Feeding variability among individual aquatic predators in experimental channels

Roger S. Wotton

Department of Biology, Darwin Building, University College London, Gower Street, London WC1E 6BT, U.K.

Mark S. Wipfli

Forestry Sciences Laboratory, USDA Forest Service, 2770 Sherwood Ln., Juneau, AK 99801, U.S.A.

Luke Watson

Department of Biology, Darwin Building, University College London, Gower Street, London WC1E 6BT, U.K.

AND

Richard W. Merritt[1]

Department of Entomology, Michigan State University, East Lansing, MI 48824, U.S.A.

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Experiments were conducted in experimental channels to study feeding variability through time and between conspecific individuals of four species of lotic predators. Large and small *Rhyacophila dorsalis* (Trichoptera: Rhyacophilidae) were given black fly larvae, mainly *Simulium ornatum* (Diptera: Simuliidae) of two size classes during laboratory feeding trials lasting up to 5 days. *Acroneuria lycorias* (Plecoptera: Perlidae) were also given black fly larvae (*Prosimulium fuscum, S. venustum*) during 11-day laboratory feeding trials. *Paragnetina media* (Perlidae) and *Isoperla signata* (Plecoptera: Perlodidae), were supplied with a mixed prey assemblage of black fly larvae and mayfly nymphs, *Baetis flavistriga* (Ephemeroptera: Baetidae), and *Epeorus vitrea* (Heptageniidae), for 9 days in field experiments. There was significant variability in the consumption of prey among individuals of *R. dorsalis*, this being true for both large and small predators. Significant among-predator and day-to-day feeding variability also occured with *A. lycorias*, *P. media*, and *I. signata*. Our experiments showed that there are significant differences in prey consumption among individual predators within a given species, and these differences need to be considered when planning, and interpreting, future studies on predator−prey interactions, particularly those conducted in experimental streams.

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La variabilité temporelle dans l'alimentation a été étudiée dans des canaux expérimentaux chez quatre espèces de prédateurs d'eau courante. Des individus de grande et de petite taille de *Rhyacophila dorsalis* (Trichoptera: Rhyacophilidae) ont été nourris de larves de mouches noires, notamment *Simulium ornatum* (Diptera: Simuliidae), de deux classes d'âge lors de tests en laboratoire d'une durée allant jusqu'à 5 jours. Des *Acroneuria lycorias* (Plecoptera: Perlidae) ont également reçu des larves de mouches noires (*Prosimulium fuscum, S. venustum*) au cours de tests en laboratoire d'une durée de 11 jours. *Paragnetina media* (Perlidae) et *Isoperla signata* (Plecoptera: Perlodidae) ont été nourris d'un mélange de proies comptant des larves de mouches noires et des larves d'éphémères, *Baetis flavistriga* (Ephemeroptera: Baetidae) et *Epeorus vitrea* (Heptageniidae) au cours d'expériences de 9 jours en nature. Il y avait une variabilité importante de la consommation de proies chez les divers individus de *R. dorsalis*, aussi bien chez les petits prédateurs que chez les grands. La consommation de proies variait également de façon importante d'une journée à l'autre et d'un individu à l'autre chez *A. lycorias*, *P. media* et *I. signata*. Nos expériences ont mis en évidence des différences importantes dans la consommation des proies chez différents individus de la même espèce; il faudra tenir compte de ces différences dans la planification et l'interprétation d'études sur les interactions prédateurs−proies, particulièrement dans les ruisseaux expérimentaux.

[Traduit par la rédaction]

Introduction

Predators play an important part in shaping stream communities and a large literature describes both theoretical and practical approaches to community-level effects (reviewed by Allan 1983 and Peckarsky 1984). Predator biology and behaviour studies have also been made at the population level, including the way predators interact with their prey (Allan 1983; Peckarsky 1984). Information gained from studies at this level is important in understanding the role of predators in communities.

