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Feeding while evading predators by a lotic mayfly: linking short-term foraging behaviours to long-term fitness consequences

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Abstract Laboratory experiments were performed to quantify the combined effects of food abundance (low, high) and predation threat, imposed using a model fish (safe, risky) on fitness correlates (i.e. growth, time to emergence, adult body mass, fecundity, egg size) of the mayfly *Baetis tricaudatus*. These effects were determined by rearing larvae under different combinations of food abundance and predator threat. Fitness correlates were significantly affected by food abundance, predation threat or the interaction of these factors. High food abundance and the absence of predation threat significantly increased larval growth rates, adult body mass, fecundity, egg size, and decreased time to emergence. Long-term effects of predator threat and food abundance on fitness correlates of *B. tricaudatus* were compared to previously conducted short-term patch choice trials to test for concordance between short-term measures of patch choice and their potential longer-term fitness consequences. This comparison indicated that patches that were utilized the most were those that yielded the highest fitness benefits. These results suggest that behavioural costs of balancing mortality risk due to predation against food acquisition by *B. tricaudatus* can have strong fitness consequences.

Key words Fitness · Trade-off · Life history · Foraging mayfly

Introduction

Foragers are thought to routinely balance the conflicting demands of adopting one behaviour against the costs and benefits of adopting others (Stephens and Krebs 1986; Dill 1987; Dudley et al. 1990; Lima and Dill 1990; Ludwig and Rowe 1990). When foragers trade off the benefits of food ingestion against the costs of mortality risk due to predation, in terms of feeding patch selection, individuals should select patch types that yield the highest fitness benefits (Cooper 1984; Dill 1987; Gilliam and Fraser 1987; Abrahams and Dill 1989; Nonacs and Dill 1990). The majority of studies examining the risk of mortality versus resource acquisition dilemma have used short-term experiments, often conducted over several hours, to describe forager responses to spatial variation in food abundance and predation risk (see reviews by Stephens and Krebs 1986; Dill 1987; Lima and Dill 1990). The results from these short-term studies are then compared to an a priori outcome which is considered optimal. Despite the importance of linking short-term foraging behaviours to fitness, few studies have determined this relationship or quantified the costs and benefits of selecting patches which vary in both resource abundance and mortality risk due to predation (Werner and Hall 1988; Nonacs and Dill 1990; Blanckenhorn 1991; Scrimgeour and Culp 1994).

Quantifying the fitness benefits of foraging patch selectivity can be accomplished by performing short-term patch choice trials to identify individual patch preferences, followed by long-term studies in which individuals are reared under fixed combinations of predation risk and food abundance. For instance, Blanckenhorn (1991) used this approach to determine fitness benefits of water striders, *Gerris remigis*, selecting patches that differed solely in prey abundance. When provided with two prey patches differing in the density of *Drosophila* prey, gerrids selected high prey density patches. Individuals reared in high prey density patches grew more rapidly compared with those reared in low prey abundance patches. While this example indicates concordance be-

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tween short-term patch choice and fitness in a relatively simple scenario (i.e. spatial variation in prey abundance), fitness consequences associated with more complex scenarios, such as the case where foragers must balance the conflicting demands of food acquisition and predator avoidance, are not well understood.

The lotic food-web consisting of periphytic algae, mayfly larvae of *Baetis tricaudatus* Dodds and the longnose dace fish predator *Rhinichthys cataractae* (Valenciennes) provides a useful system to empirically determine the fitness benefits of patch choice selection. Mayfly larvae graze upper stone surfaces ingesting algal and associated particulate material (Scrimgeour et al. 1991; Culp and Scrimgeour 1993). While the duration of the feeding period is size-dependent, both small and large larvae feed during the hours of darkness (Culp and Scrimgeour 1993). Feeding on exposed surfaces during the night makes them vulnerable to a nocturnal minnow, the longnose dace (Culp 1989; Culp et al. 1991). Previously completed patch choice experiments indicate that *B. tricaudatus* larvae provided with simultaneous access to feeding patches that varied in predation risk according to the presence of a live fish (safe, risky), and food abundance (low, high), spent the majority of time in safe, high-food patches. Decreasing amounts of time were spent in safe, low-food patches, risky, high-food patches and risky, low-food patches, respectively (Scrimgeour et al. 1994b). Food ingestion rates were also highest in safe compared to risky, and in high food compared to low-food patches, respectively (Scrimgeour 1992; Scrimgeour et al. 1994b). These results suggest that selection of safe versus risky and high versus low food patches should have strong fitness consequences.

