

CONSEQUENCES AND PLASTICITY OF THE SPECIALIZED PREDATORY BEHAVIOR OF STREAM-DWELLING STONEFLY LARVAE¹

BARBARA L. PECKARSKY, CATHY A. COWAN,² AND CHESTER R. ANDERSON

Department of Entomology, Cornell University, Ithaca, New York 14853 USA and
Rocky Mountain Biological Laboratory, P.O. Box 519, Crested Butte, Colorado 81224 USA

Abstract. The purpose of this study was to determine experimentally the potential mechanism(s) favoring specialized foraging behavior of stream-dwelling predatory stonefly larvae (*Megarcys signata*), and whether this specialized behavior was fixed or flexible. We measured stonefly growth rates after 10 d of conditioning on *Baetis bicaudatus* (Ephemeroptera) or one of two alternative mayfly prey species in replicated circular plexiglass flow-through chambers powered by water from a stream in western Colorado. We then compared attacks per encounter (as an index of predator choice) of conditioned stoneflies to those of unconditioned controls given equal densities of all three prey types. We conducted additional behavioral observations to determine whether predators differentially encountered the alternative prey types on natural substrates, and to determine whether predator-prey microhabitat overlap was a mechanism explaining differential prey encounter rates among prey species. *Megarcys* exhibited a stereotyped attack bias toward swimming mayflies, such as *Baetis*, following the simple rule, "attack any prey that swim," which results in *Megarcys*' selection of prey types that swim in response to stonefly encounters. This behavior remained unmodified after extended experience with alternate but palatable nonswimming mayfly species. A potential fitness advantage (measured as relative growth rate) of this behavioral specialization occurred for female *Megarcys*, but not for males. Female *Megarcys* grew faster on *Baetis* diets because they ate more *Baetis*, not because *Baetis* was a more intrinsically profitable prey item (in terms of promoting predator growth). Further, high feeding rates on *Baetis* were a result of disproportionately high encounter rates and attacks per encounter with *Baetis* compared to the other mayfly species. Our data are consistent with the hypothesis that this predatory behavior arose and is maintained in female stoneflies due to a fitness advantage to individuals specializing on a relatively abundant, easily recognized prey resource. We speculate that this specialized behavior has not been lost in male stoneflies, for which we did not measure a fitness advantage, because there is no strong selection pressure against it. Effective pre- and post-contact prey defenses may exert enough selection pressure to prevent stoneflies from evolving specialization on alternative mayfly types.

Key words: artificial stream channels; attacks per encounter; behavioral plasticity; encounter rates; fitness; growth rates; mayflies; prey profitability; prey selection; specialization; stoneflies; streams.

INTRODUCTION

An intriguing challenge in evolutionary ecology is to determine why some foragers have evolved specialized feeding behavior. Considerable attention has been paid to the notion that the major selection pressure leading to the evolution of specialized feeding behavior is energy maximization (e.g., Schoener 1971, Werner and Hall 1974, Townsend and Hughes 1981, Krebs and McCleery 1984, Pyke 1984, Stephens and Krebs 1986). The general argument supporting this view is that foragers maximize fitness by specializing on the most energetically profitable food types. Assumptions implicit in this argument are that: (1) specialists are more efficient foragers than generalists; (2) forager fitness is

limited by energy intake rate; (3) acquisition of the most profitable food is not outweighed by some other fitness cost such as increasing risk of predation or parasitism; (4) ranking of prey value by foragers is independent of prey encounter rates; and (5) forager recognition of profitable food types is instantaneous.

Recent investigations have cast doubt on the generality of all of these assumptions, challenging the notion that evolution should favor the existence of specialization from an energy efficiency standpoint (Futuyma and Moreno 1988). Fox and Morrow (1981) review the evidence from studies of specialization among terrestrial insect herbivores, concluding that there are no consistent differences in feeding efficiency between specialists and generalists (assumption 1). Glasser (1984) presents a theory suggesting that if resources are abundant relative to forager population size, obligate specialists will be favored; but where resources are scarce, an obligate generalist strategy will

¹ Manuscript received 26 May 1992; revised 15 March 1993; accepted 11 April 1993.

² Present address: California EPA, Department of Pesticide Regulation, Worker Health and Safety Branch, 1220 N Street, Suite 620, Sacramento, California, USA.

be the most efficient. Where the ratio of population size to resource abundance fluctuates, the energy-maximizing foraging strategy should be facultative specialization.

Increasing documentation exists that the energetically profitable diet may not necessarily provide the best mix of nutrients (Royama 1970). If not, natural selection should favor maximizing the nutritional value of potential diet items rather than simply the net energy gain per unit time (Greenstone 1979, Taghon 1981, Waldbauer and Friedman 1991) (assumption 2). Further, many recent empirical and theoretical studies consider the trade-offs between maximizing foraging efficiency and minimizing risk of predation (e.g., Werner and Mittlebach 1981, Sih 1982, Winterhalder 1983, Gilliam and Fraser 1987, Gilliam et al. 1989, Kohler and McPeck 1989). In other words, natural selection should favor foraging behaviors that maximize not only fecundity, but also survivorship (assumption 3).

An alternative explanation for the evolution of specialized foraging behavior is that the diet that maximizes forager fitness may be a function not only of intrinsic prey value, but also of prey encounter rate (assumption 4). Theoretical and experimental evidence shows that foragers will switch preferences, attacking disproportionately whichever of two prey types is more abundant (Lawton et al. 1974, Murdoch et al. 1975, Fullich and Greenwood 1979, Greenwood and Elton 1979). Presumably, such frequency-dependent selection is driven not by the intrinsic value of each prey item, but by responses of foragers to differential prey encounter rates (but see Hughes 1979, who differentiates encounter rates from prey densities). Murdoch et al. (1975) suggest that such flexible behavior is more efficient, and therefore, should be favored by natural selection. However, switching should not occur if (1) one prey type has such high value that regardless of its abundance, its relative rank can never be transposed with that of alternative prey, or (2) foragers are consistently generalists.

Hughes (1979) modifies the classic energy maximization model, relaxing the often unrealistic assumptions that prey recognition is instantaneous and that ranking of prey value is independent of prey encounter rates (assumptions 4 and 5). His modified model predicts that forager specialization should only be favored when profitable prey are easy to recognize (by some relatively simple physical properties, such as size, movement pattern, or distance from the predator) and their relative ranking is unambiguous (their profitability is significantly higher than that of alternative prey). Stein et al. (1984) likewise suggest that a predator's ability to discriminate among prey types may result in a foraging behavior that is inconsistent with the predictions of diet models based on energy costs and benefits alone.

Stoneflies from many geographic regions prey selectively on mayflies of the family Baetidae (Malmqvist

and Sjöström 1980, Molles and Pietruszka 1983, Walde and Davies 1987, Fuller and DeSteffan 1988, Peckarsky and Penton 1989, Peckarsky et al. 1990). Stoneflies are not strict dietary specialists, since dipteran larvae (Chironomidae and Simuliidae) may also be abundant in their guts (Peckarsky 1985); but data are insufficient to conclude whether feeding on these prey types is disproportionate to their abundance in the habitat, and little is known about the behavioral interactions between stoneflies and dipteran prey (Allan and Flecker 1988, Fuller and deSteffan 1988).

Studies of behavioral interactions between predatory perlotids and mayfly prey in simple arenas without substrates (e.g., Peckarsky and Penton 1989) have indicated that selectivity on baetid mayflies was a result of a highly specialized foraging behavior. (Thus we will refer to them as behavioral specialists.) Compared to other mayfly species, stoneflies attacked baetids more frequently per encounter (defined as predator-prey contact), because these prey primarily swam in response to stonefly contact, a hydrodynamically conspicuous evasive behavior. Other mayflies had high rates of attack per encounter if they swam to evade stoneflies, and attacks could be stimulated on unacceptable prey types by artificially oscillating them (Peckarsky and Wilcox 1989). Thus, a low incidence of swim responses to stoneflies was an effective post-contact defense; and stoneflies appear to be operating under a simple rule: "attack prey that swim once encountered," perhaps only recognizing individuals as prey if they swim. This decision rule results in stonefly specialization on swimming mayflies such as Baetidae. Thus, predatory stoneflies were not actively rejecting other prey types after encounters (active behavioral selection: Greene 1985), but prey defensive behavior coupled with stereotypical predator behavior was the mechanism explaining the pattern (fixed behavioral selection: Greene 1985).

We do not, however, know what selection pressures might have favored the evolution of this specific response, or whether this behavior is evolutionarily fixed or environmentally flexible. Also, we were not satisfied with our evaluation of relative predator-prey encounter frequencies measured in simple arenas without substrates (Peckarsky and Penton 1989). We know that alternative (nonswimming) mayflies are palatable, and may become more vulnerable to stonefly predation with the removal of substrate refuges, but we have not determined whether higher prey mortality is due to greater encounter frequencies or to increased attacks per encounter in the absence of refuges.

The purpose of the present study was to distinguish experimentally between an energy maximization and an encounter frequency (resource abundance) hypothesis to determine the potential mechanism(s) favoring specialized foraging behavior of stream-dwelling predatory stonefly larvae. These hypotheses are not mutually exclusive, because the most energetically prof-

TABLE 1. Summary of predator-prey combinations for growth and conditioning experiments. *N* = number of replicates per treatment level. No. = prey ration. *n* = number of mayflies measured. *R.* = *Rhithrogena*, *E.* = *Epeorus*.