Many factors controlling the behaviour of aquatic predators have been examined. These include the effect of predator density on prey numbers, and vice versa (Wotton and Merritt

1988; Lancaster et al. 1991), the effect of hunger on predation (Molles and Pietruszka 1983), the effect of life stage and sex on predation (Malmqvist and Sjöström 1980; Allan et al. 1987; Peckarsky and Cowan 1991), the role of prey-size selectivity by predators (Malmqvist and Sjöström 1985).

In the course of experiments, some authors have noted differences in feeding behaviour between individual predators. Malmqvist and Sjöström (1980) found that the stonefly *Dinocras* displayed variation in the rate at which *Baetis* mayfly prey were taken, with pulses every 2.5−4 days. Similarly, Allan et al. (1987) described experiments with stonefly nymphs feeding on *Baetis* mayfly nymphs where "a particular individual in any given trial may or may not behave according to the average outcome."

The objective of our study was to examine the feeding variability among individual conspecific predators over time.

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[1]Author to whom correspondence should be sent.

Materials and methods

I. Animals used in experiments

Predators used in experiments were caddisfly larvae, *Rhyacophila dorsalis* (Curtis) (Trichoptera: Rhyacophilidae), and the stonefly nymphs, *Acroneuria lycorias* (Newman), *Paragnetina media* (Walker) (Plecoptera: Perlidae), and *Isoperla signata* (Banks) (Plecoptera: Perlodidae). Black fly larvae (Diptera: Simuliidae) were used as prey because all the predators feed on them naturally (Davies 1981, 1991; Wiley and Kohler 1981; Martin and Mackay 1982, 1983; Wipfli 1992). *Prosimulium fuscum* Syme and Davies and *Simulium venustum* (Say) were used in trials with *A. lycorias* nymphs. *Simulium ornatum* Meigen larvae were used in trials with the caddisfly larvae, these species coexisting with the respective predator species. In trials with *P. media* and *I. signata*, a mixed-prey assemblage was used and consisted of *Baetis flavistriga* McDunnough (Ephemeroptera: Baetidae), and *Epeorus vitrea* (Walker) (Ephemeroptera: Heptageniidae) nymphs and black fly larvae. These prey were chosen because they were the three most abundant prey cohabiting with the predators, all three occurring at nearly equal densities.

II. Experimental stream construction and operation

We investigated variation in feeding by individual predators using the standardized conditions provided by replicated stream channels. Our channels were similar to those developed by Walde and Davies (1984), but smaller for field transport. Experiments with predacious stonefly nymphs were carried out using 40 circular channels (each of volume 500 mL) (Wipfli 1992). The outer circumference of the channel base was 29 cm and total base area was 64 cm². Water entered individual channels through single tubes, circulated at a uniform velocity, then exited through an elevated centre drain covered with 250 μm mesh screen. Water current velocity was estimated for each channel by measuring the time it took a neutrally buoyant float to complete 20 revolutions.

Paragnetina media and *I. signata* experiments were conducted in the field. Stream water was gravity fed to a stream unit as described above, passed through the channels, then returned to the stream. Minimum and maximum water temperatures were 8.0 and 19.5°C, respectively, during the 9-day experiment. Current velocity was maintained near 21 cm s⁻¹ (range 19–23 cm s⁻¹).

Laboratory experiments with *A. lycorias* used dechlorinated, carbon-filtered tap water that was continuously recirculated through the channels from a 500 L cooling tank. Water temperature was kept at 10°C, and mean current velocity was maintained near 21 cm s⁻¹ (range 19–23 cm s⁻¹ across channels).

Rhyacophila dorsalis experiments were conducted in the laboratory using a modified version of the experimental stream unit which could fit on a bench top. It consisted of 11 channels, allowing 10 replicate trials and a control to be run concurrently. Due to laboratory constraints, channels were fed with tap water, which was shown to have little effect on either predators or prey, and water current velocity was maintained near 30 cm s⁻¹.

