily on prey active in the water column of streams (Allan 1978). Further, mermithid parasites have been observed in both larval and adult *Baetis* (Vance and Peckarsky 1992). Near maturity a single worm may occupy the entire abdominal cavity, either killing or completely and permanently sterilizing mayflies, resulting in zero fecundity. Depending on the infectivity of this parasite, it has the potential to exert a very strong direct effect on mayfly fitness. Yet this species retains numerical dominance in the system year after year, apparently favorably competing with other grazers for periphyton resources (Ode 1990).

The success of *Baetis* despite its high fitness costs associated with swimming behavior suggests that other pressures override selection against swimming (Peckarsky 1991b). For example, *Baetis* may use its vagility to exploit patchy benthic algae (Kohler 1984) that is less available to more sedentary mayflies. Apparently swimming behavior improves foraging efficiency and confers a competitive advantage to *Baetis* (Padilla et al. 1990, Ode 1990) that counterbalances direct and indirect predatory losses. *Baetis* is also quick to recolonize after disturbances (Peckarsky 1986), effectively discriminating among different resource levels by nocturnal drifting and sampling food patches. Further, these mayflies maintain high feeding rates even in habitats with very low levels of food (Peckarsky et al. 1993). This improved foraging efficiency enables *Baetis* uniquely to complete two generations per year in this high elevation system, including the very fast-growing, lower fecundity summer generation, and slower growing, high-fecundity overwintering generation (Peckarsky et al. 1993).

Although movement is an essential part of the foraging behavior of all mayflies, the model suggests that the benefits of a highly vagile life style diminish along a continuum from *Baetis* to heptageniids to *Ephemerella*. In contrast to the similarity of the hypothetical mortality curves, I suggest that the resource acquisition/fecundity curves vary among the three types of mayflies (Fig. 7), due to striking differences in their foraging behaviors, and account for the shifts in the location along the mobility axis of the predator avoidance behavior that maximizes fitness (d). Thus, contrasting resource acquisition modes account for the evolution and maintenance of alternative predator avoidance syndromes. For all three mayflies, however, resource acquisition curves should decline at some point along the mobility axis where the energetic costs of swimming (metabolic costs of interruption of feed-

ing) and the survivorship costs of increased predation exceed the benefits of moving to obtain food. That point differs among species from *Baetis* (high mobility) to heptageniids (intermediate mobility) to *Ephemerella* (low mobility) as a consequence of variation in morphology and feeding behavior.

In the absence of predators, *Baetis* swims as part of a saltatory food search behavior. As shown in this study, the lower the food resources, the more they swim. The rising limb of the resource acquisition curve (Fig. 7 upper) illustrates the advantage of increased mobility to *Baetis* foraging efficiency. While swimming in the absence of predators increases their resource acquisition rate, we have demonstrated experimentally (Peckarsky et al. 1993) that predator-induced increases in rates of swimming reduce resource acquisition and fecundity (falling limb of the resource acquisition curve). I would argue that for selection to maintain swimming as a foraging and predator avoidance behavior, the fecundity and mortality curves need to be parallel at the high end of the prey mobility axis, resulting in the shaded area where the distance between them (d = fitness) them is maximum. In other words, the fecundity costs of swimming to avoid predators cannot outweigh the mortality benefits of swimming away from predators.

In contrast, heptageniids crawl within and between food patches, also moving as food patches become depleted. They rarely encounter stoneflies because they often crawl away from predators before being contacted (80% encounters, Peckarsky et al. 1994). This pre-contact predator detection enables them to avoid using more energetically costly, disruptive, and conspicuous swimming behavior, which has been shown in this study to reduce resource acquisition in one heptageniid species (*E. longimanus*). Thus, crawling to acquire resources and avoid predators results in the highest fitness for heptageniid mayflies, maximizing the difference (d) between fecundity and mortality due to predation (Fig. 7 center).

Despite very high encounter rates with stoneflies (Peckarsky et al. 1994), *Ephemerella*'s considerable energy investment in physical defense (the costs of which have not been measured), results in feeding behavior that is largely unaffected by the presence of stoneflies. *Ephemerella* also crawls to forage within and between detritus patches, but as shown in this study, stopping or posturing to avoid stoneflies does not reduce their feeding rates. Thus, the fecundity curve is flat at the low mobility end of the axis (Fig. 7 lower), suggesting a range (shaded area) of foraging and predator avoidance behaviors (freeze, posture, and crawl) that maximize their fitness (d). The differences in shape between the resource acquisition curves of *Ephemerella* and the other two mayflies show that a more sedentary life style is not costly to *Ephemerella* because its food source (detritus) may be less depletable than the periphyton resource of the other two mayflies. Thus, I would spec-

ulate that *Ephemerella* can forage in one place longer without incurring a cost in resource acquisition.

Future work on this system should test hypotheses suggested by this model to explain the intriguing success of *Baetis*, its dominance over other species of grazing mayflies, and the selection pressures maintaining different predator avoidance syndromes. More detailed information is needed to understand how prey mobility affects rates of resource acquisition and fecundity with and without predators. Further, studies need to address how selection pressures from predation, parasitism, and competition singly and interactively affect the population dynamics of these mayflies and their resources. An analysis of this broader context of predation effects on mayfly behavior will enable us to develop a better understanding of the consequences of the alternative predator avoidance syndromes, both in terms of population dynamics of each species and community level interactions among species.

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