

Feeding while avoiding predators: evidence for a size-specific trade-off by a lotic mayfly

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Abstract. Laboratory experiments were performed to test the hypothesis that the trade-off between predator avoidance and food acquisition was affected by forager size. Groups of small and large larvae of the mayfly *Baetis tricaudatus* were presented simultaneously with foraging patches representing all combinations of two levels of predation risk (predators present or absent) and two levels of food (low, high). We hypothesized that forager body size would affect patch use because field observations in a Rocky Mountain stream suggested that small *Baetis* experience twice the per-capita risk of mortality of large larvae as a result of predation by a nocturnal minnow. Small larvae also spend more time feeding over a diel period than large larvae. Our results showed that relative patch selection was significantly affected by the interaction between predation risk and *Baetis* size. Although the presence of a predator reduced patch use, the reduction was less pronounced for large *Baetis* than for small individuals, suggesting that large *Baetis* accepted more risk when risky patches contained more food. Food intake rates of small *Baetis* in safe, high-food patches was four times higher than in safe, low-food patches. For large *Baetis*, the presence of a predator in high-food patches reduced food intake to a greater extent than in low-food patches. Greater use of risky, high-food patches by large *Baetis* compared with small *Baetis* was associated with differences in the distance at which larvae responded to predators by initiating a drift response. The mean distance at which large *Baetis* reacted to predators by drifting out of patches was almost four times lower in risky, high-food patches than in risky, low-food patches. Mean reactive distances of small *Baetis* to the predatory minnow were similar to those of large *Baetis* in low-food patches and did not vary with food level.

Key words: foraging, food-patch use, behavioural trade-off, predation risk, food reward, behaviour, mayfly, streams.

A major focus of behavioural ecology has been to understand the way in which animals integrate the costs and benefits of different foraging choices with resultant effects on distributional and feeding responses (Sih 1980, Cerri and Fraser 1983, Werner et al. 1983, Fraser and Emmons 1984, Werner and Gilliam 1984, Milinski 1985a, Fraser and Huntingford 1986, Gilliam and Fraser 1987, Sih 1987, Holbrook and Schmitt 1988, Pitcher et al. 1988, Nonacs and Dill 1990). Numerous studies have shown that an animal's sex (Abrahams and Dill 1989), starvation level (Sih 1982, Kohler and McPeck 1989), and parasite load (Milinski 1985b), influence foraging de-

cisions (see Stephens and Krebs 1986, Dill 1987, Lima and Dill 1990 for reviews). For instance, ontogenetic habitat shifts and size-specific diel vertical migrations are considered to be size dependent responses to the assessments of feeding benefits versus predator avoidance (Holmes 1984, Werner et al. 1983, Power 1984, Dill 1987, Ludwig and Rowe 1990). However, empirical tests of this hypothesis are lacking, and the response of different sized foragers to spatial variation in both predation risk and food reward has not been evaluated.

Body size may have potentially important consequences to evaluating and responding to the costs and benefits of various behavioural options. For instance, components of the predation cycle, including encounter, attack rate, and capture efficiency are often related to prey

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body size (Allan et al. 1987, Dixon and Baker 1988). Foragers of different sizes also consume different amounts of food per unit time and can differ in the amount of time spent feeding.

The common lotic food chain consisting of algae (*Navicula*), mayfly grazers (*Baetis tricaudatus*) Dodds, and minnow predators (*Rhinichthys cataractae* Valenciennes) provides an ideal system for determining if the predation risk-food reward trade-off is influenced by forager size. Baetid mayflies inhabit fast flowing, stony streams and graze on algae, bacteria, and other particulate material present on upper stone surfaces, exposing them to predatory minnows (Kohler and McPeck 1989, Scrimgeour 1992, Culp and Scrimgeour 1993). Field observations on the diel feeding periodicity of small and large *Baetis* have shown that small larvae feed on upper stone surfaces throughout the day and night, whereas large *Baetis* have a short nocturnal feeding bout (8–10 h) (Scrimgeour 1992, Culp and Scrimgeour 1993). The particularly low mass of stomach contents in large *Baetis* during the day suggests that they feed at an extremely low rate, if at all, during this period (Scrimgeour 1992, Culp and Scrimgeour 1993). When they feed on upper stone surfaces at night, *Baetis* larvae are preyed upon by a nocturnal predator, the longnose dace (*Rhinichthys cataractae*), and analyses of gut contents of *Rhinichthys* suggest that *Baetis* are an important prey item of this minnow (Culp 1989, Scrimgeour 1992). Further, a field estimate of mortality risk during the hours of darkness from *Rhinichthys* for small larvae (<3 mm total body length) was almost twice that for large larvae (>5 mm total body length) (Scrimgeour 1992).

