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Differential behavioural responses of mayflies from streams with and without fish to trout odour

ANGUS R. McINTOSH*†§ AND BARBARA L. PECKARSKY†§
*Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand
†Department of Entomology, Cornell University, Ithaca, NY 14853, U.S.A.
§Rocky Mountain Biological Laboratory, PO Box 519, Crested Butte, CO 81224, U.S.A.

Address for correspondence: A.R. McIntosh, Department of Entomology, Cornell University, Ithaca, NY 14853, U.S.A.

SUMMARY

1. In streams, mayflies (Order Ephemeroptera) are at risk from fish feeding visually in the water column. The effect of fish odour on the behaviour of *Baetis bicaudatus* from a fishless stream and a trout stream was investigated in four large oval tanks supplied with water from the fishless stream.
2. For each mayfly population, mayfly positioning on the substratum and movement in the water column (drift) were measured during the day and night, over 3 days. Brook trout (*Salvelinus fontinalis*) odour was added to two tanks to test the effect of a threat from fish.
3. Throughout the experiment more mayflies from the trout stream were observed on the substratum surface and in the water column during the night than the day, but the magnitude of night drift was less in tanks with fish odour.
4. *Baetis* from the fishless stream also displayed a nocturnal periodicity in drift and positioning, but their night-time drift was not affected by the presence of fish odour. On the first day of the experiment, however, more mayflies were observed on the substratum surface and drifting in tanks without fish odour during the day.
5. Sensitivity to fish odour may enable mayflies to alter their behaviour according to the risk of predation from fish.

Introduction

In many streams, mayfly nymphs (Order Ephemeroptera) are at risk from fish such as trout that feed visually. Visually feeding fish have a large influence on the behaviour of mayflies. They present a higher predation risk during the day (Jenkins, 1969; Ware, 1973; Ringler, 1979; Angradi & Griffith, 1990; McIntosh & Townsend, 1995). To reduce the risk of predation, many mayflies drift less during the day where visually feeding predatory fish are present (Flecker, 1992; Douglas, Forrester & Cooper, 1994; McIntosh & Townsend, 1994). Consequently, a diel periodicity in the drift of mayflies is regularly observed in streams with trout (Elliott, 1967; Waters, 1972; Müller, 1974; Allan, 1987; Brittain & Eikeland, 1988; Sagar & Glova, 1992) but not in streams where visually feeding fish are absent (Malmqvist, 1988; Flecker, 1992; Douglas *et al.*, 1994; McIntosh & Townsend, 1994). This relationship is common, but how variations in the threat of trout predation induce this phenomenon is unclear.

In the laboratory the nocturnal drift periodicities of mayfly nymphs often persist irrespective of the presence of fish (Ciborowski, Pointing & Corkum, 1977; Ciborowski, 1983; Kohler, 1985; McIntosh & Townsend, 1994). However, some studies have shown that mayflies do alter their behaviour in response to fish chemicals (Cowan & Peckarsky, 1994; Douglas *et al.*, 1994; Scrimgeour, Culp & Cash, 1994). Here we report the results of a study of the behavioural responses of a mayfly, *Baetis bicaudatus* Dodds, from a

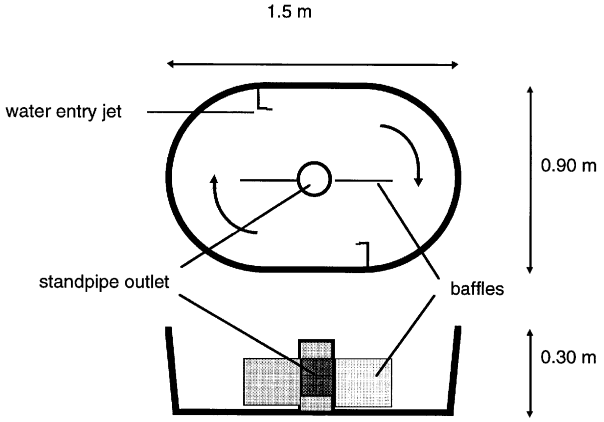

Fig. 1 The design of the flow-through tanks used in the experiments.

trout stream and a fishless stream. We tested whether the presence or absence of brook trout (*Salvelinus fontinalis* Mitchill) odour differentially affected the behaviour of *Baetis* from the two streams.