III. Predator feeding trials

Rhyacophila dorsalis experiments

Rhyacophila dorsalis larvae and black fly larvae were collected in June and September from the River Darent in Kent, U.K. Black fly larvae were brought to the laboratory attached to leaves of *Ranunculus* sp., and *R. dorsalis* were collected from stones located in fast-flowing reaches, the caddisfly larvae invariably being found closely attached to stone surfaces. The predators were placed into separate polyethylene bags and carried to the laboratory, with the black fly larvae, in a cooler. In the laboratory, black fly larvae were kept in a large aquarium (50-L capacity) with water circulated using air pumps. *Rhyacophila dorsalis* larvae were placed individually in containers sealed with net mesh at each end and kept in the same aquarium.

The caddisfly larvae were "starved" (kept without access to prey) for 12 h in the June experiment and for 24 h in the September experiment. Limited time prevented us from starving predators for identical time periods in the two experiments. At the beginning of the first trial in each experiment, 20 black fly larvae, 10 small (3.5 ± 0.5 mm overall length, mean ± SD, mean dry mass 0.3 mg, converted from length to dry mass using data in Smock 1980), and 10 large (6.4 ± 0.4 mm overall length, mean ± SD, mean dry mass 0.8 mg), were placed into each of the 11 circular channels and allowed to attach. Ten *R. dorsalis* larvae (mean dry mass 68 mg, range 49–84 mg, in the June experiment and mean dry mass 13 mg, range 9–22 mg in the September experiment, converted from overall length measurements using the length–mass relationship given by Smock 1980), were placed 1 to each of the 10 channels and feeding trials were run for 24 h. The 11th channel contained only black fly larvae as a control to examine whether mortality resulted from factors other than predation.

After 24 h in each trial, *R. dorsalis* larvae were removed, placed back in their numbered isolated enclosures, and black fly larvae recovered from each channel. The number of live and dead whole black fly larvae within each size category in each channel was recorded. Channels were then cleaned of debris and reset for the next trial. After starvation of the *R. dorsalis* larvae, the same procedure was repeated.

The June experiment with larger predators involved three successive trials, with each *R. dorsalis* larva returned to the same channel. The September experiment, with smaller *R. dorsalis*, had five successive trials using the same larvae in each channel.

Acroneuria lycorias experiments

Acroneuria lycorias nymphs were collected from the Medora River, Keweenaw County, Michigan, U.S.A., and transported to the laboratory in a cooler containing water that was oxygenated by using air pumps. Black fly larvae were collected from local streams closer to the laboratory and transported using the same procedure as above, because multiple collections were necessary.

Acroneuria lycorias nymphs were fed black fly larvae up to the onset of experiments to eliminate feeding variability that may result from starvation. One *A. lycorias* nymph (not sexed) was placed into each of 10 channels with 30 third-instar black fly larvae. Mean predator dry body mass of stonefly nymphs was 42 mg (range 17–64 mg). As with the previous experiments, the control treatment used only prey and as with the treatment containing predators, the control treatment was replicated 10 times for a total of 20 channels.

Experimental trials were conducted in the laboratory and allowed to proceed for 11 days. The number of remaining black fly larvae in each channel was recorded every 24 h and the number of larvae consumed was obtained by subtraction from 30. Dead and injured larvae were removed and replaced with live larvae. Thus, each channel contained 30 prey at the start of every 24-h interval.

Paragnetina media *and* Isoperla signata experiments

Experiments with *P. media* and *I. signata* were conducted in the field during May 1990 at Morgan Creek, Marquette County, Michigan, U.S.A. The protocol for these experiments was similar to that with *A. lycorias*, but prey consisted of a mixed prey assemblage; equal ratios (10:10:10) of third instar black fly larvae, *Baetis*, and *Epeorus* nymphs, and the experiments extended over 9 days. Mayfly nymphs used were approximately equal in body length to the black fly larvae (ca. 4–5 mm, dry mass range 1.0–1.2 mg; Smock 1980). *Epeorus* nymphs were observed clinging to rocks, and crawled rather than swam upon encountering predators. *Baetis* nymphs commonly swam in response to encounters with predators, and black flies commonly drifted. Predators and prey were collected from Morgan Creek on the day the experiments commenced. Predators were not sexed at the time of collection. *P. media* nymphs averaged 41 mg dry mass (range 19–93 mg), and *I. signata* nymphs averaged 9 mg dry mass (range 7–12 mg). Gravel substrate was added to cover the bottoms of the channels.