Based on these observations, we hypothesized that differences in vulnerability of *Baetis* to *Rhinichthys* at night and differences in feeding periodicities of small and large *Baetis* could produce different patch-use patterns when *Baetis* have access to feeding patches varying in predation risk and food level. Differences in the length of foraging periods of small and large *Baetis* could affect the way different sized *Baetis* balance predation risk against food acquisition. Because small *Baetis* feed continuously through a diel cycle, the cost of reduced food intake due to the appearance of a nocturnal predator may be compensated by increased food intake during the day. This potential compensatory foraging response of small individuals is not avail-

able to large *Baetis* because they feed only at night. Further, since mortality risk due to predation on *Baetis* from *Rhinichthys* depends on size, large *Baetis* should spend more time in risky patches, and drift less than small *Baetis* because they experience lower risk. Large *Baetis* could spend a greater amount of time in risky, high-food patches than in risky, low-food patches by varying the distance at which they react to a predator by drifting out of risky patches. These predictions were tested in a laboratory stream system where we experimentally manipulated food level and predation risk. For both small and large *Baetis* we determined patch use (i.e., time spent in a patch), consumption rates, and drift rates in safe (predator absent) versus risky (predator present) streams. We also measured the distance at which *Baetis* reacted to *Rhinichthys* by drifting out of risky patches (i.e., drift initiation distance).

Methods

Experimental animals

Baetis tricaudatus were collected from the Bow River (51°03'N, 114°03'W), Calgary, Alberta, 22 May–4 June 1989 and 20 April–3 May 1990. Before experiments, larvae were maintained at 11°C for 2–4 wk in holding tanks in the laboratory with aerated flowing water and a 14:10 h light:dark cycle. During this period larvae were fed an ad-libitum supply of the diatom *Navicula* sp., which is commonly ingested by *Baetis* in several Albertan streams (Scrimgeour, unpublished data).

Rhinichthys cataractae were collected from the Bow River and maintained at 11°C on a diet of *Baetis* nymphs in the laboratory until used in trials. Individual *Rhinichthys* and *Baetis* were used only once per patch-choice trial.

Determining food levels

Functional response experiments using small larvae (mean body length \pm 1 SE = 2.5 ± 0.3 mm) and large larvae (5.4 ± 0.3 mm) were performed to determine food levels for use in patch-choice trials following Scrimgeour et al. (1991). These experiments were conducted in small circular streams (diameter = 10 cm, water volume = 0.25 L, planar area = 50 cm²) (Walde and Davies 1984) in which filtered and oxygen-sat-

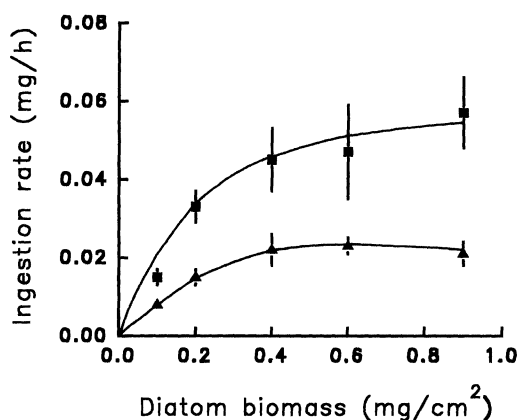


FIG. 1. Functional response curves (mean individual ingestion rate ± 1 SE) of small (\blacktriangle) and large (\blacksquare) *Baetis tricaudatus* when grazing on patches of the diatom *Navicula*.

urated water was circulated (mean velocity ± 1 SE = 7.6 ± 0.2 cm/s; water temperature 11°C) from a large 600-L reservoir fitted with an activated charcoal water filter. Feeding trials consisted of allowing an individual mayfly to forage at one of five biomass levels of *Navicula* (0.10, 0.24, 0.53, 0.68, 0.90 mg dry weight (DW)/cm²) for a 1-h period. This biomass range was determined from a preliminary set of feeding trials which determined asymptotic feeding rates; the different diatom biomass levels were created by culturing substrata in an algal medium for different lengths of time (Scrimgeour et al. 1991). Gut contents of small and large *Baetis* were estimated by dissecting out the gut. This was accomplished by placing individual larvae onto wax dissecting dishes before removing the head and peeling off the gut wall from other internal tissues. The gut contents were then carefully separated from the gut wall, dried at 40°C , and weighed to the nearest 0.01 mg on a Cahn 25 Automatic electrobalance.