Materials and methods

Experiments were conducted on late instar nymphs of winter generation *B. bicaudatus* (Cowan & Peckarsky, 1994) without black wing pads. Mayflies from a trout stream were collected from the East River, a third-order, high-altitude (2950 m) stream in the Rocky Mountains, Colorado. The East River contains large numbers of brook trout and stocked rainbow trout (*Oncorhynchus mykiss* Richardson), with smaller numbers of brown (*Salmo trutta* L.) and cutthroat (*O. clarki* Richardson) trout (Allan, 1981). *Baetis* from a fishless stream were obtained from Benthette Brook, a first-order tributary of the East River. Mayflies were collected from Benthette Brook 100 m upstream from the confluence with the East River where a waterfall prevents migration of fish from the East River, rendering Benthette Brook naturally fishless. Both streams contain large numbers of *B. bicaudatus* but two predatory perlodid stoneflies, *Megarcys signata* Hagen and *Kogotus modestus* Banks, were more abundant in Benthette Brook (see Peckarsky, 1979; Peckarsky & Penton, 1989 for a more detailed description of these sites).

We ran one experiment with mayflies from each population during July 1993 in four black oval recirculating tanks (0.9 m × 1.5 m × 0.30 m, Fig. 1). These were supplied with stream water from Benthette Brook (containing no fish odours), at a mean depth (± SE) of 0.19 (± 0.04) m and a mean current velocity of 0.24 (± 0.06) m s^{-1} inside the tanks. The tanks were lined with a 0.03 m layer of gravel from a dry stream bank and ten algae-covered cobbles from a fishless stream were included to provide food patches for the mayflies. Two of the tanks were randomly selected to receive fish odour. Brook trout odour was added to these tanks by dripping in water at a mean rate of 2.18 (± 0.04) l min^{-1} from a 200 l plastic drum fed by Benthette Brook water and containing two brook trout. The two brook trout, caught by angling, were 200–250 mm (fork length) and were fed *B. bicaudatus ad libitum* while in the tank. Thus, for each population of *Baetis*, we ran one experiment which had two treatments (with or without trout odour), with two replicates of each treatment.

Mayflies were collected between 10.00 and 14.00 h and placed in the experimental tanks at 15.00 h (mountain daylight time). In the experiment with *B. bicaudatus* from the trout stream, 500 individuals per tank (≈ 370 *Baetis* m^{-2}) were used but, for logistical reasons, 200 individuals per tank (≈ 148 *Baetis* m^{-2}) were used in the experiment with the *B. bicaudatus* from the fishless stream. These densities are at the low end of the range found in the East River and Benthette Brook (Peckarsky & Penton, 1989). We measured *B. bicaudatus* drift in the tanks by counting the number of *B. bicaudatus* moving in the water column through a cross-section of the tank over 5 min. The presence of mayflies on the substratum surface was measured by counting the number of *B. bicaudatus* visible on the substratum in the tanks. Dim red light was used for observations at night. Although some mayflies avoid red light (Heise, 1992; A.R. McIntosh, personal observation), we have observed that *Baetis* appears to behave normally when observed under red light, as have others (Allan, Flecker & McClintock, 1986; Casey, 1987; Cowan & Peckarsky, 1994). On the first day, observations started at 17.00 hours and continued every 2 h for 24 h. Over the next 2 days we made three observations during daytime at 09.00, 13.00 and 17.00 h and one night-time observation at 21.00 h.

We compared mayfly drift and positioning among fish treatments (trout odour *v* no trout odour) and time (day *v* night) on successive days (days 1 and 2) with univariate repeated measures ANOVA using Systat™ (version 5.0; Wilkinson, 1989). For these

Table 1 Repeated measures ANOVA table for (a) the mean number of *Baetis* from the trout stream visible in tanks, and (b) the mean number of *Baetis* drifting per 5 min.

Source	df	MS	*F*	*P*
(a) Positioning				
Between subjects				
Time	1	2630.88	56.24	0.002
Fish	1	5.63	0.12	0.75
Time × fish	1	1.89	0.04	0.85
Error (subjects within groups)	4	46.78		
Within subjects				
Days	1	0.96	0.42	0.55
Days × time	1	1.76	0.77	0.43
Days × fish	1	0.63	0.27	0.63
Days × time × fish	1	5.64	2.45	0.19
Error (days × subjects within groups)	4	2.3		
(b) Drift				
Between subjects				
Time	1	81.33	1.64	0.27
Fish	1	464.28	9.34	0.038
Time × fish	1	1289.40	25.94	0.007
Error (subjects within groups)	4	49.70		
Within subjects				
Days	1	4.83	3.80	0.12
Days × time	1	9.33	7.36	0.053
Days × fish	1	3.78	2.98	0.16
Days × time × fish	1	4.68	3.69	0.13
Error (days × subjects within groups)	4	1.27		

analyses we grouped observations from 09.00 to 19.00 h as a daytime measure of behaviour and observations from 23.00 to 03.00 h as a night-time measure. In order to compare behaviour during the day and night the dusk and dawn observations at 05.00 and 21.00 h and the observations from the third day (when there were no night observations) were not used in our analyses. Observations from the daytime and night-time on the two successive days were treated as the repeated variable in order to test whether the pattern of behaviour changed over time. Data satisfied the assumptions of homogeneity of variance and normality for the ANOVA.

