Mechanisms of prey selection by predaceous stoneflies: roles of prey morphology, behavior and predator hunger

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Summary. Laboratory feeding experiments using *Hesperoperla pacifica* (Banks), Perlidae, and *Megarcys signata* (Hagen), Perlodidae, as predators and *Baetis tricaudatus* Dodds and *Ephemerella altana* Allen as prey indicate a strong effect of prey morphology and mobility and predator hunger on prey selection by stoneflies. Knowledge of both dietary composition and feeding behavior was necessary to fully understand prey selection by these stoneflies.

Fasted stoneflies presented with live prey ate more *E. altana* while satiated stoneflies ate approximately equal numbers of the two mayfly species. This pattern of dietary composition was the result of a reduction of attack frequency on the slower swimming *E. altana* with predator satiation and a continued high attack rate on *B. tricaudatus* regardless of recent feeding history. In contrast, fasted *H. pacifica* fed fresh frozen mayflies ate more *B. tricaudatus* indicating the importance of differences in prey mobility in controlling dietary composition.

The high degree of similarity in patterns of feeding and mechanisms underlying those patterns for *H. pacifica* and *M. signata* suggest that they may be using similar "rules" for choosing mayfly prey and we suggest that mayfly prey are ranked by stoneflies on the basis of handling times. A general mechanistic model for stoneflies feeding on mayflies is presented and discussed.

Introduction

The central questions facing a foraging predator are: 1) What type of prey to eat, 2) Where to hunt, and 3) What search path to follow (MacArthur 1972; Krebs 1978). In this study of predaceous stoneflies (Order Plecoptera) we focused on the first question. In a general sense prey selection may be defined as the deviation of prey items included in the diet from their proportions in the environment (Hassell and Southwood 1978). Two approaches have been taken to gain an understanding of prey selection. Optimal foraging theory has attempted to predict prey choice as a function of food quality by constructing design rules for optimal prey selection (Krebs and Cowie 1976), while empirical studies have either attempted to test predictions from this theory (see Krebs and Cowie 1976; Pyke et al. 1977;

Werner and Mittlebach 1981) or have simply quantified feeding preferences, often employing one of a variety of electivity indices (Cock 1978; Lechowicz 1982).

There have been many studies of the dietary habits of predaceous stoneflies which have utilized either gut analysis alone (Muttkowski and Smith 1929; Hynes 1941; Brinck 1949; Minshall and Minshall 1966; Sheldon 1969; Tarter and Krumholz 1971; and Cather and Gaufin 1975) or a combination of gut analysis with a variety field assessments of prey availability (Mackereth 1957; Vaught and Stewart 1974; Siegfried and Knight 1976; Fuller and Stewart 1977; Snellen and Stewart 1979; Johnson 1981; Allan 1982). In each of these latter studies many prey occurred in the guts of stoneflies in frequencies which differed from their occurrence in benthic samples indicating "apparent" prey selection. However, as pointed out by Allan (1982) and Peckarsky (1982) prey selection determined from field data may be mainly the result of the juxtaposition of the life cycles of stoneflies and their prey and not the result of active prey selection.

A direct approach to studying prey selection, controlled experiments, has been largely ignored in studies of stonefly feeding ecology. The most recent review of aquatic insect predator-prey relations (Peckarsky 1982) cites three experimental field studies of stonefly-prey interactions (Peckarsky 1980; Peckarsky and Dodson 1980a b) and only one laboratory study of prey selection by stoneflies (Malmqvist and Sjöström 1980). However, these studies already present intriguing data concerning interactions between stoneflies and their prey. The field studies indicate sophisticated mechanisms of avoidance of stoneflies by mayflies and the laboratory study presents a challenge to conventional wisdom regarding prey selection by showing that *Dinocras cephalotes*, a perlid stonefly, is not size selective when preying on *Baetis rhodani*. The present laboratory study of stoneflies was undertaken to add to this base of experimental information on prey selection that will eventually aid in the interpretation of the more complex field situation.