Dates of trial	<i>Megarcys</i>		Prey available		Prey size classes (mg dry mass)			
	<i>N</i>	Sexes	Types	No.	$\bar{X} \pm 1 \text{ SE}$	<i>n</i>	$\bar{X} \pm 1 \text{ SE}$	<i>n</i>
11–25 June 1990	3	males + females	<i>Baetis</i>	20	large: 0.64 ± 0.04	20	small: 0.28 ± 0.04	20
			<i>Cinygmula</i>	20	large: 0.44 ± 0.07	19	small: 0.27 ± 0.07	20
			<i>Ephemerella</i>	20	large: 1.86 ± 0.06	20	small: 0.87 ± 0.06	20
11–22 September 1991	10	females	<i>Baetis</i>	15	0.44 ± 0.03	23		
			<i>R. robusta</i>	15	0.45 ± 0.03	19		
			<i>E. deceptivus</i>	15	0.56 ± 0.01	26		
11–22 September 1992	10	males	<i>Baetis</i>	15	0.49 ± 0.02	62		
			<i>R. robusta</i>	15	0.66 ± 0.03	65		
			<i>E. deceptivus</i>	15	0.81 ± 0.01	53		

itable prey may also be encountered with the highest frequency. Tests were also devised to determine whether specialized stonefly foraging behavior was fixed or flexible. Our specific objectives were to:

1. assess the plasticity of predatory preferences by comparing the attack behavior of fresh-caught (control) stoneflies to those of stoneflies conditioned on diets of three different mayfly prey species for an extended period;

2. determine whether there is a potential fitness advantage of specializing on one prey type by comparing the growth rates of conditioned stoneflies who have fed on the three different prey species;

3. evaluate whether any observed growth advantages are due to differences in prey profitability by comparing the growth per unit prey eaten and per milligram of prey eaten by stoneflies conditioned on different prey types;

4. determine whether observed growth advantages are due to differential encounter rates among prey types resulting in higher predation rates on the preferred mayfly species; and

5. distinguish the mechanism(s) explaining differential prey encounter rates among the following alternatives: concentration of prey search in the habitat of the preferred prey (habitat selection, Holbrook and Schmitt 1992), or differential pre-contact predator detection capabilities of prey.

METHODS

Species of predators and prey

Megarcys signata (Perlodidae) is one of two numerically dominant predatory stoneflies (the other being *Kogotus modestus*) that feed on mayflies in the East River and its tributaries in Gunnison County, Colorado (Peckarsky 1985, 1991). *Megarcys* is univoltine, having an asynchronous emergence period (in late June through mid-August) during the abbreviated summer season at this high elevation site (2950 m). *Megarcys* larvae have a pronounced sexual size dimorphism, with females emerging about twice as big as males (Peckarsky and Cowan 1991).

Megarcys feeds selectively on *Baetis bicaudatus*

(Peckarsky and Penton 1989), the numerically dominant mayfly in these streams (Peckarsky 1991), and females eat significantly more than do males (Peckarsky and Cowan 1991). As stated in the *Introduction*, stonefly diets also include dipteran larvae (Chironomidae and Simuliidae, Peckarsky 1985), but the mechanism explaining this pattern has yet to be investigated. Other mayfly species common in the stoneflies' habitat, but rare in their diets, are the Heptageniidae *Epeorus deceptivus*, *E. longimanus*, *Cinygmula mimus*, *Rhithrogena robusta*, and *R. hageni*, and the ephemereid *Ephemerella infrequens* (Peckarsky 1985, 1991). These mayflies are all univoltine. *Baetis*, however, has a short, nonsynchronous summer generation in July and August that strongly overlaps with a longer overwintering generation. Thus, *Baetis* larvae are present in the stream over the entire 12 mo of the year, whereas larvae of other mayfly species are absent during a summer recruiting period, the timing of which varies depending on the species. Combinations of the predator with three prey species were selected on the basis of temporal overlap in the natural habitat. For each experiment *Baetis* was always one alternative prey, and two other species were used that were the most abundant when each experiment was conducted (Table 1).

Experimental design

Growth experiment.—To determine whether behavioral specialization on one prey type conferred a fitness advantage to stoneflies (objective 2), we measured their growth rates in replicated circular plexiglass flow-through chambers (15 cm diameter) powered by gravity-fed filtered stream water from a fishless first-order tributary (Benthette Brook; 1990) or from a third-order reach of the East River (1991, 1992). Chambers were housed in a translucent vinyl greenhouse (Weatherport) beside the East River. A more complete description and illustrations of the system are provided in Peckarsky and Cowan (1991). Chambers were filled with ≈ 1 cm of gravel overlain by one granite rock taken from the East River. Flows in the chambers were spatially variable depending on the location relative to the water delivery jets, ranging from 3 to 22 cm/s. Since

the water supply system was natural streamwater, fluctuations in water chemistry and temperatures paralleled those of the natural stream.

In June 1990, we preweighed late instar individual male and female stoneflies on a Cahn microbalance (anaesthetized with Alka Seltzer, blotted, and placed in tared pharmaceutical capsules), and then reared them in chambers containing 20 prey individuals (predetermined by prey exploitation rates) of one of two size classes and one of three different mayfly species (see Table 1 for combinations). The smallest and largest available sizes of each prey species were collected from the East River. To determine the feeding rates of *Megarcys* over the conditioning period for use in prey profitability measurements (objective 3) we counted prey remaining in each chamber every 2 d (also determined by exploitation rates), and added new prey to bring densities back up to original levels. At the end of a 10-d conditioning period, we removed and reweighed predators, and destructively sampled chambers counting all remaining prey. We conducted three replicates per treatment level (predator sex: two levels; prey type: three levels; and prey size: two levels), limited by numbers of chambers and feasibility of conducting post-conditioning observations on large numbers of stoneflies within an acceptably short period of time.

Since predator age might affect behavioral plasticity, we conducted experiments in September 1991 and 1992 using early instar recruits of the next generation of *Megarcys* who were large enough to be predatory on mayflies (Allan 1982). Also, since no prey size effects were observed in 1990, we only used one prey size class in subsequent trials (Table 1). In 1991 we selected the largest individuals present in the stream to maximize feeding rates. While late instar male and female *Megarcys* larvae are easily distinguished externally by conspicuous precursors of adult reproductive structures, these structures were not present in early instars. We assumed, therefore, that reproductive development and sexual size dimorphism would not be present in these early instars and expected a 50:50 sex ratio. Interestingly, all of the individuals tested were females, indicating that sexual size dimorphism appears very early in larval development of *Megarcys*. As a result, we repeated the experiment with early instar males in September 1992, distinguishing sexes of larvae under a dissecting microscope by presence or absence of the precursor of the female gonopore.

We compared the predators' relative growth rates (as a percentage of initial body size) per day among stoneflies conditioned on the three different mayfly diets by two-way (late instars = prey type \times prey size) or one-way (early instars: prey type only) MANOVA along with an analysis of other interdependent response variables: (1) gain in mass per prey individual eaten; (2) gain in mass per unit mass of prey eaten; (3) number of prey eaten per day; and (4) mass of prey eaten per

day. We used transformations where necessary to normalize data and stabilize residuals (see *Results*). Relative growth rate comparisons measured an overall fitness advantage of specializing on certain prey types (assuming that larger larvae have higher reproductive outputs as adults, Peckarsky and Cowan 1991). If such a fitness advantage was observed, subsequent separate ANOVAs and LSD multiple comparisons determined whether it was due to inherent prey value (response variables 1 and 2) or predator feeding rate (response variables 3 and 4). We conducted analyses on each predator sex separately.

Plasticity of foraging behavior.—After the 10-d conditioning period, we replaced each predator into its original chamber, but with no prey. Unconditioned male and female stoneflies of masses similar to those of the conditioned individuals were collected from the stream at this time and also placed in chambers with no prey. We did not control for differences between time in experimental chambers of conditioned vs. unconditioned stoneflies. However, the lack of significant treatment effects suggested no systematic experimental artifacts. After a 24-h starvation period the foraging behavior of each conditioned stonefly was compared to that of the unconditioned controls. We starved the stoneflies prior to observations, both to control hunger levels, and because previous work showed that starved individuals were much more responsive to prey than are well-fed ones, but had similar patterns of prey preferences (Peckarsky and Penton 1989).

We presented each stonefly with equal densities of all three prey types, but only the same size class of prey with which it had been conditioned (seven each, approximating mean natural total mayfly densities, Peckarsky 1991), and compared their foraging behavior to that of the unconditioned control stoneflies (randomly assigning control stoneflies to one size class or the other). We recorded attacks per encounter on audio tape for each predator for a period of 10 min between 0900 and 1100 Mountain Daylight Time, a period when stoneflies were actively feeding and when observations were practical. We used attacks per encounter as the behavioral response variable, since this is the only predator behavior that varied significantly between mayfly prey types (Peckarsky and Penton 1989), and is the component of predator behavior where choice between prey types occurs. Thus, we could determine whether manipulation of previous encounter history affected the tendency of stoneflies to selectively attack *Baetis* (objective 1).

For late instars, we observed effects of stonefly dietary conditioning on subsequent predatory behavior in rectangular flow-through chambers (10 \times 20 cm) with Nitex substrates that were placed in the East River (as in Peckarsky and Penton 1989). For early instar observations we glued sand substrate to 15 cm diameter circular chambers creating a habitat more similar to that in which stoneflies were conditioned, and in

which stoneflies foraged more freely. In all trials viewing chambers received no substrates except one black glass refuge (2 × 2 cm) elevated on beads under which predators could hide. As in Peckarsky and Penton (1989), predators rarely used the refuges. We did not include other substrates in these trials because we wished to minimize differences in encounter rates between predators and three prey species so that the response variable, attacks per encounter, would be based on similar replication of encounters. Previous experiments suggested that encounter rates proportionate to prey densities should occur in arenas without substrates (Peckarsky and Penton 1989).