The two treatments containing predators (*P. media, I. signata*) were replicated 10 times, and the control treatment was replicated 5 times, for a total of 25 channels.
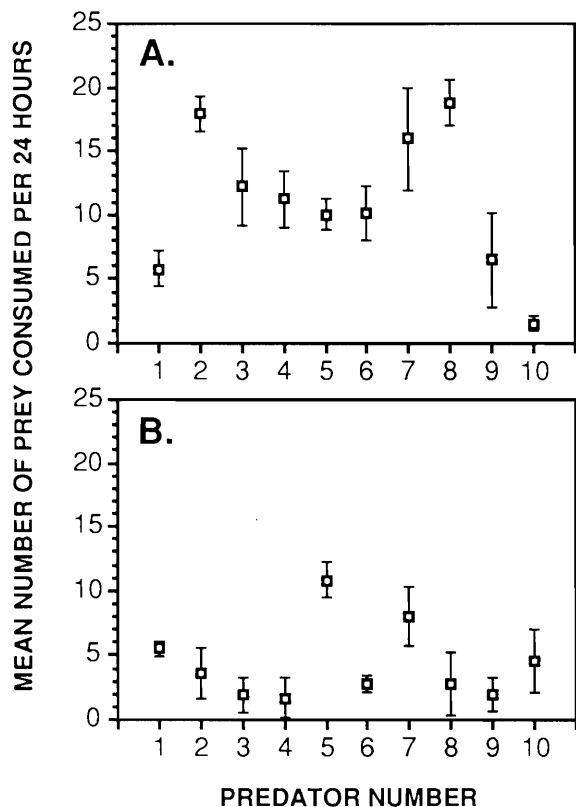
FIG. 1. Mean number of black fly larvae consumed (±SD) by large (A), and small (B) R. dorsalis larvae.

FIG. 3. Number of black fly and mayfly prey consumed by I. signata (A) and P. media (B) nymphs over 9 days during in-field feeding trials.
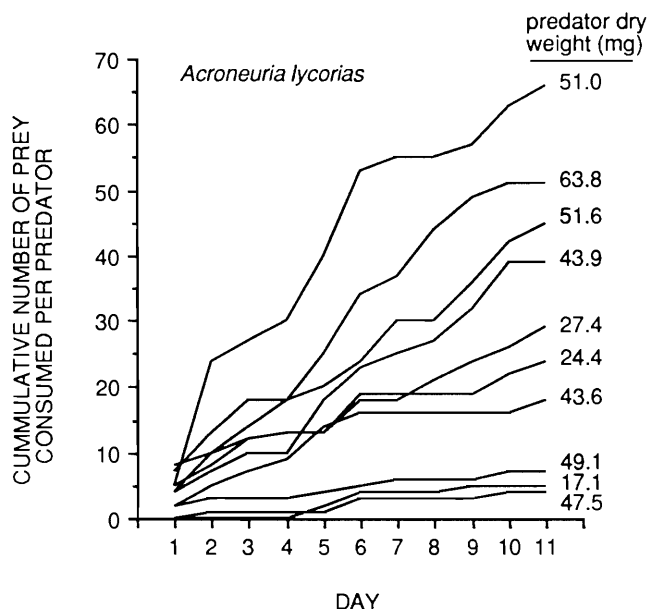

FIG. 2. Cumulative number of black fly larvae consumed by A. lycorias nymphs over 11 days during in-laboratory feeding trials.