Non-linear curve fitting (Williams and Juliano 1985, Trexler et al. 1988) using the Quasi-Newton method on SYSTAT (Wilkinson 1988) was used to discriminate among functional response models I, II, and III and to calculate model parameters, i.e., attack coefficients (a) and handling times (T_h) and their respective 95% confidence limits. The null hypothesis that ingestion rates of small and large *Baetis* were not significantly affected by diatom biomass was tested with a single-factor ANOVA on data that

were \log_{10} transformed to remedy inequality of variances.

Ingestion rates of small and large *Baetis* were significantly affected by diatom biomass (small *Baetis*, $F_{(4,25)} = 6.71$, $p < 0.001$; large *Baetis*, $F_{(4,25)} = 15.58$, $p < 0.001$). Comparison of coefficients of determination and curve fitting showed that small and large *Baetis* displayed Type II functional response curves, that is, a decelerating rise to a positive asymptote (Fig. 1). This model explained more of the variation in ingestion rate by small *Baetis* ($r^2 = 0.94$) and large *Baetis* ($r^2 = 0.96$) than the Type I (small *Baetis* $r^2 = 0.63$; large *Baetis* $r^2 = 0.57$) or Type III models (small *Baetis* $r^2 = 0.90$; large *Baetis* $r^2 = 0.55$). Asymptotic feeding rates for small and large *Baetis* were reached when diatom biomass was about 0.43 mg DW/cm². Attack coefficients were not significantly different for small and large *Baetis* (mean $\pm 95\%$ confidence intervals: small = 0.18 ± 0.04 mg DW/h, large = 0.18 ± 0.07 mg DW/h), but mean handling time of small larvae (18.9 ± 2.6 mg DW/h) was significantly greater than for large larvae (11.7 ± 4.0 mg DW/h). Based on the results of the functional response experiment, two diatom biomasses were selected to represent low (0.10 mg DW/cm²) and high (0.90 mg DW/cm²) food levels (Fig. 1).

Patch-choice trials

The effects of predation risk and food levels on patch use by small (2.9 ± 0.2 mm) and large *Baetis* (5.8 ± 0.6 mm) were investigated in a laboratory stream system where larvae were provided with simultaneous access to feeding patches that differed in predation risk and food level: safe (S), risky (R), low food (L), high food (H). Thus, larvae had access to four patch types (i.e., LR, LS, HR, HS).

Patch choice trials were conducted in circular streams (Fig. 2) that were partitioned into four equal-sized patches representing all combinations of predation risk and food level. The four patch types were blocked within replicate streams. Although the initial position of blocks (i.e., patch types) in a stream was selected at random, the position of blocks relative to each other was held constant among replicate streams. Thus LR was adjacent to LS, which was adjacent to HR, which was adjacent to HS, which was adjacent to LR; and the position of each patch in relation to the others remained the same for

each replicate trial. To control for potential position effects, each stream was rotated 90° after each replicate trial.

Food patches consisted of a single $4 \times 4 \times 1$ -cm plexiglas substrate with the top surface (16 cm^2) covered with either a low or high biomass of *Navicula*. The two biomass levels were created by culturing substrata in an algal medium for different lengths of time (Scrimgeour et al. 1991). Water temperature (day : night = 14:9°C) and diel light cycle (light : dark = 14:10 h) within the streams were based on spring field conditions. Patch-choice trials were conducted in the dark because both small and large *Baetis* feed on the upper surfaces of stones and are preyed upon by the nocturnal predator *Rhinichthys cataractae* at night. Although water circulation jets were present in only two of the four patches, mean water velocities (± 1 SE) measured directly above artificial substrata with a Novonics micro-current meter did not vary significantly (single factor ANOVA, $F_{(3,12)} = 0.97$, $p > 0.05$). Mean current velocity was $8.73 \pm 0.6 \text{ cm/s}$ for all jet-present patches and $9.58 \pm 0.8 \text{ cm/s}$ for jet-absent patches.