We conducted two-way MANOVAs (late instars: prey size × prey type) or one-way MANOVAs (early instars: prey type only) on each predator sex separately. We compared the patterns of attacks per encounter (arcsine transformed) of each of the three mayfly species (interdependent response variables) by unconditioned control stoneflies to those of stoneflies conditioned on the three different mayfly diets. For significant MANOVAs, individual ANOVAs and LSD multiple comparisons determined the source of observed differences.

Analysis of encounter rates on natural substrates.— We conducted additional behavioral observations during 1990–1992 to determine whether predators differentially encountered the alternative prey types on natural substrates (objective 4). We recorded predator–prey encounter rates on audio tape during 10-min observation periods in larger (25 cm diameter) versions of the circular flow-through chambers that were placed in an elevated plexiglass tray, such that they could be observed from above or below. Arenas received natural substrates, including gravel and six larger granite or slate rocks (three each located randomly within chambers). Rocks were not overlain on gravel so that there was no location in the arena where stoneflies or mayflies (none of which burrowed in the gravel) could be obscured from the views of observers stationed above and below the arenas.

Individual late instar *Megarcys* were starved for 24 h (to control for hunger levels) and exposed to 8, 16, 24, or 50 (*Baetis* only) prey per chamber (single-species trials, $n = 8$), representing a range of prey densities observed in nature. We tested the same prey species as those used in the growth and conditioning studies (Table 1). Further, we conducted one mixed species treatment (8 each of three mayfly species) to determine whether the presence of alternative prey affected the predator–prey encounter rates with each prey species. For mixed prey trials, we used the same combinations of prey species as in the late instar experiments (Table 1). We included male and female stoneflies in the same analysis because they showed similar encounter rate patterns.

We defined encounters as predator–prey contacts, since stoneflies rarely detect prey without first touching them (Martinez 1987). However, mayflies frequently

detect stoneflies before contact (Peckarsky 1987), and thereby evade encounters. Therefore, we compared both the frequency of encounters (contacts) and the frequency of prey responses to stoneflies without contact (interdependent response variables) by two-way MANOVA (prey type and prey density). Where MANOVAs were significant, we conducted subsequent individual ANOVAs and LSD multiple comparisons to determine the source of observed differences. For mixed prey trials we conducted multiple paired *t* tests to compare predator–prey encounter rates and non-contact prey responses to predators among prey species (experimentwise comparisons using Bonferroni-adjusted significance levels). We also recorded the location of each encounter, noting whether it was on a rock or gravel, and measured the amount of time spent by each stonefly foraging (moving) in these two microhabitats. Differences in the locations (rock or gravel) of encounters between stoneflies and each of the mayfly species were also analyzed by paired *t* tests. Microhabitat preferences of stoneflies were similarly analyzed (rock vs. gravel).

Microhabitat selection of prey species.— To distinguish the mechanism(s) explaining differential prey encounter rates among prey species (objective 5) we made repeated observations of mayfly microhabitat locations in 15-cm arenas containing rocks and gravel. We similarly observed microhabitats of alternative mayfly prey species from above and below, but in the smaller arenas (15 cm diameter) with only two sections each of gravel or a granite rock (locations randomized). These tests were conducted on *Baetis*, *Ephemerella*, and two heptageniids (*Cinygmula* and *Epeorus deceptivus*) in August 1991. We made observations at the same time every day (noon) to control for diel positioning periodicity. We placed eight mayflies in each chamber (single species only) and half the chambers received a late instar live stonefly whose mouthparts were glued to prevent predation. We analyzed preferences of each mayfly species for rocks or gravel in the presence and absence of predators by the paired Wilcoxon Signed-Ranks Test to control for possible effects of time, since we used subsequent days as replicates ($n = 5$). This experiment enabled us to identify the microhabitat use by each mayfly species and whether observed preferences were affected by the presence of a predatory stonefly.

RESULTS

Effects of dietary conditioning on predatory behavior

There were no significant effects of dietary conditioning on the predatory behavior of female *Megarcys* or early instar males (Table 2). These stoneflies had consistently high rates of attacks per encounter on *Baetis* compared to those on the other mayfly species (Fig. 1), and the pattern of attacks per encounter of alter-

TABLE 2. MANOVA tables for attacks per encounter (A/E) (arcsine transformed) and subsequent ANOVA tables (where MANOVAs were significant) and LSD tests. (ANOVA tables are only presented where $P < .10$. Complete tables are available from B. L. Peckarsky.)

Analysis	Variable	Source	ss*	df†	F	P	LSD results‡	
1990 (late instars)								
♀ <i>Megarcys</i>	MANOVA	prey type	0.484	9, 29	1.13	.372		
	MANOVA	prey size	0.966	3, 12	0.14	.935		
♂ <i>Megarcys</i>	MANOVA	prey type	0.132	9, 27	3.88	.003		
	MANOVA	prey size	0.375	3, 11	6.10	.011		
	<i>Baetis</i> A/E	model		0.514	7	9.79	.0003	control > B = C = E large > small
		prey type		0.297	3	13.19	.0003	
		prey size		0.104	1	13.86	.003	
		interaction		0.047	3	2.07	.152	
	<i>Cinygmula</i> A/E	model		0.114	7	1.09	.421	
		error		0.193	13			
	<i>Ephemerella</i> A/E	model		0.007	7	0.52	.805	
		error		0.026	13			
1991 (early instars)								
♀ <i>Megarcys</i>	MANOVA	model	0.801	9, 80	0.85	.570		
1992 (early instars)								
♂ <i>Megarcys</i>	MANOVA	model	0.502	9, 54	1.95	.06		

* Wilk's criterion.

† Numerator, denominator df for MANOVA F.

‡ B = *Baetis* diet, E = *Ephemerella* diet, C = *Cinygmula* diet.

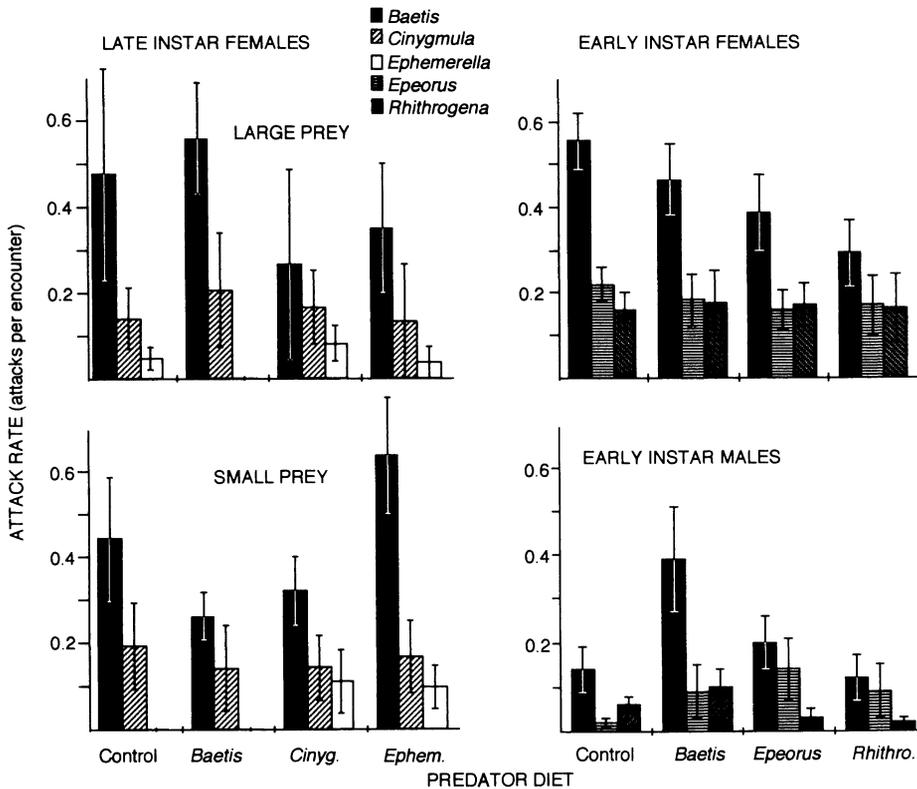


FIG. 1. Attacks per encounter ($\bar{X} \pm 1$ SE) on three different prey species offered in equal densities in flow-through arenas without substrates during 10-min trials. (See Table 1 for replication.) Control individuals were unconditioned, while others were given specified diets for 10 d before observations. (Data for late instar male *Megarcys* in Table 3.)

TABLE 3. Attacks per encounter during 10-min trials by *Megarcys* stoneflies on alternate prey species offered in equal densities in flow-through arenas without substrates (means \pm 1 SE). (See Table 1 for replication.) Control individuals were unconditioned and others were given specified diets for 10 d before observation.

Trial	Control	<i>Baetis</i> diet	<i>Cinygmula</i> diet	<i>Ephemera</i> diet
1990 (late instars), δ <i>Megarcys</i>				
Large <i>Baetis</i>	0.46 \pm 0.02	0.05 \pm 0.05	0.08 \pm 0.08	0.24 \pm 0.07
Large <i>Cinygmula</i>	0.19 \pm 0.06	0.15 \pm 0.11	0.12 \pm 0.12	0.03 \pm 0.03
Large <i>Ephemera</i>	0.02 \pm 0.02	0.06 \pm 0.06	0 \pm 0	0.02 \pm 0.02
Small <i>Baetis</i>	0.21 \pm 0.01	0.05 \pm 0.05	0.02 \pm 0.02	0.04 \pm 0.04
Small <i>Cinygmula</i>	0.06 \pm 0.06	0 \pm 0	0 \pm 0	0 \pm 0
Small <i>Ephemera</i>	0 \pm 0	0 \pm 0	0 \pm 0	0.02 \pm 0.02

native mayfly prey species did not differ between conditioned and unconditioned control stoneflies. Therefore, in early and late instar female and early instar male *Megarcys*, the apparently stereotypical behavior pattern of disproportionate attack rates on swimming mayflies was not altered by 10 d of experience with alternative, nonswimming prey.