The major questions we addressed ourselves to in this study were: 1) How do prey morphology and escape tactics affect prey selection by stoneflies, 2) How does hunger affect prey selection by stoneflies, 3) Would the "foraging rules" worked out for one species of predaceous stonefly be followed by another distantly related but ecologically similar species, 4) How is handling time for a particular prey species related to its inclusion in stonefly diets?

Materials and methods

Experimental animals

Stoneflies (Order Plecoptera) are convenient for laboratory studies of prey selection because they are large, which eases direct observations, and because many have relatively long-lived stream dwelling nymphal stages, up to 3 years, which insures the availability of experimental animals. Mayflies (O. Ephemeroptera) were selected as prey because they comprise a significant portion of the diets of carnivorous stoneflies (references on gut contents cited above) and because they are very diverse morphologically and behaviorally (Dodds and Hisaw 1924; Edmunds 1972; Edmunds et al. 1976; Peckarsky 1980). Such diversity within a group of prey is necessary to elucidate the role of prey behavior and morphology in determining inclusion in the diet of predators.

The two stonefly species used in our experiments, *Hesperoperla pacifica* (Banks), Perlidae, and *Megarcys signata* (Hagen), Perlodidae, are distributed throughout western North America (Baumann et al. 1977). Although belonging to different families, both species are tactile searching predators known to consume mayflies and appear to be ecologically similar, with *M. signata* generally found at higher elevations (Cather and Gaufin 1975; Muttkowski and Smith 1929; Fuller and Stewart 1977; Peckarsky 1980; Allan 1982). *H. pacifica* used in our experiments were collected at an intermediate elevation (2,030 m) from Jemez Creek, a third order stream in Sandoval County, New Mexico, USA. *M. signata* were collected from a high elevation (3,300 m) first order tributary of Teseque Creek, Santa Fe County, N.M. Both are high gradient streams with heterogeneous gravel and cobble substrate.

Two mayfly species, *Baetis tricaudatus* Dodds (Baetidae) and *Ephemerella altana* Allen (Ephemerellidae), were used as prey in our experiments. These two were chosen because of their contrasting morphologies and behavior. *B. tricaudatus* is a streamlined, fast swimming species that can be found on the exposed surfaces of rocks in swift riffles (Dodds and Hisaw 1924; Molles and Pietruszka personal observation). The usual reaction to a predator by this and similar species is to swim swiftly away. In contrast, *E. altana* is a robust, armored and weak swimming species that is usually found tightly clinging to aquatic vegetation or stones. When disturbed, *E. altana*, like other ephemerellids, usually remain motionless, and may raise their tails in scorpionlike fashion (Peckarsky 1980, 1982). Both mayfly species were collected from Jemez Creek. They do not occur in the section of Tesuque Creek where we collected *M. signata* although closely related species occur there.

Laboratory stream

Experiments were carried out in a laboratory stream housed in the biology department at the University of New Mexico, Albuquerque. The stream is a continuous flow oval design with water circulation maintained by a Flotec (TM) pump placed in an adjacent 760 l storage reservoir. The stream path consists of two straight 4.88 m × 40 cm × 30 cm reaches, constructed of plywood coated with ParaRock (TM) paint. These sections are connected by half circle sections 40 cm × 78 cm outside radius, constructed of Lexan (TM) plastic (Fig. 1). Throughout the experiments water velocity was 7–10 cm/sec with a depth of 17 cm. The stream
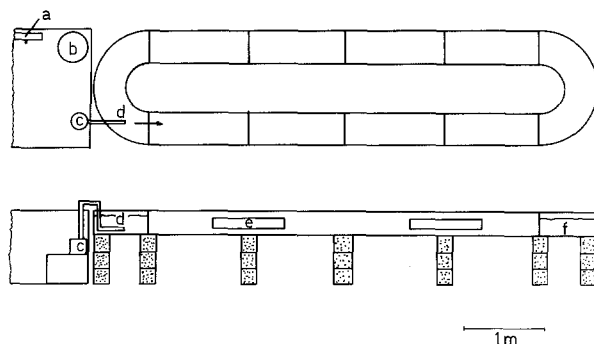