For each patch-choice trial, 30 mayflies were placed in each of four replicate streams. The density of mayfly larvae used ($638/\text{m}^2$) is within the range of densities observed in the field (Scrimgeour, unpublished data). Larvae were acclimated to experimental conditions for 38 h, including two diurnal and one nocturnal intervals, before the addition of the predators. Each stream was videotaped for 1 min in the dark using infra-red light prior to the introduction of predators to determine the distribution of mayflies and to determine whether mayflies could distinguish between diatom biomass levels (i.e., low versus high food). In the absence of predators, drift of *Baetis* is typically low (< 2 individuals/min pass a vertical line separating any two patches) and remains constant over a 1-h period (Scrimgeour 1992). Five minutes after the commencement of the dark photoperiod, one *Rhinichthys* (mean total length ± 1 SE = $63 \pm 1.4 \text{ mm}$) was placed in a low-food patch and another was placed in a high-food patch. The entire stream was again videotaped under infrared light for 1 h. Patch choice trials were performed separately for small and large *Baetis* and were replicated four times.

The presence of 5-mm mesh screen restricted *Rhinichthys* to patches designated as risky but

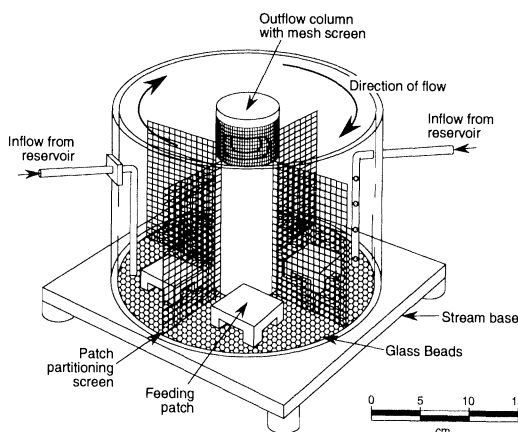


FIG. 2. Flow through laboratory streams used to determine the effects of predation risk and food level on time spent among four concurrently available patches (quadrants). Each patch contains a single 16-cm^2 feeding block with the upper surface covered with the diatom *Navicula*. Mesh screens (5 mm) prevent fish from moving among patches while allowing free movement of mayfly larvae.

allowed *Baetis* to move freely among patches. *Rhinichthys* were acclimated to experimental conditions by placing them in a set of acclimation streams adjacent to experimental streams. After a 38-h acclimation period *Rhinichthys* were selected randomly from acclimation streams and placed into patches designated as risky. Although *Rhinichthys* were present only in risky patches, odours could potentially alter the foraging behaviour of *Baetis* in safe patches. A set of additional experiments, however, showed that *Baetis* larvae do not respond to *Rhinichthys* odours by altering drift rate or position of larvae on the top, bottom, and sides of substrata (Scrimgeour et al. 1994). Thus, it is unlikely that the presence of *Rhinichthys* in a risky patch altered foraging behaviour of *Baetis* in adjacent safe patches. To minimize build-up of *Rhinichthys* odours, streams were scrubbed with hot water and detergent between trials, and water pumped into the streams from the 600-L reservoir was not recirculated.

Field observations showed marked differences in the feeding periodicity of small and large *Baetis* larvae (Culp and Scrimgeour 1993). In streams with resident populations of diurnally active fish predators, small larvae feed continuously throughout the day and night, whereas large *Baetis* feed almost exclusively at

night (Scrimgeour 1992, Culp and Scrimgeour 1993). To ensure that large *Baetis* had low amounts of food in the gut before the initiation of the dark feeding period, as in the field, plexiglas substrata with the upper surfaces covered with *Navicula* were removed from all patches during the 10-h light acclimation period and replaced with clean substrata (i.e., food absent). For patch choice trials involving small *Baetis*, feeding patches were replaced with food-absent substrata for 1 h before the commencement of the dark period. Two main advantages to adopting these protocols were 1) larvae used in patch choice trials experienced levels of starvation, and presumably amounts of food in their guts, similar to those they would have experienced in the field and 2) diatoms ingested by small larvae during the light acclimation period could be distinguished from algal material consumed during patch-choice trials by the presence of a small gap in ingested food in the foregut. Food ingested during the patch-choice trials was quantified by dissecting out the entire foregut, preserving it in 10% formalin for two days, and then removing the food bolus from the gut (Scrimgeour et al. 1991). The food bolus was then dried to constant weight at 40°C and weighed to the nearest 0.01 mg.

For each 1-h trial we calculated time spent in each patch by the 30 mayflies by dividing the total amount of time that mayflies spent in an individual patch by the total time that all mayfly larvae spent in all patches. This protocol allowed us to correct patch use for any mayfly larvae on mesh screens (<3 individuals at any one time) and for any larvae consumed during the 1-h trials (<1 individual per stream). Cumulative estimates of patch use were determined by stopping the videotape every 30 s and counting the number of mayflies in each patch. As a result, patch use was based on 120 snapshots during the 1-h trials. Low speed video play-back also allowed us to identify individual larvae that remained in the same patch during the entire 1-h period.