In contrast, there was a significant prey type and prey size effect on attacks per encounter for late instar male *Megarcys* (Table 2). In this case, unconditioned control stoneflies had a greater number of attacks per encounter on *Baetis* than did any of the conditioned stoneflies,

and attacks per encounter on large *Baetis* were higher than those on small *Baetis* (Table 3). The prey size effect reflects an extremely low overall attack rate of late instar male *Megarcys* on small prey. The prey type effect indicates that late instar male *Megarcys* conditioned on any prey species were less likely to attack *Baetis* than were fresh-caught stoneflies. But in most cases, attack rates were still higher on *Baetis* than on the other mayfly species and behavioral modifications were not consistent with expected effects of experience on predatory behavior. In other words, this result does not indicate that conditioning caused a change in pred-

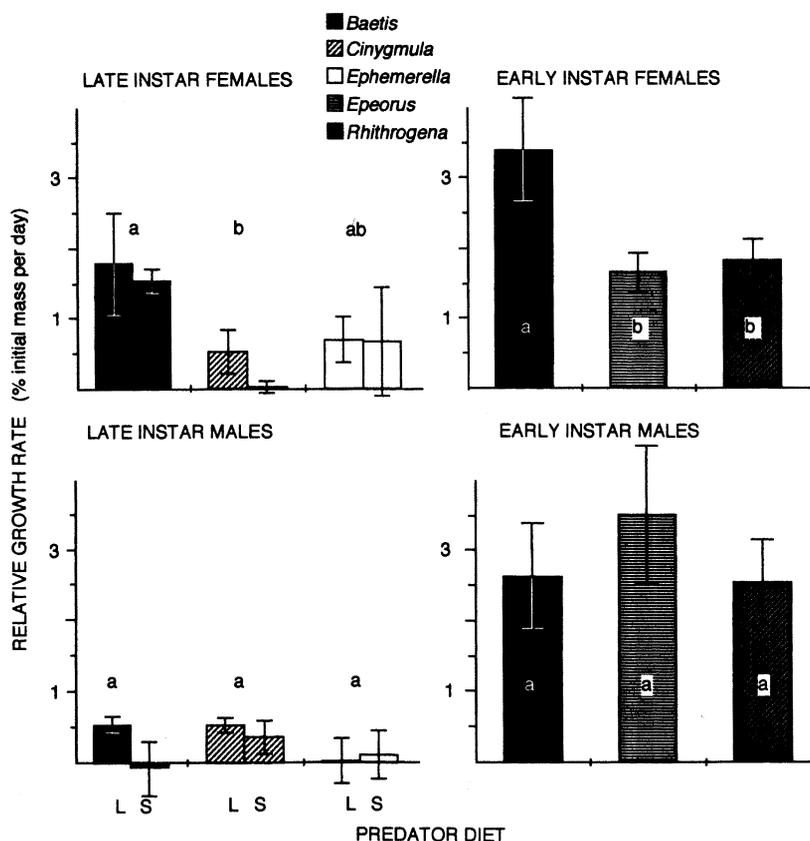


FIG. 2. Relative growth rates ($\bar{X} \pm 1$ SE) of late and early instar *Megarcys* females and males conditioned on three different diets for 10 d. (See Table 1 for sample sizes.) Growth rates denoted with different lowercase letters are significantly different (see Table 4). L = large prey; S = small prey.

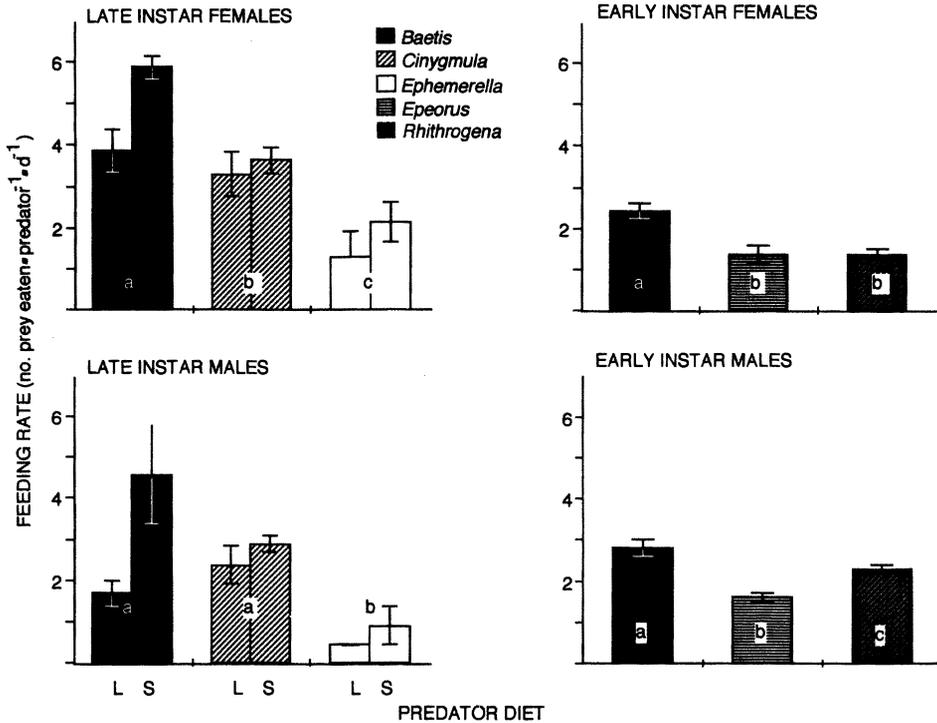


FIG. 3. Feeding rates ($\bar{X} \pm 1 \text{ SE}$) of late and early instar female and male *Megarcys* conditioned on three different diets for 10 d. Feeding rates denoted with different lowercase letters are significantly different (see Table 4).

ator preference toward the prey type on which the stoneflies had been feeding. Instead, we suspect late instar male behavior here was an experimental artifact of the treatment.

Effects of diet on growth and feeding rates

Megarcys growth rates were highly variable depending on the instar and sex of the stoneflies (Fig. 2). Late instar females grew faster than males, and generally had higher feeding rates than males (Fig. 3). Both males and females slow their feeding rates just prior to emergence, and *Megarcys* are protandrous, males emerging before females (Peckarsky and Cowan 1991). Thus, their growth and feeding rates level off before those of females as they allocate resources to reproductive maturation (Branham and Hathaway 1975). As a result, late instar males did not eat or grow much during these trials. The fastest growing *Megarcys* individuals were the early instars, although the large late instar females ate more prey per day (Fig. 3). In early and late instar females there was a significantly higher growth rate of individuals feeding on *Baetis* than on one (late instars) or both (early instars) of the other prey species (Fig. 2, Table 4). Thus, over the 10-d period of dietary conditioning, females conditioned on *Baetis* accrued more biomass than those feeding on the heptageniids or *Ephemerella*.

We then tested whether this growth advantage could be explained by higher feeding rates on *Baetis* than on

alternative prey, or by greater intrinsic prey value of *Baetis*. Comparison of the feeding rates of individual stoneflies (in terms of both numbers and mass of each prey type eaten per day) shows that early and late instar females and early instar males ate significantly more *Baetis* per day than of either of the alternative prey (Fig. 3, Table 4). Interestingly, late instar male *Megarcys* also ate more *Baetis* and *Cinygmula* than *Ephemerella* (Fig. 3, Table 4), but this did not result in corresponding mass gain differences (Fig. 2), nor were the feeding rate differences of early instar male *Megarcys* reflected in differences in patterns of growth. Late instars of both males and females also ate more small than large prey (Fig. 3, Table 4). We estimated the mass of prey eaten per predator per day by multiplying the number of prey consumed over the 10-d trial by the average mass of prey (Table 1). Interestingly, early instar female *Megarcys* also ate a greater mass of *Baetis* than of the other two prey types (Table 5), because the sizes of the three prey types were similar (Table 1).

Intrinsic value of prey was calculated in two ways: (1) growth rates of individual stoneflies per prey eaten, and (2) growth rates per unit mass of prey eaten. We used these measures because they integrate all the parameters (search and handling costs and benefits) used in the conventional estimates of prey profitability (e.g., Schoener 1971, Werner and Hall 1974, Pastorok 1981) and are independent of prey encounter rates (Stephens

TABLE 4. MANOVA tables for several measures of prey value to *Megarcys*. Complete ANOVA tables and LSD results are given where MANOVAs were significant.