Fig. 1. Diagrammatic representation of the laboratory stream. *a* compressed air, *b* Frigid Units water refrigerator, *c* FlowTec water pump, *d* water inlet, *e* viewing port, *f* Lexan plastic end section

Table 1. Range of head capsule widths (mm) of stoneflies and mayflies used in experiments

Predators			
Hesperoperla pacifica			*Megarcys signata*
Small	Medium	Large	
2.9–3.9	4.0–4.9	5.1–6.6	3.2–4.0

Prey	
Baetis tricaudatus	*Ephemerella altana*
0.6–1.1	0.6–1.45

was filled with dechlorinated tap water and maintained at 7–11 C by a Frigid Units (TM) water refrigerator and aerated with filtered compressed air. Filtration of wastes was supplied by algae allowed to grow on the sides and bottom of the stream. Excess algal growth was periodically removed from the stream with fine mesh aquarium nets. Animals were exposed to natural photoperiod augmented by full spectrum fluorescent lights.

Stoneflies were individually housed in 10.4 × 10.4 × 6.3 cm polyethylene containers into which eight 7 mm openings were bored to provide for water circulation. These openings were screened with 0.25 mm nylon screening. Cages were weighted and kept in the main current of the stream. Sixty *H. pacifica* were kept under these conditions for 4 months with only 2 deaths. Mayflies were freshly captured before each experiment and maintained in chilled aerated buckets for 1–2 days before their use.

Experimental design

Initial experiments were designed to determine whether *H. pacifica*, in a structurally simple environment, would select preferentially between *B. tricaudatus* and *E. altana* when presented in equal numbers. Furthermore, we were interested in whether hunger might affect prey selection.

Since *H. pacifica* were present in the study stream in a wide range of sizes (<1.0–>6.6 mm head capsule width) and changes in diet with size have been described for stoneflies (Fuller and Stewart 1977; Sheldon 1969, 1980), we partitioned this species into small, medium, and large size classes for the experiments (Table 1). Feeding trials were

conducted in which 5 each of *B. tricaudatus* and *E. altana* were placed into cages of the stoneflies and left overnight (18–24 h), after which the numbers of each prey species eaten were recorded. These trials were conducted with stoneflies having two feeding histories, fasted and satiated, and with prey that were either active or immobilized. Fasted stoneflies were deprived of food for 6 days prior to the feeding trial. This corresponds to ~1.5–2 X the feeding pulse maxima found by Malmqvist and Sjöström (1980) for the perlid stonefly *Dinocras cephalotes*. Satiated individuals were presented with an excess of food consisting of a random mix of small insect species from Jemez Creek 24 h before the trial. In trials with immobilized prey, freshly frozen mayflies were thawed immediately prior to introduction into stonefly cages. This procedure eliminated prey mobility as a potential factor in prey selection but probably had little effect on the nutritive quality of the prey. In all trials *B. tricaudatus* and *E. altana* were carefully matched for size to avoid size selective effects.

To investigate mechanisms of prey selection that might be suggested by overnight trials, we conducted short-term, direct observations with each of the size classes of *H. pacifica*. In these, 5 each of the two mayfly species were placed within stonefly cages and monitored for 20 min during which all stonefly encounters, attacks, and captures of mayflies were recorded. Encounters were defined as any physical contact between prey and any portion of the head region (usually antennae) of a stonefly. The response of a stonefly to an encounter was considered an attack if it resulted in a marked increase in movement rate (usually with lacinia extended) directed at the prey item. Since mayfly species may differ in their defense tactics and hence in their ability to avoid contact with predators (Peckarsky 1980), we compared attack/encounter ratios in our analyses rather than absolute number of attacks. Handling times, time from capture to complete consumption, were recorded for all captures with an electronic stopwatch. As with overnight feeding trials, both fasted and satiated stoneflies were tested and prey species were size-matched; however, only active prey were used in these trials.