The number of mayflies in the drift was determined every 3 min to identify possible drift responses of larvae to predators. Because we were interested in how the presence of predators affected drift rates of small and large *Baetis*, we compared drift in predator-present streams (i.e., streams that contained *Rhinichthys* in two patches) with that in predator-absent streams (*Rhinichthys* absent from all patches). All streams

contained two low-food and two high-food patches. Drift rate was determined by counting the number of larvae that passed a vertical line between the central outflow column and the outer stream wall over a 1-min period. Because patch residence times of foragers can be affected by the distance at which they react to predators, we measured the distance between *Baetis* and *Rhinichthys* when drift was initiated in risky patches (i.e., drift initiation distance).

At the end of each trial, at least five mayflies were selected randomly (when possible, given low mayfly numbers in patches) from all patches and preserved in 10% formalin so that food intake could be determined through gut content analysis. Depletion of diatom patches during the experiment (initial biomass – final biomass) was determined by scraping diatoms from 10 low-biomass and 10 high-biomass substrata before the experiment and comparing these weights with those removed from stream patches after the 1-h patch-choice trials. Loss of diatoms to currents is minimal under this experimental set-up (Scrimgeour et al. 1991). Diatoms removed from foreguts and from plexiglas scrapings were dried at 40°C and weighed to the nearest 0.01 mg on a Cahn electrobalance.

Statistical analyses

We determined whether mayfly distributions among food patches was significantly affected by forager size and predation risk by calculating patch use (i.e., the number of larvae \times patch residence time) in each of the four concurrently available patches. Ingestion of diatoms in each patch was determined, when possible, by identifying individual larvae that remained in the same patch during the entire 1-h period. Presentation of *Baetis* larvae with simultaneous access to food patches differing in predation risk and food level creates problems with statistical analyses because estimates of patch use are not independent observations. We calculated relative patch use separately for the two safe patches (time spent in HS minus time spent in LS) and the two risky patches (time spent in HR minus time spent in LR), as previously done by Holbrook and Schmitt (1988). $\log_{10}(x + 1)$ transformations of these data removed differences in absolute patch use and allowed comparisons of relative patch use. The hypothesis that relative use of safe and risky patches was significantly affected by *Baetis* size (small, large),

predation risk (safe, risky), and the interaction of these factors was tested with a two-factor ANOVA.

A different approach was used to test the hypothesis that food ingestion rates were affected by *Baetis* size and predation risk. For this analysis, we calculated feeding rates in each of the four trials separately for the two high-food patches (mass of ingested food in HS minus mass of food ingested in HR) and in the two low-food patches (mass of ingested food in LS minus mass of food ingested in LR). Thus, we were interested in how the presence of a predator affected food intake rates when patches contained low and high food levels. Analysis of video tapes showed that several mayfly larvae remained in most patch types after the 1-h trials. Thus, we calculated a mean food-intake rate for all larvae within a given patch type, in a given stream, and then used the same patch types in different streams as replicates.

The hypothesis that mean drift rate was not significantly affected by predation risk (safe, risky), mayfly size (small, large), time since the start of the trial (covariate), and the interaction of these factors was tested using a two-factor ANCOVA on \log_{10} transformed data. Because drift in streams containing predators did not typically increase until 3 min after the addition of *Rhinichthys*, coinciding with the onset of *Rhinichthys* foraging behaviour, we restricted our analysis of drift rates to between 3 and 60 min after predator addition. The hypothesis that the mean reactive distance was not significantly affected by food level (low, high), mayfly size (small, large), and the interaction of these factors was tested with a two-factor ANOVA. Because individual larvae could not be followed when drift rates were high (i.e., just after predator addition) we restricted our analysis of drift-initiation distances to the first drift event and assumed that all drift events were responses to the addition of the predator. Finally, video taping also recorded attacks by *Rhinichthys* on *Baetis*. The hypothesis that attack rate by *Rhinichthys* was not significantly affected by *Baetis* size (small, large), food level (low, high), and the interaction of these factors was tested with a two-factor ANOVA.