In the present study we designed an experiment based on the results from these short-term patch choice trials to test the hypotheses that: (1) fitness correlates of a lotic mayfly *B. tricaudatus* are affected by predator threat and food abundance, and (2) patches selected during short-term patch choice trials are those that yield the highest fitness benefits (i.e. concordance between short-term patch choice decisions and fitness consequences). These hypotheses were tested by rearing larvae under different combinations of predator threat, using a model predator, and food abundance and measuring larval growth rates, time to emergence, adult body mass, fecundity and egg size.

Material and Methods

Study animals and experimental design

Mayfly larvae (body length $\bar{x} \pm 1$ SE = 2.8 ± 0.01 mm) were collected from the Bow River, Alberta, Canada ($51^{\circ} 03' N$, $114^{\circ} 03' W$) between 1 to 7 April 1990 and reared in small, circular Plexiglas streams (i.e. microcosms, volume = 0.25 l, planar area = 50 cm²) with recirculating filtered, aerated water (Scrimgeour et al. 1994a). Water was pumped into each stream from one of two large (>500 l) reservoirs. Water temperature (day:night = 14:10°C) and light (day:night = 12:12 h) was cycled on a diel basis. The bottom of each stream was covered with a single layer of 4 mm glass beads

to serve as a substratum, and five rectangular plexiglas blocks (3×2×1 cm) provided feeding patches. Feeding patches were elevated above the stream bottom on smaller plexiglas blocks (1×1×1 cm). Previous observations showed that *B. tricaudatus* feed primarily on these feeding patches with little time spent grazing glass beads (G.J. Scrimgeour, unpublished data).

The experiment represented a two-factorial design with food abundance [i.e. algal biomass = low (L), high (H)] and predator threat [safe (S), risky (R)] as factors. Groups of ten larvae were reared in each of eight replicate streams representing each combination of predation threat and food abundance (i.e. LS, HS, LR, HR). Although each stream contained ten larvae, streams were treated as replicates by creating a mean for each response variable based on all larvae present in an individual stream. Thus, each combination of food abundance and predator threat was replicated eight times. Lastly, replicate streams, within the food abundance treatment, were randomly positioned on two large tables to ensure that treatment effects could not be attributed to stream position effects.

Two levels of food abundance (i.e. algal biomass) were established by adding phosphorus, as KH_2PO_4 , into one reservoir but not the other. After the addition of nutrients, each stream was inoculated with a 50 ml volume of algal stock, consisting predominantly of the diatoms of *Navicula*, *Gomphonema* and *Nitzschia* species, which has been scraped from upper surfaces of stones from the Bow River on 26 March 1990. Algal growth in streams receiving water from the high nutrient reservoir increased rapidly compared to streams that received water from the low nutrient reservoir. Differences in algal biomass among streams receiving low and high nutrient water produced two significantly different algal biomasses on upper surfaces of feeding substrata after 2 weeks [low food abundance = 0.10 mg dry mass (DM)/cm², high food abundance = 1.10 mg DM/cm²]. An initial set of feeding trials (described in Scrimgeour 1992) showed that small *B. tricaudatus* ($\bar{x} \pm 1$ SE = 3.03 ± 0.3 mm) achieved a mean ($\bar{x} \pm 1$ SE) food intake of 0.04 ± 0.005 mg DM/h in feeding patches with a diatom biomass of 1.10 mg DM/cm². This feeding rate was significantly higher (*t*-test on \log_{10} transformed data: $t = 4.41$, $P < 0.05$) than food intake (0.01 ± 0.002 mg DM/h) on low algal biomass substrata (0.10 mg DM/cm²). These rates of food intake are similar to those achieved on natural stones from the Bow River (Scrimgeour 1992).