Analysis	Variable*	Source	ss†	df‡	F	P	LSD results§
1990 (late instars)							
♀ <i>Megarcys</i>	MANOVA	prey type	0.0147	10, 16	7.53	.0001	
	MANOVA	prey size	0.1205	5, 8	11.68	.002	
	RGR	model	6.608	5	1.91	.166	B > C
		prey type	6.122	2	4.43	.036	
		prey size	0.308	1	0.45	.517	
		interaction	0.177	2	0.13	.881	
		error	8.288	12			
	Prey value no.	model	0.473	5	0.70	.636	
		error	1.628	12			
	Prey value mass	model	1.610	5	1.59	.237	
		error	2.436	12			
	Feeding rate no.	model	37.36	5	11.41	.0003	
		prey type	30.03	2	22.93	.0001	B > C > E
		prey size	5.12	1	7.82	.016	small > large
		interaction	2.21	2	1.68	.227	
	error	7.86	12				
Feeding rate mass	model	1.297	5	1.32	.320		
	error	2.359	12				
♂ <i>Megarcys</i>	MANOVA	prey type	0.0054	10, 14	117.60	.0001	
	MANOVA	prey size	0.0179	5, 7	76.87	.0001	
	RGR	model	1.069	5	1.00	.459	
		error	2.570	12			
	Prey value no.	model	0.148	5	0.20	.956	
		error	1.631	11			
	Prey value mass	model	0.515	5	1.06	.431	
		error	1.065	11			
	Feeding rate no.	model	33.53	5	7.01	.003	
		prey type	20.21	2	10.56	.002	B = C > E
		prey size	7.47	1	7.81	.016	small > large
		interaction	5.841	2	3.05	.085	
		error	11.49	12			
	Feeding rate mass	model	0.458	5	0.87	.531	
		error	1.157	11			
1991 (early instars)							
♀ <i>Megarcys</i>	MANOVA	model	0.0183	10, 44	128.10	.0001	
	RGR	model	17.92	2	3.82	.035	B > Ep = R
		error	60.97	26			
	Prey value no.	model	0.945	2	0.28	.756	
		error	4.339	26			
	Prey value mass	model	33.59	2	0.27	.765	
		error	1614.48	26			
	Feeding rate no.	model	7.343	2	12.57	.0002	B > Ep = R
		error	7.597	26			
	Feeding rate mass	model	0.010	2	7.33	.003	B > Ep = R
		error	0.018	26			
	1992 (early instars)						
♂ <i>Megarcys</i>	MANOVA	model	0.0156	10, 34	23.76	.0001	
	RGR	model	4.576	2	0.45	.6453	
		error	107.43	21			
	Prey value no.	model	0.165	2	1.19	.325	
		error	1.463	21			
	Prey value mass	model	0.653	2	0.31	.736	
		error	2.144	21			
	Feeding rate no.	model	5.660	2	17.58	.0001	B > R > E
		error	3.380	21			
	Feeding rate mass	model	0.159	2	1.390	.270	
		error	1.195	21			

* Relative growth rates (RGR = body mass gained per unit initial body mass); prey value no. (mass gained per prey eaten); prey value mass (mass gained per unit mass of prey eaten); feeding rate no. (prey eaten per day); and feeding rate mass (mass of prey eaten per day, log [y] transformed 1990).

† Wilk's criterion.

‡ Numerator, denominator df for MANOVA F.

§ B = *Baetis*, C = *Cinygmula*, E = *Ephemera*, Ep = *Epeorus*, R = *Rhithrogena*.

TABLE 5. Feeding rate of *Megarcys* (mass of prey eaten per predator per day) conditioned on three different diets for 10 d (mean ± 1 SE). Feeding rates with different superscript letters were significantly different (see Table 4).

Trial	Feeding rate (prey mass eaten per predator per day)		
	Predator diet		
1990 (late instars)			
♀ <i>Megarcys</i>	<i>Baetis</i>	<i>Cinygmula</i>	<i>Ephemerella</i>
Large prey	2.32 ± 0.31	1.48 ± 0.24	2.43 ± 1.13
Small prey	1.83 ± 0.08	0.98 ± 0.06	1.85 ± 0.42
♂ <i>Megarcys</i>			
Large prey	1.12 ± 0.06	1.08 ± 0.21	0.85 ± 0.01
Small prey	1.39 ± 0.41	0.82 ± 0.06	0.82 ± 0.41
1991 (early instars)			
♀ <i>Megarcys</i>	<i>Baetis</i>	<i>Rhithrogena</i>	<i>Epeorus</i>
	0.106 ± 0.008 ^a	0.062 ± 0.006 ^b	0.078 ± 0.011 ^b
1992 (early instars)			
♂ <i>Megarcys</i>	1.363 ± 0.09	1.508 ± 0.730	1.318 ± 0.09

and Krebs 1986). Also, they do not require any black box calculations based on difficult assumptions (Mitchell 1981, Palmer 1983, Anholt 1986, McClintock 1986). Interestingly, *Baetis* was not the most valuable prey item per prey individual eaten or per unit mass of prey eaten (Table 6). Thus, all prey types (per individual or per unit mass) were of equivalent profitability from the standpoint of promoting growth of *Megarcys*. Thus, our results indicate that feeding rate rather than prey value was responsible for the observed growth advantage to female *Megarcys* of feeding on *Baetis*.

Predator-prey encounter rates on natural substrates

Encounter rates between predators and all prey types increased significantly with prey density (Fig. 4A, Table 7). Given the same density of alternative prey types on natural substrates, *Megarcys* encounter rates with *Baetis* and *Ephemerella* were significantly higher than those on the heptageniids at all prey densities in both

single (Fig. 4A) and mixed (Table 8) prey trials. One explanation for this pattern was that under all conditions the heptageniids (*Cinygmula*, *Epeorus*, and *Rhithrogena*) showed a high frequency of predator avoidance responses before predator contact (Fig. 4B, Table 7). In contrast, *Baetis* and to a greater extent, *Ephemerella*, rarely responded to *Megarcys* without contact.

We further sought to explain this pattern by examining the microhabitat overlap of *Megarcys* with that of *Baetis*. *Megarcys* foraged during these trials primarily on gravel, with the result that significantly more predator-prey encounters occurred with all prey species in the preferred microhabitat of the predators (Fig. 5, Table 9). Further, in the absence and presence of predators, both *Baetis* and the heptageniids preferred rocks over gravel, whereas *Ephemerella* preferred gravel (Fig. 6, Table 10). These microhabitat preferences are consistent with the hypothesis that microhabitat overlap is a mechanism resulting in high encounter

TABLE 6. Prey value for *Megarcys* in terms of gain in mass per number of prey eaten (No.) and gain in mass per unit mass of prey eaten (Mass) over the 10-d conditioning period on three different diets (mean ± 1 SE). None of the prey values were significantly different (see Table 4).

Trial	Measure		Measure		Measure	
	No.	Mass	No.	Mass	No.	Mass
1990 (late instars)						
♀ <i>Megarcys</i>	<i>Baetis</i>		<i>Cinygmula</i>		<i>Ephemerella</i>	
Large prey	.388 ± .065	.646 ± .109	.178 ± .095	.394 ± .210	.441 ± .163	.236 ± .087
Small prey	.257 ± .039	.826 ± .127	.005 ± .029	.020 ± .110	.043 ± .478	.034 ± .561
♂ <i>Megarcys</i>						
Large prey	.227 ± .072	.342 ± .108	.137 ± .004	.301 ± .009	-.003 ± .504	.001 ± .268
Small prey	-.030 ± .060	-.117 ± .207	.081 ± .060	.288 ± .211	.178 ± .130	.194 ± .142
1991 (early instars)						
♀ <i>Megarcys</i>	<i>Baetis</i>		<i>Rhithrogena</i>		<i>Epeorus</i>	
	.460 ± .110	1.05 ± 2.5	.359 ± .038	.801 ± .08	.493 ± .208	.874 ± .37
1992 (early instars)						
♂ <i>Megarcys</i>	.210 ± .064	.431 ± .131	.220 ± .063	.334 ± .095	.468 ± .139	.575 ± .171

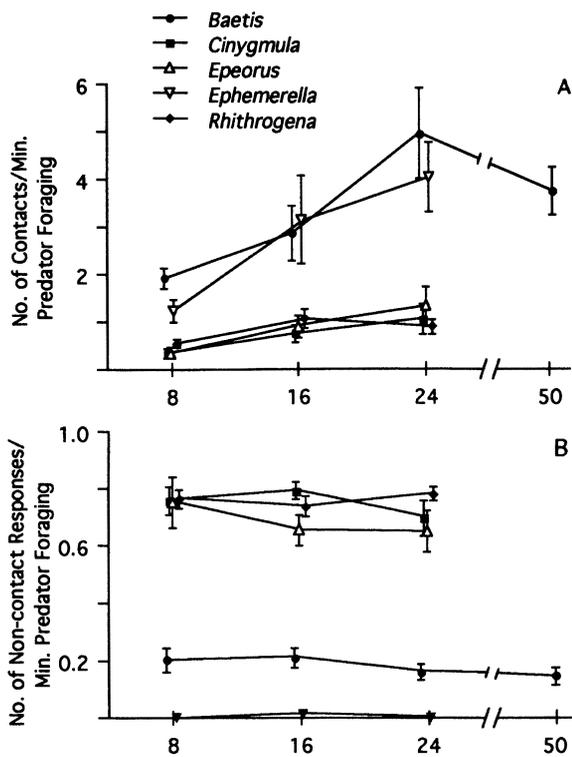


FIG. 4. Encounter rates (contacts: upper) and responses by prey to predators without contact (lower) for late instar *Megarcys* ($\bar{X} \pm 1$ SE, $n = 8$ 10-min trials) over the entire range of prey densities tested (single prey species trials). Observations were made in arenas with natural substrates.

rates between *Megarcys* and *Ephemerella*. However, microhabitat overlap does not explain the disproportionately high encounter rates of *Megarcys* on *Baetis*. Other experiments designed to determine the temporal and spatial overlap of predators and prey on rock surfaces (tops, bottoms, and sides) suggest that high en-

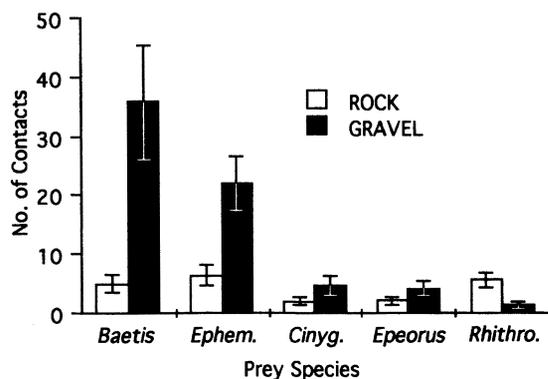


FIG. 5. Location of predator-prey encounters in arenas with substrates for late instar *Megarcys* ($\bar{X} \pm 1$ SE, $n = 8$ 10-min trials). *Cinyg.* = *Cinygmula*, *Ephem.* = *Ephemerella*, *Rhithro.* = *Rhithrogena*.

counter rates between *Megarcys* and *Baetis* are not a simple function of spatial and temporal microhabitat overlap (B. L. Peckarsky and C. A. Cowan, unpublished data), but may instead reflect the high mobility of *Baetis* compared to that of other mayflies. Interestingly, high levels of mobility (drift responses to encounters with stoneflies) is the reason why numbers of *Baetis* on rocks and gravel do not add up to 8 in chambers with predators (Fig. 6, top graph).