IV. Statistical analyses

Daily prey consumption data were analyzed using one-way ANOVA for R. dorsalis experiments and one-way ANCOVA with day as the covariate for all stonefly experiments ($P = 0.05$). To determine if temperature affected P. media and I. signata feeding rates, possible correlations of the size of predacious stonefly nymphs and water temperature, with prey consumption dat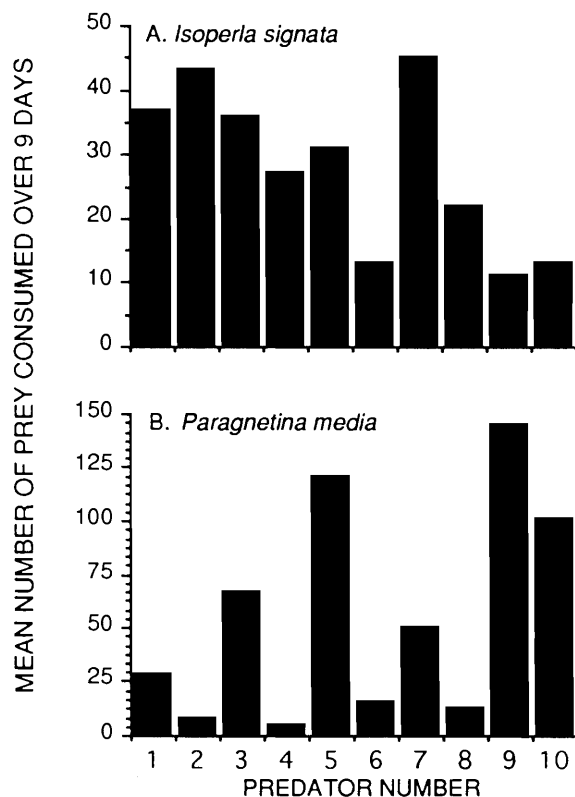a, were also examined for field experiments. Transformation by $\sqrt{(x + 1)}$ was used to normalize data and homogenize sample variances where necessary.

Results

Rhyacophila dorsalis *experiments*

There was no significant difference in the number of small and large black fly larvae taken by R. dorsalis larvae, and so consumption data for large and small prey were therefore grouped. There was a significant difference in the number of black fly larvae consumed by individual predators for both small ($F = 17.96$, $P < 0.001$) and large ($F = 20.76$, $P < 0.001$) R. dorsalis larvae (Fig. 1). Individual larvae displayed a consistent pattern of consumption during both trials through time as evidenced by the pattern of mean ± SD for each predator. Large predators consumed more black fly larvae (median = 11) than did small R. dorsalis larvae (median = 3), and this despite the "starvation time" being twice as long for the latter group. In the June experiments, mortality of black fly larvae in controls averaged 1.7 larvae per trial, and in the September experiments, 1.8 larvae per trial. Nonconsumptive prey mortality in the June experiments averaged 2.9 prey per predator (range, 0–10) and in the September experiments 4.5 prey per predator (range, 0–12). There was considerable variation in nonconsumptive mortality among individuals in both experiments.

Acroneuria lycorias *experiments*

Acroneuria lycorias nymphs also showed significant among-individual differences in the number of black fly larvae consumed ($F = 6.45$, $P < 0.001$) (Fig. 2). There was no significant relationship between predator size (as measured by
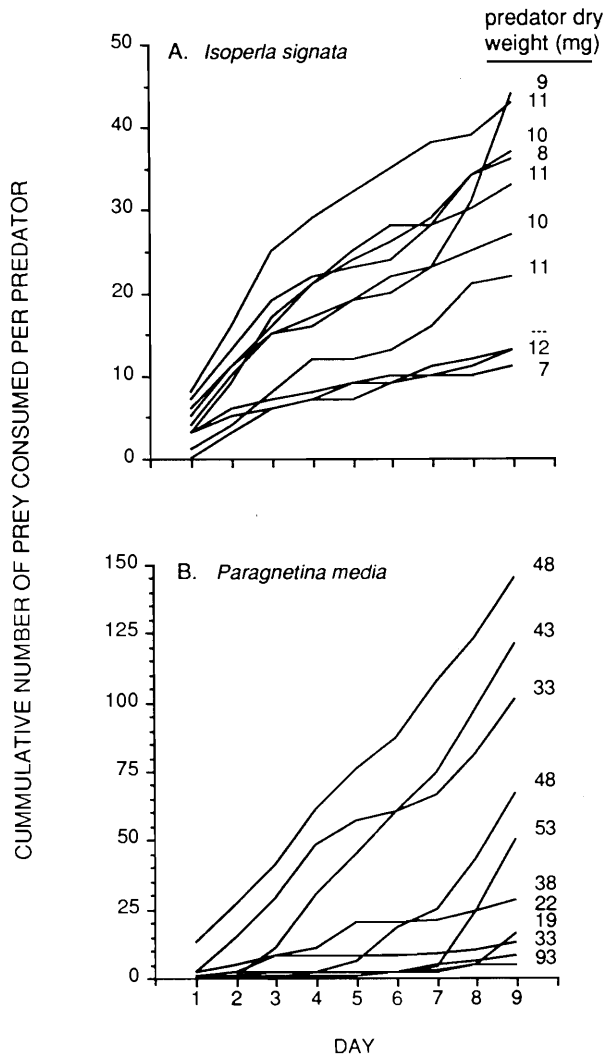
FIG. 4. Cumulative number of prey consumed by *I. signata* (A) and *P. media* (B) nymphs over 9 days during in-field feeding trials.