Experiments involving *M. signata* were designed to determine if, under the same experimental conditions, another large predaceous stonefly would exhibit patterns of foraging similar to *H. pacifica* without having a natural history of exposure to the prey items presented. In these experiments only short-term, direct observations were conducted since our observations of *H. pacifica* indicated that 20 min were sufficient to observe normal feeding. These trials were refined over earlier ones, by immediately replacing individuals of each mayfly species eaten, thereby avoiding the potential bias of changing encounter probabilities as a consequence of differential consumption of the two prey species. As with *H. pacifica*, both fasted and satiated *M. signata* were tested and only size-matched, active prey were used. The size of *M. signata* used in these experiments is representative of the range of sizes present in Tesuque Creek, where the species was represented by a single cohort, and most closely matched the small *H. pacifica* (Table 1).

All the above direct observations were conducted in daylight. Nighttime observations of 5 fasted *H. pacifica* and 5 satiated *M. signata* were also conducted using a Noctron IV (TM) night viewing scope to validate the easier daylight observations. This was necessary since it has been suggested that stonefly nymphs are most active at night (Vaught and

Table 2. Results of 24 h feeding trials for *Hesperoperla pacifica*. Values are Wilcoxon rank sum T statistics (Conover 1980) indicating a tendency for preference for either *Baetis tricaudatus* or *Ephemerella altana*. Negative values indicate a tendency for *Baetis*, positive values indicate a tendency for *Ephemerella*

Feeding category	Hesperoperla size class			
	N	Small	Medium	Large
Fasted/live prey	20	2.669***	1.651	−1.552[1]
	20	2.883***	1.312	1.605
	20	−	2.581**	0.975
Satiated/live prey	20	1.149	−0.639	0.106
	20	−1.232	−	−
Fasted/dead prey	20	−3.354***	−2.659[2]***	−1.628
	20	−2.825***	−	−
Satiated/dead prey	20	−0.791	−2.231[1]*	−1.165[3]

1 = number of replicates (N) reduced to 18
2 = number of replicates (N) reduced to 19
3 = number of replicates (N) reduced to 17

* $P<0.05$, ** $P<0.01$, *** $P<0.005$

Stewart 1974; Hynes 1976). We expected that, if the major activity period occurred at night rather than during the day, attack frequencies (attack/encounter ratios) would be higher than those found during daylight trials.

All statistical analyses of results were based on the methods of Siegel (1956) and Conover (1980). Wilcoxon rank sum tests were used to determine whether stoneflies preferentially consumed one or the other of the mayfly prey. Mann-Whitney U tests were used to compare attack/encounter ratios and handling times.

Results

Hesperoperla pacifica

In overnight feeding trials hunger and prey mobility were shown to have significant effects on prey selection by at least some size classes of *H. pacifica* (Table 2). Small, fasted *H. pacifica* consumed more *E. altana* than *B. tricaudatus* ($P<0.005$) in both trials. However this was true for only one of three trials for medium *H. pacifica* ($P<0.01$) while all three trials with large, fasted individuals yielded random results. In contrast satiated *H. pacifica* of all three size classes appeared to feed randomly. Presentation of frozen mayflies produced a dramatic reversal of results in which small and medium, fasted *H. pacifica* selected *B. tricaudatus* over *E. altana* ($P<0.001$) and there was a strong, though non-significant, trend toward selection of *B. tricaudatus* by large individuals.

We questioned the apparently random feeding by large *H. pacifica* irrespective of feeding history. A review of the raw data suggested that this size class may be able to overeat its food supply (i.e., to consume more prey items than were present in experimental arrays) during overnight trials, thus clouding any apparent selectivity in feeding.