In summary, a combination of differential prey responses to stoneflies before contact, and microhabitat overlap, may explain the differences in predator-prey encounter rates observed on natural substrates.

DISCUSSION

Behavioral plasticity

Neither early nor late instar *Megarcys* altered their responses to mixed prey assemblages to favor an alternate prey type on which they had been feeding for

TABLE 7. MANOVA tables for encounter rates (predator-prey contacts), and responses by prey without predator contact, per 10-min trials.

Variable	Source	ss*	df†	F	P	LSD results‡
MANOVA	prey type	0.080	8, 228	72.46	.0001	
MANOVA	prey density	0.685	6, 228	7.9	.0001	
Log (encounter rates)						
	model	74.88	7	28	.0001	
	prey type	51.04	4	33.64	.0001	B > E > R = Ep = C
	prey density	15.86	3	13.94	.0001	24 > 16 > 8
	interaction	1.65	8	0.53	.8339	
	error	43.62	115			
Arcsine square root (noncontact responses)						
	model	20.83	7	143.38	.0001	
	prey type	20.78	4	250.32	.0001	R = C = Ep > B > E
	prey density	0.049	3	0.80	.4987	
	interaction	0.081	8	0.47	.8747	
	error	2.3861	115			

* Wilk's criterion.

† Numerator, denominator df for MANOVA F.

‡ B = *Baetis*, E = *Ephemerella*, C = *Cinygmula*, Ep = *Epeorus*, R = *Rhithrogena*.

TABLE 8. Encounter rates (contacts) and noncontact prey responses in mixed prey trials between stoneflies and mayflies in arenas with substrates. Means \pm 1 SE of 8 10-min trials.

Variable	Prey species			<i>p</i> *		
	<i>Baetis</i> (B)	<i>Cinygmula</i> (C)	<i>Ephemerella</i> (E)	B-C	B-E	C-E
Encounter rates	1.347 \pm 0.370	0.341 \pm 0.127	1.054 \pm 0.244	0.0318	0.2259	0.0192
Noncontact responses	0.221 \pm 0.083	0.787 \pm 0.072	0.048 \pm 0.048	0.0040	0.1241	0.0001

* Probability of a greater absolute value of Student's *t*.

TABLE 9. Paired *t* tests of locations of predator-prey encounters in arenas with natural substrates at all prey densities in single and mixed prey trials (8 of each of 3 prey species). Values are probabilities of a greater absolute value of *t*; *n* = 8.

Prey species	Prey density			Mixed	Direction
	8	16	24		
<i>Baetis</i>	0.0199	0.0019	0.0129	0.0454	gravel > rock
<i>Cinygmula</i>	0.0331	0.0342	0.2434	0.3159	gravel > rock
<i>Ephemerella</i>	0.0050	0.0092	0.0082	0.0189	gravel > rock
<i>Epeorus</i>	1.0000	0.1970	0.1036	—	gravel = rock
<i>Rhithrogena</i>	0.0169	0.0479	0.0195	—	rock > gravel

10 d. Stoneflies consistently focused their attacks on *Baetis* regardless of prior conditioning. Thus, predatory stoneflies of this and a related species (*Kogotus modestus*; B. L. Peckarsky, unpublished data) showed no modification of prey preference as a result of recent experience. Previous studies of these predators also deemed them inflexible on a shorter time scale, in that they did not exhibit "switching" behavior to disproportionately feed on the most abundant prey type (Peckarsky and Penton 1989). Even in the absence of their favored prey (*Baetis*), stoneflies had low attack and consumption rates on alternative prey that were comparable to their low attack and consumption rates on alternate prey types in the presence of *Baetis*. Unlike other aquatic invertebrate predators (Odonata: Bergelson 1985; Hemiptera: Jeffries 1988; Diptera: Jin and Sprules 1988; mysidacean Crustacea: Folt 1984), stoneflies did not alter their feeding behavior in the presence of alternate prey types (Peckarsky and Penton 1989). Bergelson (1985) suggests that frequency-dependent prey selection (switching) should occur if the more abundant prey type also has a high probability of capture. Since prey types other than *Baetis* have generally low capture probabilities (Peckarsky and Penton 1989), the observed inflexibility of stonefly responses to manipulated prey densities supports this suggestion.

There are several possible mechanistic explanations for this pattern of inflexible behavior. First, stoneflies are a relatively old order of aquatic insects (Plecoptera), and may not have the neurological machinery to learn new behaviors. We doubt that this is true, since other studies have demonstrated that Plecoptera are capable of learning the location of shelters that reduce their exposure to predatory trout (Feltmate and Williams

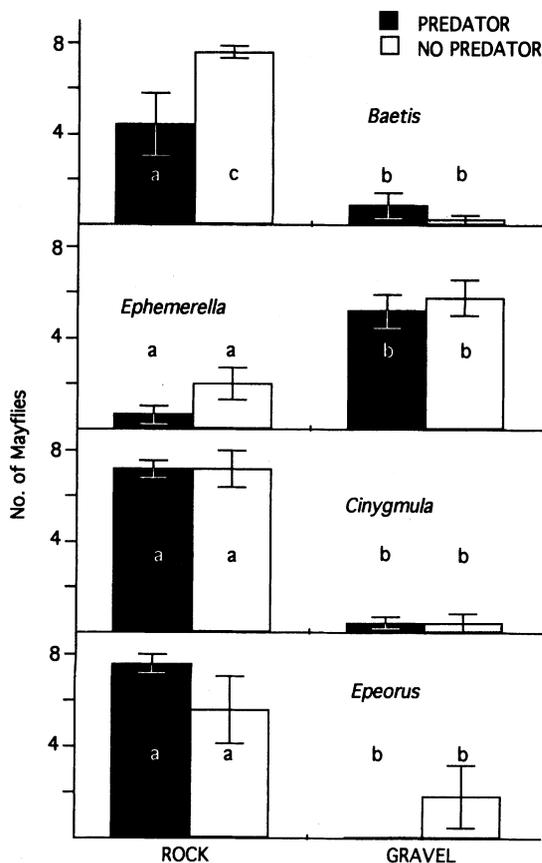


FIG. 6. Microhabitat preferences of each mayfly species in arenas with and without predators ($\bar{X} \pm 1$ SE, *n* = 5). Locations were measured in arenas with natural substrates. Histogram bars with different letters are significantly different.

TABLE 10. Paired Wilcoxon signed ranks tests of microhabitat preferences of prey species with and without predators; $n = 5$.

Prey species	No predator		Predator	
	Ranking	P^*	Ranking	P^*
<i>Baetis</i>	rock > gravel	<.05	rock = gravel	<.10
<i>Cinygmula</i>	rock > gravel	<.05	rock > gravel	<.05
<i>Ephemerella</i>	gravel > rock	<.05	gravel > rock	<.05
<i>Epeorus</i>	rock > gravel	<.05	rock > gravel	<.05

* Probability of a greater absolute value of T .

1991). Further, foraging flexibility has been observed in insect orders with older lineages than the Plecoptera (e.g., Odonata: Blois 1985, Johansson 1990). The fact that most evidence of induction of feeding preferences or learning to switch to more abundant prey types has been obtained from studies of the more derived insect orders (Papaj and Prokopy 1989, Bell 1990): e.g., Lepidoptera (Jermy et al. 1968, deBoer and Hanson 1984, Dethier 1988), and Hymenoptera (Johnson 1991) may simply indicate investigator bias. Finally, Hewett's (1988) observation that ciliate protozoans (*Didinium*) performed better on prey sizes on which they were conditioned suggests that complicated neuronal pathways are not a required mechanism of foraging plasticity.

A second possible explanation for why we did not observe effects of conditioning is that the time scale of our experiments might have been inadequate. Ten days may be too short a period for stoneflies to become conditioned to alternative prey types. However, Johansson (1990) reported that odonate larvae were able to learn to feed on novel prey items in 2 d, and Johnson (1991) found that desert seed-harvester ants learned new seed-harvesting techniques very quickly (within 10 d). Therefore, we suspect that 10 d was a reasonable time period within which to expect stoneflies to learn to attack alternative but palatable prey types. Neither is it probable that the stoneflies forgot the 10 d of conditioning experience during the 24 h starvation period preceding the behavioral observations. There is little evidence of memory in insects, with the exception of the Hymenoptera. For example, Johnson (1991) showed that desert seed-harvester ants had long memories, taking about three times longer (30 d) to lose their novel behaviors than to acquire them. Therefore, we suspect that 1 d was too short a time period for stoneflies to forget 10 d of experience.