Results

In the absence of predators, the total number ($\bar{x} \pm 1$ SE) of small (22.5 ± 0.7) and large *Baetis*

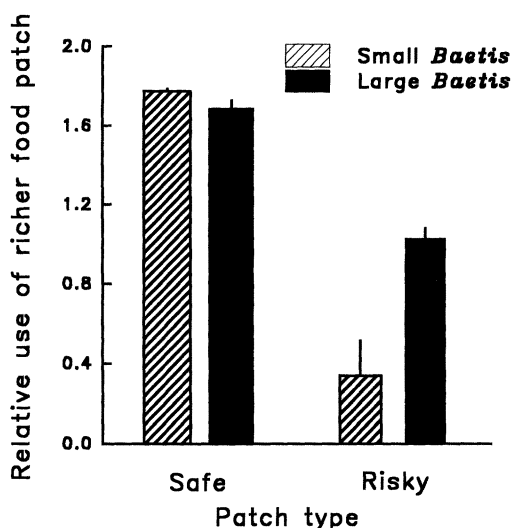


FIG. 3. Effect of predation risk and forager size on mean (± 1 SE) relative patch use by *Baetis tricaudatus* when larvae had simultaneous access to patches differing in predation risk and food level. Relative patch use by small and large *Baetis* was determined separately for safe and risky patches by calculating the relative use of the two safe patches (time spent in high-food safe minus time spent in low-food safe) and the two risky patches (time spent in high-food risky minus time spent in low-food risky) after $\log_{10}[x + 1]$ transformation. ANOVA indicated that relative patch use was significantly affected by the interaction between *Baetis* size and predation risk.

(23 ± 0.7) in high-food patches was four times higher than in low-food patches (small = 5.3 ± 0.3 , large = 4.8 ± 0.5). After the introduction of predators, total time spent in safe, high-food patches also remained four times higher than in safe, low-food patches.

Relative use of the richer patch was significantly affected by predation risk ($F_{(1,15)} = 92.34$, $p < 0.001$), mayfly size ($F_{(1,15)} = 10.16$, $p < 0.01$), and the interaction of these factors ($F_{(1,15)} = 14.58$, $p < 0.005$). Although the presence of a predator reduced relative use of high-food patches, the reduction was less pronounced for large than for small *Baetis* (Fig. 3).

As insufficient (< 1 individual per patch) numbers of small *Baetis* were present in risky patches at the end of trials, algal ingestion rates could only be measured on larvae from safe patches. Small *Baetis* present in feeding patches during the entire 1-h period ingested more food in safe, high-food patches (0.023 ± 0.001 mg DW per individual/h) than in safe, low-food

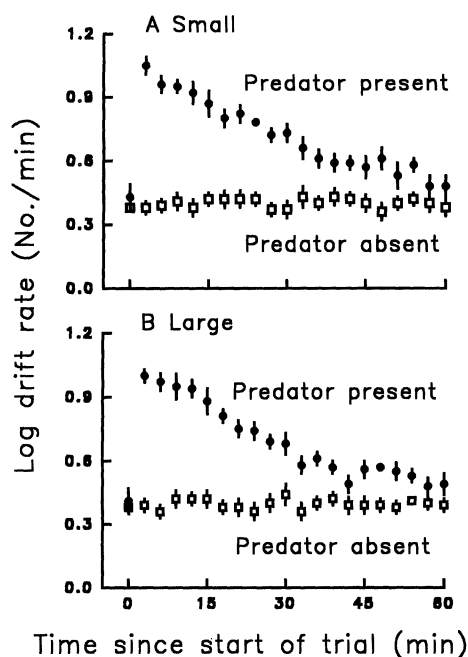


FIG. 4. \log_{10} mean drift rates (± 1 SE) of (A) small and (B) large *Baetis tricaudatus* in streams containing predators (\bullet) compared with those without (\square). Standard error may not be shown if included in the symbol.

patches (0.006 ± 0.002 mg DW per individual/h) ($t = 6.9$, $p < 0.001$). For large *Baetis* the presence of a predator in high-food patches (mass of ingested food in HS minus mass of food ingested in HR) reduced food intake *Baetis* to a greater extent (0.055 ± 0.005) than in low-food patches (mass of ingested food in LS minus mass of food ingested in LR = 0.0102 ± 0.002) ($t = 8.10$, $p < 0.001$).

Small and large *Baetis* foraged throughout the 1-h trials, and depletion of the diatom mat during trials was low ($<10\%$ initial biomass). Because *Rhinichthys* continued to forage through the 1-h trials, it is unlikely that the level of predation risk varied appreciably through the experimental period.