During direct (daylight) observations both fasted and satiated *H. pacifica* were very active resulting in both high rates of encounters ($\bar{x}_{fasted}$, $N=30=40.77$, $\bar{x}_{satiated}$, $N=30=50.93$) and attacks ($\bar{x}_{fasted}$, $N=30=30.40$, $\bar{x}_{satiated}$, $N=30=22.27$). During the 20 min of observation all three size class-

Table 3. Comparisons of feeding success during direct observation of *Hesperoperla pacifica* and *Megarcys signata*. Values are Wilcoxon rank sum T statistics ($N=10$, all trials) (Conover 1980). Negative values indicate a tendency to prefer *Baetis tricaudatus*, positive values indicate a tendency to prefer *Ephemerella altana*

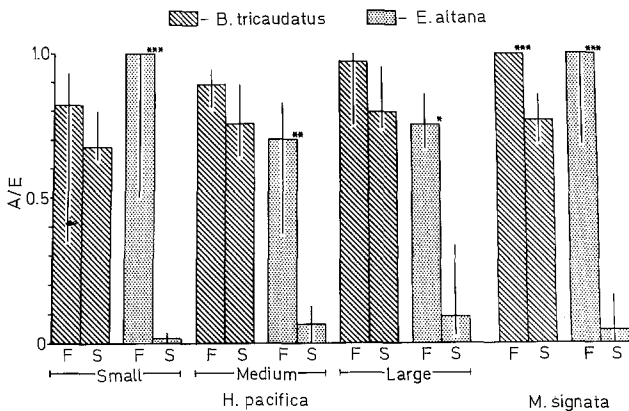| | Hesperoperla pacifica | | | Megarcys signata |
	Small	Medium	Large	
Fasted	2.530**	2.521**	2.275*	2.682**
Satiated	1.342	1.000	1.089	−1.518

* $P<0.05$, ** $P<0.01$, *** $P<0.005$

Fig. 2. Comparison of attack/encounter ratios for *Hesperoperla pacifica* and *Megarcys signata* showing median values and interquartile ranges. Significance levels determined by Mann-Whitney U tests (N = 10, all trials) ***$P<0.001$, **$P<0.002$, *$P<0.05$

es of fasted *H. pacifica* consumed significantly more *E. altana* than *B. tricaudatus*, while when satiated consumption by all three size classes was random (Table 3). This greater consistency of behavior between size classes under direct observation reinforces our suspicion of a deficiency in the design of overnight feeding trials.

Direct observation also revealed somewhat surprising mechanisms underlying these patterns. *H. pacifica* exhibited a high frequency of vigorous attacks on *B. tricaudatus* whether fasted or satiated (Fig. 2). Likewise, fasted *H. pacifica* vigorously attacked (and usually consumed) almost all *E. altana* encountered. However, satiation led to an order of magnitude reduction in attack/encounter ratios for *E. altana* for all three size classes ($P<0.05$). These satiated *H. pacifica* would walk over almost all *E. altana* encountered without showing a visible response while persisting in vigorous attacks on *B. tricaudatus*.

Constancy of response to *B. tricaudatus* and variable response to *E. altana* coupled with differences in attack/capture ratios explain the patterns of apparent dietary "selection" indicated in both feeding trials and direct observations (Tables 2 and 3). Fasted *H. pacifica* attacked *E. altana* with high frequency and with a high rate of successful captures (43.41%). Fasted individuals also attacked the quicker *B. tricaudatus* with a high frequency but with a much lower rate of success (3.01%). Hence dietary data for fasted *H. pacifica* indicate "selection" or "preference" for *E. altana*. Satiated individuals on the other hand appeared to exhibit no "preference". The mechanisms underlying this pattern

Table 4. Comparison of attack/encounter ratios from daytime versus nigthttime direct observation trials, in large fasted *H. pacifica* and satiated *M. signata*

| | H. pacifica | | M. signata | |
	N	median A/E (range)	N	median A/E (range)
B. triaudatus				
Day	10	0.974 (0.704–1.00)	10	0.769 (0.068–0.970)
		ns		ns
Night	5	0.908 (0.457–0.954)	5	0.563 (0.316–0.875)
E. altana				
Day	10	0.750 (0.026–0.975)	10	0.044 (0–0.400)
		ns		ns
Night	5	0.883 (0–1.00)	5	0.036 (0–0.556)

are a continued high rate of attack on *B. tricaudatus* coupled with a low success rate and a highly reduced attack rate on *E. altana* coupled with a high success rate. The result is an approximately equal number of captures of the two mayfly species.