A third possible explanation for inflexible predator behavior is that stoneflies may become conditioned to *Baetis* at some early critical developmental stage, after which their behavior cannot be modified by experience. This explanation is also improbable, because we observed inflexible predator behavior in early instar *Megarcys* of both sexes, not long after they were big enough to be predatory.

The simplest explanation for the observed behavioral inflexibility is that it is genetically fixed, and therefore, not responsive to environmental fluctuations. Via

(1991) demonstrated that even more prolonged experience (three generations) of three specialized pea aphid clones did not result in shifts of specialization on different host plants. Further, experience with novel host plants did not affect the relative performance of specialists. Via suggested that these results were consistent with the hypothesis that selection is operating against movement to a different host plant, because the aphids cannot improve their fitness by doing so. In a review of host-associated differences in fitness of insects, Futuyama and Peterson (1985) speculate that host-associated genotypes of specialists are usually superior in fitness, which would select against shifts to new resources.

Why did stoneflies evolve specialized predatory behavior?

Why, then, has *Megarcys* evolved such inflexible specialization on swimming mayflies, such as *Baetis*? Is there a measurable advantage to this feeding behavior in terms of fitness-related parameters? We have documented previously that larger female stoneflies are more fecund (Peckarsky and Cowan 1991). Therefore, fast growth rates and larger larval body size probably confers a fitness advantage to females. Stonefly males drum the substrates with their abdomens to court females, and responsive females usually answer, leading to copulation. However, preliminary observations of the reproductive biology of *Megarcys* suggest that larger males may have no advantage over smaller males in terms of reproductive success (B. W. Taylor and B. L. Peckarsky, unpublished data). If behavioral specialization on *Baetis* confers a fitness advantage (at least for females), we expected higher growth rates on stoneflies conditioned on a *Baetis* diet.

Female *Megarcys* grew faster on *Baetis* diets than on alternative prey, but there were no observed growth differences for male *Megarcys* conditioned on alternative mayfly diets. Late instar males did not grow much during the trials, but we also measured no growth advantage of eating *Baetis* for earlier instar males, which had high growth rates during trials. First, we will describe the mechanism resulting in the growth advantage to female *Megarcys* feeding on *Baetis*. Then we will speculate on why *Megarcys* might have evolved this specialized behavior and why we still observe consistent, inflexible attack behavior in *Megarcys* males

even though such behavior did not confer any observable benefit.

Our data show that female *Megarcys* grew faster on *Baetis* diets because they ate more *Baetis* during the trials, not because each *Baetis* individual or unit mass of *Baetis* was of greater intrinsic value. Other studies of predatory stoneflies have similarly shown that attacks were not biased toward more energetically profitable prey (Allan and Flecker 1988). Interestingly, although Allan et al. (1987) have also shown that *Megarcys* is size-selective for large *Baetis*, we observed no growth advantage for this species when feeding on their preferred prey size class. All *Megarcys* ate more *Baetis* because they encountered more *Baetis* than other mayflies offered in equal densities, and they attacked more *Baetis* per encounter. These data combined with similar rates of captures per attack among mayfly prey species (Peckarsky and Penton 1989) result in higher capture and consumption rates on *Baetis* than on other prey types. In the natural stream system, the bias toward high encounter rates on *Baetis* is probably even more pronounced, because *Baetis* is relatively more abundant than the other mayflies (Peckarsky 1985, 1991). Other predatory stoneflies have been shown to eat disproportionately the most abundant groups of aquatic insects (Feminella and Stewart 1986).

Thus we would speculate that the evolution of specialized stonefly behavior arose as a response to a relatively common, temporally and spatially predictable prey resource that is particularly easy to recognize. By following the simple rule, "if it swims, attack it" female *Megarcys* have achieved an attack bias toward *Baetis*, which maximizes their fitness. If *Baetis* or other swimming mayflies (families Baetidae, Leptophlebiidae, Oligoneuriidae, Siphonuridae) have been abundant (as they are in the present) in the habitats of predatory stoneflies throughout their evolutionary history, individuals specializing on this easily recognized prey type might have been favored due to disproportionately high predator-prey encounter rates. A test of this hypothesis would require observation of predatory stonefly behavior in habitats where they have existed for long periods devoid of swimming mayfly species. Unfortunately we know of no such habitats (which may explain the inflexibility of their behavior). Other empirical and theoretical studies support an encounter rate hypothesis as a reasonable scenario for the evolution of specialized predatory behavior (Real and Caraco 1986, Osenberg and Mittlebach 1989).

Since the reward for specializing on *Baetis* is clear for female *Megarcys*, and such swimming prey are easily recognized, switching to nonswimming prey types would require a major behavioral change that provides no clear benefit. Alternative prey species were of similar intrinsic value, but due to their morphology and behavior are of generally lower vulnerability to stonefly predation (Molles and Pietruszka 1983, 1987, Fuller and DeSteffan 1988, Peckarsky and Penton 1989, Ful-

ler and Rand 1990). Ephemerelellidae are hard-bodied, spiny, and rarely swim when encountered by predatory stoneflies. These attributes make them relatively invulnerable prey types, except when in post-molt condition (Soluk 1990). Heptageniidae also rarely swim when encountered by stoneflies, but even more interesting is our observation in the present study that they can detect and avoid stoneflies before contact, dramatically lowering their rates of encounters with predators. Thus, these pre- and post-contact prey defenses may exert selection pressure against stonefly specialization on alternative mayfly types. Also, nonswimming mayflies rarely occur in high densities in this region (Peckarsky 1991). It is under these conditions that switching is theoretically less likely to occur (Murdoch et al. 1975, Hughes 1979). Studies of predatory odonate larvae have similarly shown that their prey selection behavior neither conforms to predictions of optimal diet models, nor to frequency-dependent selection ("switching") models (Sherratt and Harvey 1989, Harvey and White 1990). These predators select one prey type regardless of manipulated relative abundances of alternative prey.

Despite the fact that we did not measure a growth advantage to selective predation by males, we suspect that this specialized foraging behavior has been retained in males for similar reasons: because there is no strong selection pressure against specializing on *Baetis*. Further experimentation on their reproductive biology will also verify preliminary observations that size, and possibly growth rate, have no effect on male *Megarcys* reproductive success. It is possible, however, that developmental or metabolic differences between males and females resulted in female but not male growth rates responding to predation rate differences between prey species. Males used in these experiments were much smaller than females, and at different developmental stages than females. Further, growth rates of early instar males were highly variable, which reduced the potential for observing responses to different prey species.

In summary, predatory stoneflies exhibit a stereotyped attack bias toward swimming mayflies. As a result of following the simple rule, "attack any prey that swim," they specialize on prey types that swim in response to stonefly encounters (e.g., *Baetis*). This behavior was not modified through extended experience with alternate, but palatable, nonswimming mayfly species. Thus, the relative ranking of *Baetis* in the diets of these stoneflies was not altered by manipulating predator-prey encounter rates. A potential fitness advantage (measured as relative growth rate) of this behavioral specialization occurs for females, but not for males. Observed growth advantages of female *Megarcys* were due to disproportionately high encounter rates with *Baetis* as well as to the bias in attacks per encounter, resulting in disproportionate feeding rates on *Baetis* compared to those on other prey species. *Baetis*

was not an intrinsically more valuable prey type (in terms of predator growth rates per prey individual or per unit of prey biomass eaten). Therefore, female *Megarcys* grew faster on *Baetis* diets because they ate more *Baetis*, not because *Baetis* was a more profitable prey item.

Our data are consistent with the hypothesis that this predatory behavior arose and is maintained in female stoneflies due to a fitness advantage to individuals specializing on a relatively abundant, easily recognized prey resource. We also speculate that this specialized behavior has not been lost in male stoneflies because there is no fitness cost associated with it. Further, effective pre- and post-contact prey defenses may exert enough selection pressure to prevent stoneflies from evolving specialization on alternative mayfly types.

ACKNOWLEDGMENTS

We thank Marge Penton and Billie Kerans for helping us with the field and lab work for this project. Billie Kerans gave us valuable statistical advice. Discussions with Chuck Greene, Nelson Hairston, Jr., Drew Harvell, and other members of Cornell's Aquatic Ecology Lunch Bunch, especially Gilson Moreira, Peter Ode, Alex Flecker, and Sarah Vance made this a much more lucid document than it would otherwise have been. Thanks also to Dan Soluk, Jim Collins, and an anonymous reviewer for improving the presentation of this manuscript. Donna Bunce provided clerical support. This work was supported by NSF Grant Number BSR-8906737 to B. L. Peckarsky.