Algal biomass on Plexiglas substrata in each stream was monitored throughout the trials by randomly removing two 16 mm² areas from two substratum in each stream at weekly intervals. Algal scrapings were dried at 40°C for 2 days and weighed to the nearest 0.001 mg to estimate biomass. Previous algal growth experiments in small streams indicated that algal biomass increases through time (G.J. Scrimgeour, unpublished data). A small proportion of this material enters the water column, eventually clogging the central outflow column causing water to overflow and, if left unattended, resulting in the emigration of mayfly larvae. To overcome this problem, and to maintain initial low and high food abundance levels, algae on upper surfaces of feeding patches were reduced by gently brushing surfaces with a stout brush.

Predation threat on *B. tricaudatus* was imposed using a model *R. cataractae* that had been dried, attached to a 15-cm piece of wire and covered with a thin plastic film. The threat of predation was imposed on *B. tricaudatus* by moving the model across the substratum 6 times during the dark period (i.e. once every 1.5 h). On each occasion, the model was moved in an upstream direction at a velocity of 0.70 cm/s to resemble probing and rooting foraging behaviours (Beers and Culp 1990). Because mayfly larvae of *B. tricaudatus* display strong anti-predator responses to the predator model which closely resemble those displayed to live *R. cataractae*, we have assumed that mayfly larvae perceive the model as an indicator of impending mortality risk due to predation. In the majority of cases larvae respond to the model by entering the drift, presumably after recognition of hydrodynamic cues, rather than coming into direct contact with the model (Scrimgeour et al. 1994a, 1994b; G.J. Scrimgeour, unpublished observations).

Our experimental design was based on testing for sub-lethal effects of predator threat on fitness correlates. While the experiment

does not test for effects of predators on larval survival, our results from previous experiments indicate that the movement of the *R. cataractae* model through streams results in significant increases in drift and the movement of mayfly larvae to the undersurfaces of substrata, which could be associated with a latency period accompanied with reduced food intake rates (Scrimgeour et al. 1994a).

Measurement of fitness correlates

Larval growth rates were estimated by removing larvae at weekly intervals from each stream, placing them in a petri dish and measuring total body length (posterior of abdomen to anterior of head) under 12 \times magnification. After measurement, larvae were returned to their respective stream. Removal of larvae and their measurement took less than 20 sec per individual. Larval mortality during the entire experimental period (i.e. 4–9 week period) was approximately 15% and did not vary appreciably among treatments (range=12–18% mortality).

Larvae were reared in streams under one of the fixed combinations of predation threat and food abundance until emergence as adults. Fine mesh netting (mesh size=2 mm) was secured over the tops of streams to ensure that adults could be collected and identified as originating from a particular stream. Adult *B. tricaudatus* undergo two moults (i.e. sub-imago and imago stages) before becoming sexually mature, and the relationship between adult length and egg size can change during this period (Clifford 1970). We standardized the developmental stage of mayfly adults by ensuring that all adults had completed their second moult before they were preserved in formalin. The presence of adults was checked daily and adults were preserved in individual vials containing 10% formalin for 2 days. After this period adult males were dried at 40 $^{\circ}$ C for 2 days to determine biomass. Adult females were removed from the formalin solution after 2 days and all eggs from the thoracic and abdominal cavities removed under 25 \times magnification to determine fecundity.

Removal of eggs under high magnification ensured that chorionic material could be separated from the eggs. We calculated the mass of all eggs, and the mass of chorionic material combined with the remaining viscera, by drying each separately and combining these weights to estimate total female mass. Mean egg size (i.e. egg dry mass) for each female was calculated by dividing the dry mass of all eggs by fecundity.