dry mass) and the number of prey eaten ($r = 0.55$, $P > 0.05$), and there were no obvious pulses in the number of blackfly larvae consumed (Fig. 2).

Paragnetina media *and* Isoperla signata *experiments*

Both *P. media* and *I. signata* conspecifics showed a significant among-individual difference in prey consumption ($F = 11.77$, $P < 0.001$ for *P. media*; $F = 4.39$, $P < 0.001$ for *I. signata*) (Figs. 3A and 3B). As with *A. lycorias*, prey consumption and body size of predators were not significantly correlated ($r = 0.094$ for *P. media*, $r = 0.077$ for *I. signata*) (Figs. 4A and 4B).

Feeding rates were positively correlated with water temperature for *I. signata* ($r = 0.817$, $F = 16.1$, $P < 0.01$), but not for *P. media* ($P > 0.05$). Interspecific (*P. media* vs. *I. signata*) sample variance (S^2) of 9 day cumulative prey consumption was also significantly different ($F = 4.03$, $P < 0.05$) (Fig. 5).

Nonconsumptive prey mortality was high for some, but not all, predators (*P. media*; mean $= 4.7$ prey per predator over 9 days, range, $0-11$; and *I. signata*, mean 5.3 prey per predator over 9 days, range, $0-21$).
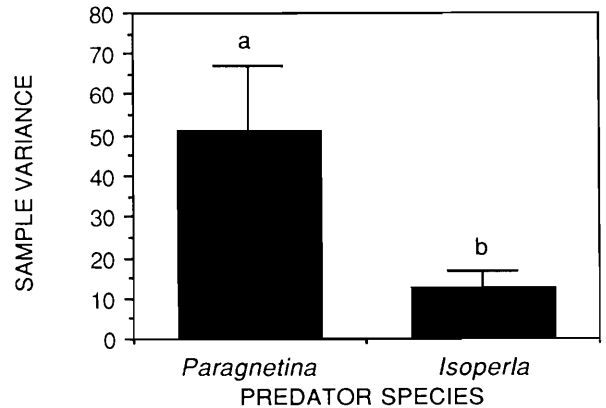

FIG. 5. Sample variance ($\pm$SD) of the daily number of prey consumed by *P. media* (a) and *I. signata* (b) nymphs averaged across 10 predators. Means significantly different, $P < 0.05$.

Discussion

Two factors known to affect predation can be discarded as explanations for the variation between individual conspecific predators in our study: the numbers of predator and prey were constant at the start of trials, and diel effects were overcome by conducting each trial for 24 h. In the two experiments with *R. dorsalis*, larvae were starved for a fixed period between trials in each experiment, thus also removing this potential source of variability among predators. Stonefly nymphs were not starved prior to feeding trials and this could have resulted in different hunger levels between predators, and initially different consumption rates. However, the lack of a starvation period did not appear to be a contributing factor in among-predator feeding differences, as these differences remained consistent throughout the duration of the feeding trials.