Megarcys signata

Both fasted and satiated *M. signata* were very active during daylight observations resulting in high rates of encounters ($\bar{x}_f$, $N=10=21.30$, $\bar{x}_s$, $N=10=68.50$) and attacks ($\bar{x}_f$, $N=10=18.50$, $\bar{x}_s$, $N=10=29.80$). Like *H. pacifica*, fasted *M. signata* consumed significantly more *E. altana* than *B. tricaudatus* while satiated individuals appeared to forage randomly (Table 3). The mechanisms underlying this pattern of feeding were almost identical to those for *H. pacifica* (Fig. 2). Fasted *M. signata* showed high attack/encounter ratios for both *B. tricaudatus* and *E. altana*. In contrast, satiated individuals continued to attack *B. tricaudatus* at a high, though reduced ($P<0.001$), rate while showing an order of magnitude reduction of rate of attack on *E. altana* (a significantly greater reduction than for *B. tricaudatus* $P<0.001$). Again, as for *H. pacifica*, there was a great difference in the percentages of attacks that resulted in successful captures of *B. tricaudatus* (3.75%) versus *E. altana* (22.05%). These results show that under our laboratory conditions not only were the patterns of foraging of these two distantly related stonefly species similar but so were the processes underlying those patterns.

Comparisons of direct observations conducted at night with the daytime observations presented above support the validity of daytime observations. At night fasted *H. pacifica* encountered and attacked *E. altana* and *B. tricaudatus* at a somewhat higher frequency than during the day ($\bar{x}_{encounters}$ $N=5=63.80$, $\bar{x}_{attacks}$ $N=5=43.80$). While satiated *M. signata* showed somewhat lower frequencies at night ($\bar{x}_{encounters}$ $N=5=41.00$, $\bar{x}_{attacks}$ $N=5=18.20$). However comparisons of day and night attack/encounter ratios indicate no significant difference in response to the mayflies upon encounter for either stonefly species (Table 4).

Table 5. Comparison of handling times for *Baetis tricaudatus* and *Ephemerella altana* by *Hesperoperla pacifica* and *Megarcys signata* using the large sample approximation of the Mann-Whitney U statistic. Values are median handling times (range)

	Hesperopera pacifica										
	Small				Medium				Large		
N	Ht_B	Ht_E	N	N	Ht_B	Ht_E	N	N	Ht_B	Ht_E	N
11	0:23 **	1:07	25	24	0:10 ***	1:02	38	38	0:06.5 ***	0:28.5	52
(0:07–5:34)		(0:10–20:00)		(0:04–0:51)		(0:09–6:50)		(0:02–0:31)		(0:08–6:44)	

	Megarcys signata		
N	Ht_B	Ht_E	N
31	1:43 *	5:15	31
(0:08–11:30)		(0:07–40:00)	

Handling times for prey

The next step in our research was to try to gain insights into factors underlying the different treatment of *E. altana* and *B. tricaudatus* by both stonefly species. Since in our experimental design prey abundance and habitat structure were held constant, we looked to the prey species themselves. The main difference that we could discern between the prey species was a difference in the amount of time that it took the stoneflies to subdue and consume individuals of the two mayfly species, generally referred to as handling time in the literature on foraging. Our estimates of handling times (Table 5) show that *E. altana* requires a significantly greater handling time than *B. tricaudatus* for both *H. pacifica*, all size classes, and *M. signata*. The difference in median handling time for the two mayfly species ranges from 3X to 6X.

Discussion

The results of this study seriously call into question the meaning of the terms prey "preference" or prey "selection" as they have been used in the ecological literature, particularly when they are based on indirect evidence such as stomach contents of predators. When fasted and presented with live prey both *H. pacifica* and *M. signata* generally consumed more *E. altana* than *B. tricaudatus*. If this were the only result considered we might conclude that both species "prefer" *E. altana*. Yet, the fact that small and medium fasted *H. pacifica* consumed more frozen *B. tricaudatus* than *E. altana* shows that the difference in mobility between the two species was pivotal in producing the higher consumption of live *E. altana* and that once prey mobility was removed as a factor consumption shifted to *B. tricaudatus*, perhaps indicating a "true preference" for that species. Even with these results, however, the picture is incomplete without knowledge of the mechanisms underlying the patterns. These mechanisms were elucidated only through direct observations.