Statistical analyses

A two factor ANCOVA with food abundance (low, high), predation threat (safe, risky) as factors, and time as the covariate was used to determine whether initial algal biomass levels (i.e. low algal biomass=0.10 mg DM cm 2 , high algal biomass=1.10 mg DM cm 2) remained constant through time in low-food versus high-food streams. An ANCOVA design was also used to test the hypothesis that larval size was not significantly affected by predation risk, food abundance, time and the interaction of these factors. The hypotheses that time to emergence, adult body mass, fecundity and egg size were affected by predation threat, food abundance and the interaction of these factors were tested with a two-factor ANOVA. Where appropriate, data were transformed to meet assumptions of ANCOVA and ANOVA analyses. Comparisons of slopes of ANCOVA designs were compared using orthogonal contrasts and main treatment effects from ANOVA comparisons were identified using Tukey's multiple range test. All statistical analyses were performed within SAS (SAS 1988).

Results

Growth rates of larvae were significantly affected by the interaction between time, food abundance and predation threat (ANCOVA: $F_{(1,223)}=7.63$, $P<0.01$; Fig. 1). Com-

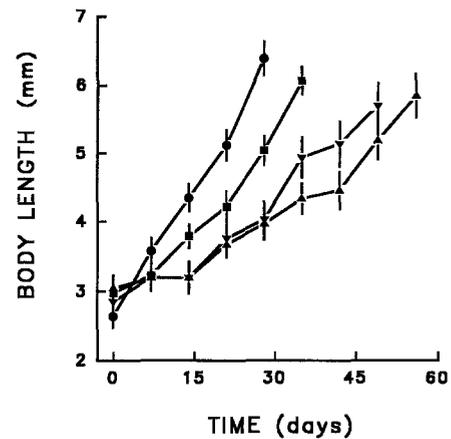


Fig. 1 Effects of predation threat (safe, risky) and prey abundance (low, high) on mean larval growth rates ($\bar{x}\pm$ SE) of *Baetis tricaudatus*. Symbols represent larvae reared under different combinations of predation risk and prey abundance: ● safe, high food, ■ safe, low food, ▼ risky, high food, ▲ risky, low food

parison of \log_{10} growth trajectories indicated that, with one exception, the slopes of all lines were significantly different from each other ($P<0.0001$). In contrast to all other comparisons, there was no significant difference between growth rates of individuals reared in risky, low-food streams and risky, high-food streams. Growth rates were typically highest when larvae were reared in safe, high-food streams, exceeding those reared in safe, low-food streams. Larval growth rates were even lower in risky, high-food streams and risky, low-food streams. Food abundance, measured as algal biomass, was significantly greater (ANCOVA: $F_{(1,223)}=527.85$, $P<0.001$) in high-food streams (overall $\bar{x}\pm$ SE=1.10 \pm 0.04 mg cm 2) than in low-food streams (0.10 \pm 0.004 mg cm 2) throughout the experiment. Because algal biomass (i.e. food abundance) in streams was not significantly affected by predation threat, time, or the interactions of these factors ($P>0.05$), initial differences in food abundance between high-food streams and low-food streams remained constant throughout the experimental period.

Mean time of larvae to emergence (Table 1) was significantly affected by predator threat (males: $F_{(1,31)}=121.7$, $P<0.0001$; females: $F_{(1,31)}=110.69$, $P<0.001$) and food abundance (males: $F_{(1,31)}=8.08$, $P<0.01$; females: $F_{(1,31)}=7.36$, $P<0.001$), whereas the interaction of these terms were not significant (males: $F_{(1,31)}=0.10$, $P>0.05$; females: $F_{(1,31)}=2.23$, $P>0.05$). Tukey's multiple range test on main effects indicated time to emergence was significantly lower when larvae were reared in safe versus risky and high-food versus low-food streams.