There were considerable intra- and inter-specific differences in predation by stoneflies. Unlike the caddisfly larvae, consumption rates within a given species of stonefly were not significantly related to predator body size in our experiments, even though a wide range of predator sizes was used. However, interspecific consumption rate differences may have been related to predator body size. Stonefly nymphs can also show marked preferences for some prey, which will elicit attacks whether the predator is starved or satiated (Molles and Pietruszka 1983; Peckarsky and Penton 1989).

Sexual differences may have contributed to differences in individual feeding patterns, as *R. dorsalis*, *A. lycorias*, and *I. signata* predators were not sexed. However, there was a spread of patterns among individuals and no evidence of bimodality. This factor was eliminated in *P. media* experiments because only females were used. Sex differences in prey consumption arise from the need for females to acquire energy reserves for egg production (Peckarsky and Cowan 1991; Lederhouse et al. 1982).

None of the predators moulted during the experiments with *R. dorsalis*, *A. lycorias*, and *I. signata*, so the effects of ecdysis on depressing consumption rate, thus producing pulses of predation (Malmqvist and Sjöström 1980), can be discounted. However, four individuals moulted during the *P. media* trials, and this may have accounted for some of the observed variability. Each of the *P. media* nymphs that moulted had different premoult feeding habits; one predator stopped feeding 1 day prior to moulting, the others stopped 2, 3, and 4 days prior to

moulting. However, they all began feeding within 24 h following ecdysis. It was not determined whether parasitism or infections with pathogens affected the behaviour of individual predators but no obvious signs of these two factors were observed during our study.

We also have no explanation as to why some caddisfly larvae and stonefly nymphs killed and, in many cases, mutilated prey without eating them. Stonefly nymphs were frequently observed encountering, attacking, and handling prey as witnessed during normal feeding bouts, but then predators released the injured prey. This often occurred several times in sequence with several prey. Attacking and handling prey may have been a "predisposition" response by predators upon encountering prey, but then satiation may have affected consumption. Black fly larvae were victims of nonconsumptive attack by predators more frequently than were mayfly nymphs, especially in attacks by *I. signata*, presumably because predators are likely to have higher prey capture success with the more vulnerable, less mobile prey. Mayfly nymphs typically swim, crawl, or drift upon encountering stonefly predators (Peckarsky 1980; Williams 1987). In our experiments, we observed infrequent predator-avoidance success with black fly larvae relative to the mayflies. Black fly larvae generally remained stationary upon attack.

Explanations of the consistent differences in feeding pattern shown among individuals of both predacious caddisfly larvae and stonefly nymphs may lie in the ability of some individuals to learn different approaches to predation (Shettleworth 1984), or to have a different phenotypic expression of slightly different genotypes (Partridge and Green 1985). Martin and Mackay (1983) have demonstrated that larvae of different *Rhyacophila* species grow most efficiently on slightly different diets, and intraspecific differences in feeding strategy may also be important in promoting the optimal growth of individuals.

Keeping predators in a restricted space under adverse conditions can provike deviant and (or) aggressive behaviour. Peckarsky (1984) stated that laboratory experiments (in artificially restrictive environments) usually produce unstable type II functional responses. In our experiments, the smaller predator, *I. signata*, invoked more nonconsumptive prey mortality than did the larger predator, *P. media*. However, this may well have been a species attribute rather than one solely of size.

The results of our experiments may not truly reflect what happens in the natural environment, but differences in the performance of individual predators were real. Attention should be focused at the level of the individual when considering the role of predators in lotic systems, and the variability in predator performance observed throughout this study should be considered when planning and interpreting studies on predator — prey interactions.

Acknowledgments

Allan, J.D. 1983. Predator — prey relationships in streams. *In* Stream ecology: Application and testing of general ecological theory. *Edited by* J.R. Barnes and G.W. Minshall. Plenum, New York. pp. 191 – 229.

Allan, J.D., Flecker, A.S., and McClintock, N.L. 1987. Prey size selection by carnivorous stoneflies. Limnol. Oceanogr. **32**: 864 – 872.