The relation between degree of dietary selectivity and hunger was also understandable only after conducting direct observations. If one considered only the relative numbers of the two mayfly species consumed, (Tables 2 and 3) one would conclude that both stonefly species were selective feeders when hungry and random feeders when satiated which is at variance with the predictions of optimal foraging theory and the results of empirical studies (Ivlev 1961; Charnov 1976; Pastorok 1980). However, the attack/encounter ratios determined from direct observations (Fig. 2) indicate behavior that is actually consistent with this previous work. When fasted, both *H. pacifica* and *M. signata* attacked the two mayfly species with approximately equal frequency. In contrast, when satiated, attack/encounter ratios were overwhelmingly biased toward *B. tricaudatus*. Thus in our experiments dietary composition relative to prey availability was inadequate for understanding either rankings of prey or overall dietary specialization.

The results of direct observations show what we think is an extraordinarily high degree of similarity in foraging behavior between *H. pacifica* and *M. signata*. Both species showed a hunger-dependent variable response to *E. altana* and a nearly constant response to *B. tricaudatus*. This is an extremely exciting result because it suggests that the rules for foraging for these predators are similar and that a common currency may be used to make "decisions" concerning this extremely important ecological process. However, these results are also puzzling because of the questions they raise. For example, "If *E. altana* is so easy to capture why not persist in high attack/encounter ratios whether one is hungry or not?" or conversely "If *B. tricaudatus* is so difficult to catch why persist in attacking the species?" We think that the answers to these questions are related to the greater handling times for *E. altana*. This conclusion is consistent with much of foraging theory which has predicted that a primary criterion for ranking of prey should be handling time (Schoener 1971; Krebs 1978).

It is likely that the difference in handling times between the two mayfly species is caused primarily by a difference in body form and amount of armor. *E. altana* is much more robust than *B. tricaudatus* and appears to possess more chitonous armor. [In this regard it is interesting to note that one common name for the family Ephemerellidae is "spiny crawlers" (McCafferty 1981).] As a consequence even the very largest *B. tricaudatus* can be swallowed very quickly

while the robust *E. altana*, if they can be swallowed whole, require more time. Larger *E. altana* are usually eaten piecemeal which requires crushing of the tougher exoskeleton of this species. Hence it appears that more energy must be invested in handling by a predator feeding on *E. altana* than one feeding on *B. tricaudatus*. However, *B. tricaudatus* still requires 6–14 times the number of attacks per successful capture. This would seem to more than compensate for the difference in handling times and suggests a more equal ranking of the two mayfly species. Yet, one critical fact remains to be considered. As mentioned in the section on experimental design, *E. altana* and *B. tricaudatus* were matched for size when used in the feeding trials to avoid any possible size selective effect. *B. tricaudatus* at maximum size appears to be approximately 1/4 to 1/5 as massive as terminal instar *E. altana*. Hence our estimates of handling times for *E. altana* are a gross underestimate of the maximum handling time for the species. In fact we have observed another large *Ephemerella* sp. successfully repel the attacks of *M. signata*. One might ask, "Why don't the stoneflies just avoid large *E. altana* and continue to attack small individuals as vigorously as they do all *B. tricaudatus*?" We think the answer lies in the habit of intermediate sized *Ephemerella* spp. assuming a scorpion-like posture upon contact with a stonefly. Peckarsky (1980, 1982) hypothesizes that this behavior functions to make individuals "appear" larger to predators. We suggest that as a consequence, stoneflies, largely tactile predators, have a difficult time assessing the actual size of intermediate and large-sized *Ephemerella* spp. including *E. altana*. Hence many attacks on such individuals would result in extremely high investments in prey handling or fail entirely. The few encounters that we have observed between stoneflies and very large Ephemerellids, some of which have actually appeared to counterattack, suggest that some attacks might even result in injury to the stonefly.