Mean body mass of adults (Table 2) was significantly affected by predation threat (males: $F_{(1,31)}=14.48$, $P<0.05$; females: $F_{(1,31)}=42.66$, $P<0.001$) and food abundance (males: $F_{(1,31)}=4.54$, $P<0.05$; females: $F_{(1,31)}=13.93$, $P<0.001$), whereas the interaction of these terms was not significant (males: $F_{(1,31)}=0.02$, $P<0.05$; females: $F_{(1,31)}=0.07$, $P<0.05$). Male and female body

Table 1 Comparison of mean time to adult (days) ($\bar{x}\pm\text{SE}$) for male and female *Baetis tricaudatus* when reared in safe or risky conditions with low or high food abundance

	Safe	Risky
Male		
Low food	32.96 \pm 1.51	52.01 \pm 1.86
High food	27.35 \pm 1.39	47.51 \pm 2.23
Female		
Low food	34.29 \pm 1.30	50.60 \pm 2.00
High food	26.69 \pm 1.10	48.40 \pm 2.49

Table 2 Comparison of mean ($\bar{x}\pm\text{SE}$) adult mass (mg dry mass) for male and female *Baetis tricaudatus* when reared in safe or risky conditions with low or high food abundance

	Safe	Risky
Female		
Male		
Low food	1.10 \pm 0.078	0.77 \pm 0.042
High food	1.30 \pm 0.113	0.95 \pm 0.108
Female		
Low food	1.49 \pm 0.093	0.93 \pm 0.094
High food	1.83 \pm 0.086	1.24 \pm 0.076

Table 3 Comparison of mean ($\bar{x}\pm\text{SE}$) fecundity and egg size ($\text{mg}\times 10^{-5}$ dry mass) of *Baetis tricaudatus* when reared in safe or risky conditions with low and high food abundance

	Safe	Risky
Fecundity		
Low food	700.18 \pm 57.52	442.59 \pm 42.24
High food	993.77 \pm 61.07	332.42 \pm 62.54
Egg size		
Low food	67.74 \pm 3.23	55.78 \pm 1.24
High food	81.17 \pm 2.69	50.94 \pm 3.15

mass was significantly higher when reared in safe versus risky streams and in high-food versus low-food streams (Tukey's multiple range test: $P<0.05$).

Mean female fecundity was significantly affected by food abundance ($F_{(1,31)}=10.48$, $P<0.05$), predation threat ($F_{(1,31)}=66.94$, $P<0.05$) and the interaction of these factors ($F_{(1,31)}=5.75$, $P<0.05$; Table 3). The significant interaction arises because females reared in safe, high-food streams were, on average, 3 times more fecund than in risky, high-food streams, but only 1.5 times more fecund in safe, low-food streams than in risky, low-food streams. Differences in fecundity are not surprising because of the positive relationship between fecundity and body mass (Fig. 2). This relationship is defined as: fecundity = $50.36 + 426.38$ body mass (mg DM) ($F_{(1,31)}=19.31$, $P<0.01$, $r^2=0.39$).

Mean egg size was significantly affected by predation threat (ANOVA: $F_{(1,31)}=306.45$, $P<0.001$), food abundance ($F_{(1,31)}=36.64$, $P<0.001$) and the interaction of these factors ($F_{(1,31)}=124.08$, $P<0.001$; Table 3). The significant interaction probably arises because females from

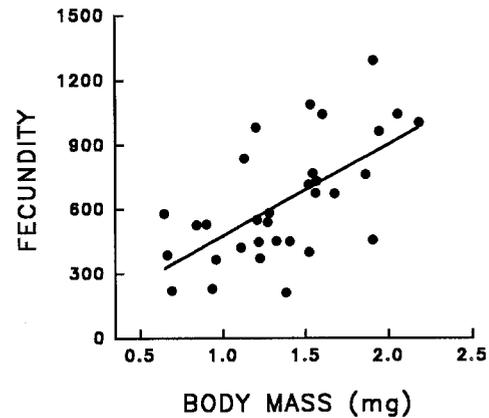


Fig. 2 Relationship between fecundity and body mass for *Baetis tricaudatus* reared in laboratory streams under different predation risk (safe, risky) and prey abundance (low, high) regimes