Davies, D.M. 1981. Predators upon black flies. *In* Black flies: the future for biological methods in integrated control. *Edited by* M. Laird. Academic Press Inc., London. pp. 139 – 158.

Davies, D.M. 1991. Additional records of predators upon black flies (Simuliidae: Diptera). Bull. Soc. Vector Ecol. **16**: 256 – 268.

Lancaster, J., Hildrew, A.G., and Townsend, C.R. 1991. Invertebrate predation on patchy and mobile prey in streams. J. Anim. Ecol. **60**: 625 – 641.

Lederhouse, R.C., Finke, M.D., and Scriber, J.M. 1982. The contributions of larval growth and pupal duration to protandry in the Black Swallowtail Butterfly, *Papilio polyxenes*. Oecologia, **53**: 296 – 300.

Malmqvist, B., and Sjöström, P. 1980. Prey size and feeding patterns in *Dinocras cephalotes* (Plecoptera). Oikos, **35**: 311 – 316.

Martin, I.D., and Mackay, R.J. 1982. Interpreting the diet of *Rhyacophila* larvae (Trichoptera) from gut analyses: an evaluation of techniques. Can. J. Zool. **60**: 783 – 789.

Martin, I.D., and Mackay, R.J. 1983. Growth rates and prey selection of two congeneric predatory caddisflies (Trichoptera: Rhyacophilidae). Can. J. Zool. **61**: 895 – 900.

Molles, M.C., Jr., and Pietruszka, R.D. 1983. Mechanisms of prey selection by predacious stoneflies: roles of prey morphology, behaviour and predator hunger. Oecologia, **57**: 25 – 31.

Partridge, L., and Green, P. 1985. Intraspecific feeding specializations and population dynamics. *In* Behavioural ecology: Ecological consequences of adaptive behaviour. *Edited by* R.M. Sibly and R.H. Smith. Blackwell, Oxford. pp. 207 – 226.

Peckarsky, B.L. 1980. Predator — prey interactions between stoneflies and mayflies: Behavioral observations. Ecology, **61**: 932 – 943.

Peckarsky, B.L. 1984. Predator — prey interactions among aquatic insects. *In* The ecology of aquatic insects. *Edited by* V.H. Resh and D.M. Rosenberg. Praeger, New York. pp. 196 – 254.

Peckarsky, B.L., and Penton, M.A. 1989. Mechanisms of prey selection by stream-dwelling stoneflies. Ecology, **70**: 1203 – 1218.

Peckarsky, B.L., and Cowan, C.A. 1991. Consequences of larval intraspecific competition to stonefly growth and fecundity. Oecologia, **88**: 277 – 288.

Shettleworth, S.J. 1984. Learning and behavioural ecology. *In* Behavioural ecology: An evolutionary approach. *Edited by* J.R. Krebs and N.B. Davies. Blackwell, Oxford. pp. 170 – 194.

Sjöström, P. 1985. Hunting behaviour of the perlid stonefly nymph *Dinocras cephalotes* (Plecoptera) under different light conditions. Anim. Behav. **33**: 534 – 540.

Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biol. **10**: 375 – 383.

Walde, S.J., and Davies, R.W. 1984. Invertebrate predation and lotic prey communities: Evaluation of in situ enclosure/exclosure experiments. Ecology, **65**: 1206 – 1213.

Wiley, M.J., and Kohler, S.L. 1981. An assessment of biological interactions in an epilithic stream community using time-lapse cinematography. Hydrobiologia, **78**: 183 – 188.

Williams, D.D. 1987. A laboratory study of predator — prey interactions of stoneflies and mayflies. Freshwater Biol. **17**: 471 – 490.

Wipfli, M.S. 1992. *Bacillus thuringiensis* var. *israelensis* and nontarget stream macroinvertebrates and trout: lethal and sublethal effects, predator — prey interactions, and fate of infected larval black flies. Ph.D. thesis, Michigan State University, East Lansing.

Wotton, R.S., and Merritt, R.W. 1988. Experiments on predation and substratum choice by larvae of the muscid fly, *Limnophora riparia*. Holarct. Ecol. **11**: 151 – 159.