It is interesting, in the light of the above discussion, to consider the finding by Malmqvist and Sjöström (1980) that the stonefly *Dinocras ceplalotes* does not show size selective predation on *Baetis rhodani*. In our experiments as well, large and small *Baetis tricaudatus* seemed to be attacked with equal frequency. We suggest that the handling time per calorie for these *Baetis* spp. does not change with size. However, we also suggest that handling time per calorie does change for *E. altana* and other *Ephemerella* spp. and we predict size selective predation by stoneflies on this and closely allied groups.

A graphical expression of many of the above ideas is shown in Fig. 3, which we propose as a general, mechanistic model for stoneflies feeding on mayflies. The boundaries of the morphological and behavioral diversity within the mayflies can be represented by two extremes, A and B. Group A are characterized by heavy exoskeletons, weak swimming capability, and high handling times, similar to *E. altana* in the present investigation. In contrast, B species are comprised of weakly amored, swift swimming, difficult-to-catch species such as *B. tricaudatus*. We predict a hunger-dependent, variable response to Group A species which as a consequence of ease of capture would occur in high frequencies in the diets of hungry stoneflies. With progressive satiation A/E ratios on species in Group A would decline and their proportion in the diets of stoneflies would decrease. The precise form of this decrease is arbitrary. We suggest only that the relationship is a monotonically de-
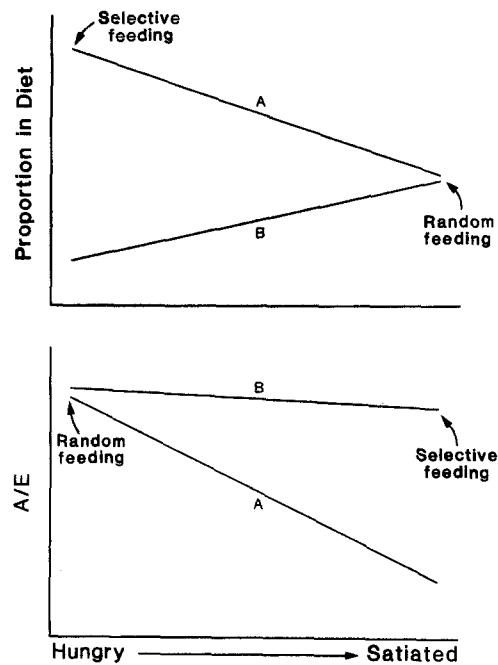

Fig. 3. A graphical model of stonefly predation on mayflies. *A* and *B* represent two widely divergent mayfly morphologies. See text for explanation

creasing function. For convenience, we represent this relationship as a straight line in Fig. 3. However, it has been suggested (Krebs and Cowie 1976) that the switch from nonselective to selective feeding may be a step function. In contrast A/E ratios on B species would decline only slightly with predator satiation and as a consequence, the proportion of these difficult-to-capture species in the diet would increase with predator satiation. Species with characteristics between the extremes A and B would be treated in an intermediate fashion. Figure 3 assumes that A and B are matched for size. We predict that the slope of the lines for Group A species would vary directly with size while the slopes for B species should not be affected by size. As a consequence of the above, as shown in Fig. 3, ones impression of feeding selectivity would depend on whether one examined dietary composition or feeding behavior (A/E ratios).

The similarity in behavior observed in stoneflies feeding at night and during the day (Fig. 2, Table 4) is worth noting since it has been assumed that stoneflies feed mainly at night (Brink 1949; Vaught and Stewart 1974; Hynes 1976). However as Allan (1982) points out, there is little direct evidence for this conclusion and some evidence to the contrary (Winterbourn 1974). In this regard, we have observed *H. pacifica* actively foraging at mid day both in our laboratory stream where several uncaged individuals not used in experiments were allowed to roam freely and in small mountain streams of the southern Rocky Mountains (Molles and Pietruszka personal observation).

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