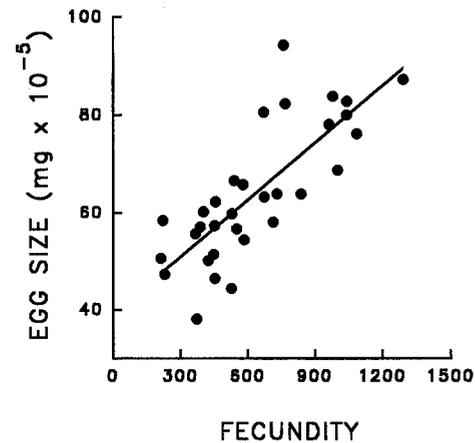


Fig. 3 Linear regression of egg size ($\times 10^{-5}$) versus fecundity for *Baetis tricaudatus* reared in laboratory streams under different combinations of predation risk and prey abundance

safe, high-food streams produced substantially larger eggs than those from other stream types. Linear regression indicated that egg size ($\times 10^{-5}$) was significantly related to fecundity [egg size (mg DM) = $39.23 + 0.039$ fecundity, $F_{(1,31)}=46.51$, $P<0.001$, $r^2=0.60$] (Fig. 3).

Discussion

Foragers are thought to face behavioural trade-offs when adopting one behaviour affects the costs and benefits of others (Stephens and Krebs 1986; Dill 1987; Dudley et al. 1990; Lima and Dill 1990; Ludwig and Rowe 1990). For instance, when feeding patches differ in both the abundance of food and in mortality risk due to predation, foragers should select patch types that yield the highest fitness benefits (Cooper 1984; Dill 1987; Gilliam and Fraser 1987; Abrahams and Dill 1989; Nonacs and Dill 1990).

We quantified fitness consequences of foraging patch selection by the lotic mayfly *B. tricaudatus* by compar-

ing larval growth and subsequent adult body characteristics after rearing larvae in streams under different regimes of food abundance and predator threat. Results from these long-term experiments were compared with short-term (1 h) patch choice experiments where larvae had simultaneous access to feeding patches that differed in predation risk (using a live fish) and food abundance. When short-term patch use patterns were ranked from high to low, time spent in a particular patch decreased from safe, high-food patches to safe, low-food patches, risky, high-food patches and risky, low-food patches, respectively (Scrimgeour 1992; Scrimgeour et al. 1994b). If short-term patch selection patterns are concordant with long-term fitness consequences, then fitness benefits in safe, high-food patches should exceed those of safe, low-food patches. Furthermore, time spent in risky, high-food patches should exceed that in risky, low-food patches.

Our results from laboratory experiments indicated that fitness correlates were significantly affected by food abundance, predation threat or the interaction of these factors. In fact, *B. tricaudatus* larvae grew more rapidly, emerged into adults more quickly, and attained a larger mean body mass in streams that contained high food abundance compared to low food abundance, and in safe compared to risky streams. Further, females displayed higher fecundity and produced larger eggs when reared in streams that contained high food abundance compared to that attained in low-food streams, and in safe compared to risky streams. In several cases fitness correlates (i.e. fecundity, egg size) were significantly affected by the interaction between food abundance and predator threat. However, in each case, fitness consequences were higher in the safe, high-food streams than in all other stream types.

Predators affect prey life history characteristics by altering growth rates, adult body size and timing and allocation of reproductive effort (Dixon and Baker 1988; Crowl and Covich 1990; Feltmate and Williams 1991; Rowe and Ludwig 1991; Skelly 1991; Peckarsky et al. 1993). One of the most striking results of our study was that predation threat imposed with a predator model significantly decreased *B. tricaudatus* larval growth, adult mass, fecundity and egg mass, and increased time to emergence (i.e. time of larvae to adult). While it is widely appreciated that the inability to avoid a predator can dramatically reduce fitness due to death, few studies have quantified the sub-lethal effects of predator intimidation on fitness. Those that have quantified sub-lethal fitness effects of predators indicate that they can be high (Crowl and Covich 1990; Flecker 1992; Macchiusi and Baker 1992; Peckarsky et al. 1993). Our results, as well as those of other studies, further suggests that although predators can exert strong population effects on their prey due to prey mortality, sub-lethal effects associated with alterations in prey foraging behaviours can potentially be strong. Further data quantifying the effects of predators on their prey in field situations is clearly required, but the results from Skelly (1991) and Feltmate and Williams (1991) in other systems suggest that fitness

effects are unlikely to be an artifact of laboratory conditions.