Attack rates on *Baetis* by *Rhinichthys* during the 1-h trials were significantly affected by *Baetis* size (two-factor ANOVA, $F_{(1,12)} = 34.6$, $p < 0.01$), but not by diatom level ($F_{(1,12)} = 0.46$, $p > 0.05$) or the interaction of mayfly size and diatom level ($F_{(1,12)} = 0.91$, $p > 0.05$). Small *Baetis* were attacked more frequently (mean number [± 1 SE] of attacks in low-food patches = 1.5 ± 0.3 , high-food patches = 2.0 ± 0.4) than large

Baetis (low-food patches = 0.5 ± 0.3 , high-food patches = 0.5 ± 0.3). While *Baetis* were attacked relatively frequently during trials, *Rhinichthys* ingested few larvae (<2 per stream) because *Baetis* were able to avoid predator attacks by drifting out of patches.

Introduction of *Rhinichthys* into streams caused a significant increase in drift rates compared with predator-absent streams (Fig. 4). The increase in drift occurred about 3 min after the introduction of *Rhinichthys* into streams and coincided with the beginning of the fish's rooting (probing the substrate with snout) and swimming behaviours (Beers and Culp 1990). ANCOVA indicated that drift rate was significantly affected by time ($F_{(1,283)} = 229.31$, $p < 0.001$), predation risk ($F_{(1,283)} = 685.91$, $p < 0.001$), and the interaction between these factors ($F_{(1,283)} = 220.09$, $p < 0.001$). Taken together these data indicate that drift rates changed in a quantitatively different manner through time in predator-present versus predator-absent treatments but were not affected by *Baetis* size.

Mean reactive distance of *Baetis* to *Rhinichthys* was significantly affected by the two-factor interaction between *Baetis* size and food level (two-factor ANOVA, $F_{(1,211)} = 49.36$, $p < 0.001$). Mean reactive distance of small *Baetis* to *Rhinichthys* was similar in low- and high-food patches, whereas the mean reactive distance for large *Baetis* was four fold lower in low-food compared with high-food patches (Fig. 5).

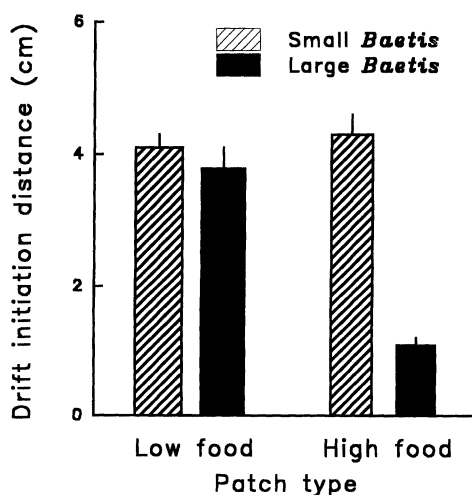


FIG. 5. Effect of food level on drift initiation distances (± 1 SE) of *Baetis tricaudatus* to *Rhinichthys cataraetae*.

Discussion

An animal's body size is an important ecological characteristic influencing a diversity of behavioural interactions (e.g., Allan et al. 1987) and life history traits (e.g., Clutton-Brock and Godfray 1991). Body size also has potentially important consequences for the way in which animals balance predation risk against food reward because both of these variables may depend upon body size (Stein and Magnuson 1976, Werner et al. 1983, Werner and Gilliam 1984, Power 1984, Sih 1987, Dixon and Baker 1988). However, no study has identified the response of different sized foragers to simultaneous variation in both food reward and predation risk, and it is not known whether foragers of different sizes balance the conflicting demands of food acquisition versus avoiding predators in the same manner.

We hypothesized that differences in per-capita mortality risk, food ingestion rates, and length of the feeding period for small versus large *Baetis* would result in size-specific patterns in patch use. Our experiments showed that the relative use of the richer patch was affected by the interaction between predation risk and *Baetis* size. Although the presence of a predator reduced selection for richer food patches, the reduction was less pronounced for large than small larvae, suggesting that the relative importance of evading predators and acquiring food can change with body size.

Although we are unable to determine why selection of richer food patches was affected by *Baetis* size, the size-dependence of mortality risk and the benefits of increased food intake from high-food patches covers most possibilities. Several studies have shown that the degree to which foragers avoid risky patches is positively related to their vulnerability to predators and that anti-predator behavioural responses can depend upon forager size (Stein and Magnuson 1976, Sih 1980, 1982, Werner et al. 1983, Power 1984). Large *Baetis* used in our experiments were close to the size of larvae that would have emerged (2–4 weeks later) from the Bow River and developed into adults and searched for mates. The greater use of risky patches by large *Baetis* may arise because the value of greater food intake increases as the length of time available for larval growth declines. Larger body size of mayfly larvae is particularly important be-

cause adult mayflies do not feed and because mayfly adult body size, a function of larval body size, is positively related to fecundity (Clifford 1970, Sweeney et al. 1986), egg size (Scrimgeour 1992), and the ability of males to obtain mates (Flecker et al. 1988).