LITERATURE CITED

- Allan, J. D. 1982. Feeding habits and prey consumption of three setipalpine stoneflies (Plecoptera) in a mountain stream. *Ecology* **63**:26–34.
- Allan, J. D., and A. S. Flecker. 1988. Prey preference in stoneflies: a comparative analysis of prey vulnerability. *Oecologia* (Berlin) **76**:496–503.
- Allan, J. D., A. S. Flecker, and N. L. McClintock. 1987. Prey size-selection by carnivorous stoneflies. *Limnology and Oceanography* **32**:864–972.
- Anholt, B. 1986. Prey selection by the predatory leech *Nephalopsis obscura* in relation to three alternative models of foraging. *Canadian Journal of Zoology* **64**:649–655.
- Bell, W. J. 1990. Searching behavior patterns in insects. *Annual Review of Entomology* **35**:447–468.
- Bergelson, J. M. 1985. A mechanistic interpretation of prey selection by *Anax junius* larvae (Odonata: Aeshnidae). *Ecology* **66**:1699–1705.
- Blois, C. 1985. Variation of predatory behaviour in *Anax imperator* larvae in relation to different prey types. *Biological Behaviour* **10**:183–214.
- Branham, J. M., and R. R. Hathaway. 1975. Sexual difference in the growth of *Pteronarcys californica* Newport and *Pternarcella badia* (Hagen) (Plecoptera). *Canadian Journal of Zoology* **53**:501–506.
- deBoer, G., and F. E. Hanson. 1984. Food plant selection and induction of feeding preference among host and non-host plants in larvae of the tobacco hornworm *Manduca sexta*. *Entomologia Experimentalis et Applicata* **35**:177–194.
- Dethier, V. G. 1988. Induction and aversion-learning in polyphagous arctiid larvae (Lepidoptera) in an ecological setting. *Canadian Entomologist* **120**:125–131.
- Feltmate, B. W., and D. D. Williams. 1991. Path and spatial learning in a stonefly nymph. *Oikos* **60**:64–68.
- Feminella, J., and K. W. Stewart. 1986. Diet and predation by three leaf-associated stoneflies (Plecoptera) in an Arkansas mountain stream. *Freshwater Biology* **16**:521–538.
- Folt, C. L. 1984. Predator efficiencies and prey risks at high and low prey densities. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **22**:3210–3214.
- Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon. *Science* **211**:887–893.
- Fuller, R. L., and P. A. DeSteffan. 1988. A laboratory study of the vulnerability of prey to predation by three aquatic insects. *Canadian Journal of Zoology* **66**:73–81.
- Fuller, R. L., and D. S. Rand. 1990. Influence of substrate type on vulnerability of prey to predaceous aquatic insects. *Journal of the North American Benthological Society* **9**:1–9.
- Fullich, T. G., and J. J. D. Greenwood. 1979. Frequency dependent food selection in relation to two models. *American Naturalist* **113**:762–765.
- Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* **19**:207–234.
- Futuyma, D. J., and S. C. Peterson. 1985. Genetic variation in use of resources by insects. *Annual Review of Entomology* **30**:217–238.
- Gilliam, J. F., Jr., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* **68**:1856–1862.
- Gilliam, J. F., D. F. Fraser, and A. M. Sabet. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. *Ecology* **70**:445–452.
- Glasser, J. W. 1984. Evolution of efficiencies and strategies of resource exploitation. *Ecology* **65**:1570–1578.
- Greene, C. H. 1985. Planktivore functional groups and patterns of prey selection in pelagic communities. *Journal of Plankton Research* **7**:35–40.
- Greenstone, M. H. 1979. Spider feeding behaviour optimizes dietary essential amino acid composition. *Nature* **282**:501–503.
- Greenwood, J. J. D., and R. A. Elton. 1979. Analyzing experiments on frequency-dependent selection by predators. *Journal of Animal Ecology* **48**:721–738.
- Harvey, I. F., and S. A. White. 1990. Prey selection by larvae of *Pyrrhosoma nymphula* (Sulzer) (Zygoptera: Coenagrionidae). *Odonatologica* **19**:17–26.
- Hewett, S. W. 1988. Predation by *Didinium nasutum*: effects of predator and prey size. *Ecology* **69**:135–145.
- Holbrook, S. J., and R. J. Schmitt. 1992. Causes and consequences of dietary specialization in surfperches: patch choice and intraspecific competition. *Ecology* **73**:402–412.
- Hughes, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. *American Naturalist* **113**:209–221.
- Jeffries, M. 1988. Individual vulnerability to predation: the effect of alternative prey types. *Freshwater Biology* **19**:49–56.
- Jermy, T., F. E. Hanson, and V. G. Dethier. 1968. Induction of specific food preference in lepidopterous larvae. *Entomologia Experimentalis et Applicata* **11**:211–230.
- Jin, E. J., and W. G. Sprules. 1988. Effects of prey composition on the feeding of *Chaoborus flavicans* larvae. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen* **23**:2165–2169.
- Johansson, F. 1990. Foraging in larvae of *Aeshna juncea* (L.): patch use and learning (Anisoptera: Aeshnidae). *Odonatologica* **19**:39–46.
- Johnson, R. A. 1991. Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. *Ecology* **72**:1408–1419.
- Kohler, S. L., and M. A. McPeck. 1989. Predation risk and

- the foraging behavior of competing stream insects. *Ecology* **70**:1811–1825.
- Krebs, J. R., and R. H. McCleery. 1984. Optimization in behavioural ecology. Pages 91–121 in J. R. Krebs and N. B. Davies, editors. *Behavioral ecology. An evolutionary approach*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Lawton, J. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pages 141–158 in M. B. Usher and M. H. Williamson editors. *Ecological stability*. Chapman and Hall, London, England.
- Malmqvist, B., and P. Sjöström. 1980. Prey size and feeding patterns in *Dinocras cephalotes* (Plecoptera). *Oikos* **35**:311–316.
- Martinez, L. A. 1987. Sensory mechanisms underlying the predator–prey interactions between perlotid stonefly nymphs and their mayfly prey. Dissertation. Cornell University, Ithaca, New York, USA.
- McClintock, J. B. 1986. On estimating energetic values of prey: implications in optimal diet models. *Oecologia* (Berlin) **70**:161–162.
- Mitchell, R. 1981. Insect behavior, resource exploitation and fitness. *Annual Review of Entomology* **26**:373–396.
- Molles, M. C., Jr., and R. D. Pietruszka. 1983. Mechanisms of prey selection by predaceous stoneflies: roles of prey morphology, behavior and predator hunger. *Oecologia* (Berlin) **57**:25–31.
- Molles, M. C., Jr., and R. D. Pietruszka. 1987. Prey selection by a stonefly: the influence of hunger and prey size. *Oecologia* (Berlin) **72**:473–478.
- Murdoch, W. W., A. Avery, and M. B. E. Smythe. 1975. Switching in predatory fish. *Ecology* **56**:1094–1105.
- Osenberg, C. W., and G. G. Mittelbach. 1989. Effects of body size on the predator–prey interactions between the pumpkinseed sunfish and gastropods. *Ecological Monographs* **59**:405–432.
- Palmer, A. R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *Journal of Experimental Marine Biology and Ecology* **73**:95–124.
- Papaj, D. R., and R. J. Prokopy. 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology* **34**:315–350.
- Pastorok, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* **62**:1311–1324.
- Peckarsky, B. L. 1985. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? *Canadian Journal of Zoology* **63**:1519–1530.
- . 1987. Mayfly cerci as defense against stonefly predation: deflection and detection. *Oikos* **48**:161–170.
- . 1991. Habitat selection by stream-dwelling predatory stoneflies. *Canadian Journal of Fisheries and Aquatic Science* **48**:1069–1076.
- Peckarsky, B. L., and C. A. Cowan. 1991. Consequences of larval intraspecific competition to stonefly growth and fecundity. *Oecologia* (Berlin) **88**:277–288.
- Peckarsky, B. L., S. C. Horn, and B. Statzner. 1990. Stonefly predation along a hydraulic gradient: a test of the harsh-benign hypothesis. *Freshwater Biology* **24**:181–191.
- Peckarsky, B. L., and M. A. Penton. 1989. Mechanisms of prey selection by stream-dwelling stoneflies. *Ecology* **70**:1203–1218.
- Peckarsky, B. L., and R. S. Wilcox. 1989. Stoneflies prefer hydrodynamically conspicuous prey. *Oecologia* (Berlin) **79**:265–270.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* **15**:523–576.
- Real, L., and T. Caraco. 1986. Risk and foraging in stochastic environments. *Annual Review of Ecology and Systematics* **17**:371–390.
- Royama, T. 1970. Factors governing the hunting behavior and selection of food by the great tit (*Parus major* L.). *Journal of Animal Ecology* **39**:619–668.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**:369–404.
- Sherratt, T. N., and I. F. Harvey. 1989. Predation by larvae of *Pantala flavescens* (Odonata) on tadpoles of *Phyllomedusa trinitatis* and *Physalaemus pustulosus*: the influence of absolute and relative density of prey on predator choice. *Oikos* **56**:170–176.
- Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* **63**:786–796.
- Soluk, D. A. 1990. Postmolt susceptibility of *Ephemerella* larvae to predatory stoneflies: constraints on defensive armour. *Oikos* **58**:336–342.
- Stein, R. A., C. G. Goodman, and E. A. Marschall. 1984. Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* **65**:702–715.
- Stevens, D. W., and J. R. Krebs. 1986. *Foraging theory. Monographs in Behavior and Ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Taghon, G. 1981. Beyond selection: optimal ingestion rate as a function of food value. *American Naturalist* **118**:202–214.
- Townsend, C. R., and R. N. Hughes. 1981. Maximizing net energy returns from foraging. Pages 86–108 in C. R. Townsend and P. Calow, editors. *Physiological ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Via, S. 1991. Specialized host plant performance of pea aphid clones is not altered by experience. *Ecology* **72**:1420–1427.
- Waldbauer, G. P., and S. Friedman. 1991. Self-selection of optimal diets by insects. *Annual Review of Entomology* **36**:43–64.
- Walde, S. J., and R. W. Davies. 1987. Spatial and temporal variation in the diet of a predaceous stonefly (Plecoptera: Perlodidae). *Freshwater Biology* **17**:109–116.
- Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by bluegill sunfish (*Lepomis macrochirus*). *Ecology* **55**:1042–1052.
- Werner, E. E., and G. G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. *American Zoologist* **21**:813–830.
- Winterhalder, B. 1983. Opportunity-cost foraging models for stationary and mobile predators. *American Naturalist* **122**:73–84.