Studies on life history patterns of larval aquatic insects have demonstrated the importance of temperature and food quantity and quality on larval growth and body size characteristics of adults (Butler 1984; Sweeney 1984; Hawkins 1986; Sweeney et al. 1986). The effect of predators on life history characteristics of aquatic insects is poorly understood, although the recent study by Feltmate and Williams (1991) is a notable exception. Using enclosures they found that exposure of the stonefly, *Paragnetina media*, to rainbow trout, *Oncorhynchus mykiss* (Richardson), reduced larval size, adult condition and fecundity. Similarly, the presence of predatory pumpkinseed sunfish, *Lepomis gibbosus*, reduced the proportion of third and fourth instar chironomid larvae of *Chironomus tentans* that moulted (Macchiusi and Baker 1992). Our results indicate that predation threat, using a model *R. cataractae*, significantly reduced larval growth rates and significantly increased the length of time to emergence as adults. Reduced growth rates of larval *B. tricaudatus* is ecologically important for at least two reasons. First, since adults do not feed, adult body size is determined by foraging activities of the larvae. Second, because fecundity is positively related to body size, an increase in body mass increases adult fecundity (Butler 1984; Sweeney 1984; Sweeney et al. 1986; Peckarsky et al. 1993). Reduced growth rates under low food and risky conditions is consistent with the contention that organisms mature at a larger size when growth is rapid and later at a smaller size when growth is slow (Stearns and Koella 1986), i.e. they adopt a slow life style (Sih 1987).

Larger adult size is generally interpreted as selectively advantageous because of the positive correlation between body size and fecundity. Furthermore, large adult body mass can potentially increase the competitive ability of males to procure mates. The fact that male heptagenid mayflies of *Epeorus longimanus* collected from mating pairs were significantly larger than those collected randomly from mating swarms suggests a benefit of increased body size (Flecker et al. 1988).

The relationship between egg size and fecundity has been addressed from both theoretical and empirical perspectives (Lloyd 1987; Godfray and Parker 1991). The nature of this trade-off is linked to balancing the benefits of producing fewer, but potentially fitter offspring (i.e. larger offspring from larger eggs), against producing more, but potentially less fit offspring (i.e. smaller offspring from small eggs). For animals of different sizes, egg size can be negatively related (Ware 1975; Sinervo and Licht 1991), unrelated (Duncan 1987; Bradford and Stephenson 1992) or positively related to egg number (Bradford and Stephenson 1992).

Our experiments showed a significant, positive relationship between egg size and fecundity for *B. tricaudatus*. Although few other studies quantified the relationship between egg size and fecundity for mayfly larvae, Clifford (1970) observed positive relationships

between body size and fecundity and body size and egg size for the leptophlebid mayfly, *Leptophlebia cupida*. While Clifford did not show the relationship between egg size and fecundity, the strong non-linear relationships between egg size and body size suggest that egg size and fecundity were also likely positively related. As large eggs can only be produced by reducing fecundity, the positive relationship between egg size and fecundity for *B. tricaudatus* suggests that larger females are sacrificing fecundity to produce larger eggs. However, high fecundity, combined with the positive relationship between fecundity and body size, suggests that the solution to the egg size versus fecundity trade-off by *B. tricaudatus* is dominated by producing very high numbers of small eggs rather than low numbers of large eggs.

In summary, the results of the present study have shown that short-term foraging decisions by the mayfly *B. tricaudatus* have long-term fitness consequences and that these consequences are concordant with those predicted from short-term patch selectivity patterns. Comparison of rankings between time allocation patterns and fitness correlates were concordant with the predictions that fitness consequences in safe patches should exceed those in risky patches, and that fitness consequences in high food abundance patches should exceed those in low food abundance patches. While the combination of short-term behavioural experiments and long-term studies is useful to empirically determine the adaptive value of behavioural trade-offs, the importance of such trade-offs to larger scale population and community characteristics requires field experimentation.

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