Alternatively, differences in feeding periods of small and large *Baetis* may explain differences in time spent in risky, high-food patches. Because small *Baetis* feed continuously through a diel cycle, the cost of reduced food intake due to the appearance of a nocturnal predator may be compensated for by increased food intake during the day. This potential compensatory foraging response of small individuals is not displayed by large *Baetis* because they feed exclusively during the night, presumably to avoid high risk of mortality from day-active trout predators (Culp and Scrimgeour 1993, Cowan and Peckarsky 1994). In fact, the shift by *Baetis* from diurnal to nocturnal activity with increasing size (Culp and Scrimgeour 1993) is consistent with the findings of several other studies (Allan 1978, Flecker 1992, Culp and Scrimgeour 1993, Cowan and Peckarsky 1994) and is hypothesized to be a general response to size-selective predators such as trout, which feed during the day (Allan 1978, Flecker 1992). Thus, the abundance of trout in the Bow River system (Culp et al. 1992) may indirectly dictate the way in which their *Baetis* prey balance the conflicting demands of acquiring food and evading predators at night.

Numerous studies have shown that the behavioural responses of foragers to predators are influenced by forager size (Peckarsky 1987), sex (Abrahams and Dill 1989), level of starvation (Kohler and McPeck 1989), and parasite load (Milinski 1985b). In a similar fashion, these factors should have important consequences for the way in which foragers balance predation risk against food reward. There is some evidence to support this hypothesis. For example, Kohler and McPeck (1989) investigated the effects of predation risk, food reward, and hunger level on the foraging behaviour of *Baetis*. They found that, in the presence of mottled sculpin (*Cottus bairdi*), starved *Baetis* foraged longer than fed larvae on the top surface of artificial substrata (Kohler and McPeck 1989). Similarly, Abrahams and Dill (1989) observed that the amount of food required to offset mortality risk due to predation of guppies from predatory fish

was less for females than males. Our results suggest that forager size also influences the behavioural trade-off between predation risk and food reward and should be included in foraging models that attempt to predict spatial and temporal foraging patterns.

Patch residence times may depend upon the distance at which foragers react to an approaching predator (Ydenberg and Dill 1986, Dill and Ydenberg 1987, Dill and Houtman 1989). A general prediction is that patch residence time will be inversely related to the forager's reactive distance (i.e., the distance at which prey flee from a predator). Our findings showed that the greater use of risky, high-food patches compared with risky, low-food patches by large *Baetis* was accompanied by a food-dependent reactive distance response. The distance at which large *Baetis* reacted to *Rhinichthys* declined four-fold when patches contained high food. In contrast, the distance at which small *Baetis* fled from *Rhinichthys* was unaffected by food level. The ability to vary drift-initiation distances should be adaptive because it allows stream herbivores, such as *Baetis*, to exploit a food resource that shows high spatial and temporal variation (Richards and Minshall 1988, Scrimgeour and Winterbourn 1989, Scrimgeour 1992), or where the benefits of greater food intake change with life-history stage. This mechanism may be particularly important for varying patch-residence times, especially when a predator, like *Rhinichthys*, has a short reactive distance (< 2 cm) (Beers and Culp 1990). We are unable currently to identify the causal mechanisms underlying the flexibility in size-specific drift-initiation distance displayed by *Baetis* as related to food reward, but they could be related to size-specific differences in the sensory abilities, speed at which mayfly larvae swim away from predators, or the result of prior experiences with predators.

Despite differences in patch selectivity between small and large *Baetis*, larvae mostly used safe over risky patches, and within this selection regime, high-food over low-food patches. Although our results are based on short-term estimates of patch use, selection of safe rather than risky patches over longer periods should lead to increased survival. Selection of high-food patches over low-food patches, evident from functional response experiments, should be beneficial because of greater food intake and

potential increases in growth rates, adult body size, fecundity, and egg size (Scrimgeour 1992). Whether patch selectivity patterns by *Baetis* affect fitness will require longer term studies where larvae can be reared to adults under different combinations of predation risk and food level.

Lastly, our results from laboratory experiments suggest that the distribution of *Baetis* larvae was affected by presence of a nocturnal predator and food abundance. Further work is required to describe distribution patterns of *Baetis* in natural streams, including field experiments to determine how these larger-scale patterns are affected by spatial and temporal variation in the distribution of predators and algal biomass.

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