Results

We were able to observe mayflies grazing on cobbles and drifting in the water column of the tanks by day and night. They were most often seen grazing on the tops and sides of cobbles, but also took up positions in the gravel and on the sides of the tanks. Excursions in the water column usually lasted for less than one circuit of the tank but some individuals were observed to make up to three circuits of the tank.

Trout stream Baetis

The effect of our experimental manipulations on *Baetis* behaviour depended on the source of the mayflies. *Baetis* from the trout stream showed a strong nocturnal periodicity in both positioning and drift. Throughout the experiment we observed significantly more mayflies, on the substratum surface and in the drift, by night than by day (Fig. 2a and b), as indicated by the significant between-subjects time effect (Table 1a and b). Initially the addition of trout odour had no effect on the number of mayflies visible on the substratum during the day or the night, but it did affect the number of mayflies drifting. More mayflies drifted during the night in tanks without fish odour compared with those with fish odour, indicated by the significant between-subjects time–fish odour interaction (Table 1b). The trout odour addition, however, did not affect positioning as indicated by the lack of a significant effect of fish odour in the analysis (Table 1a). Although there were no significant differences among days (Table 1a and b), there was a small reduction in the nocturnal peak in drift on the second day (Fig. 1b).

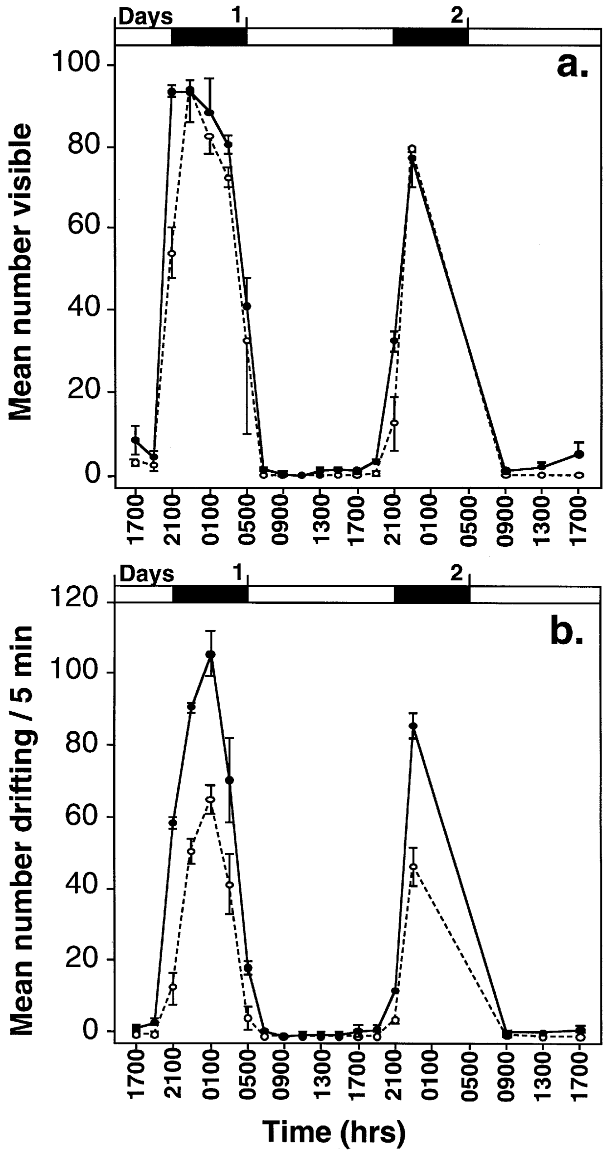

Fig. 2 Patterns of (a) the mean number of *Baetis* visible on stone surfaces, and (b) the mean number of *Baetis* drifting per 5 min over the course of the experiment with *Baetis* from the trout stream in tanks with (○) and without (●) brook trout odour. The error bars indicate 1 SE and the horizontal black bars indicate times of darkness.

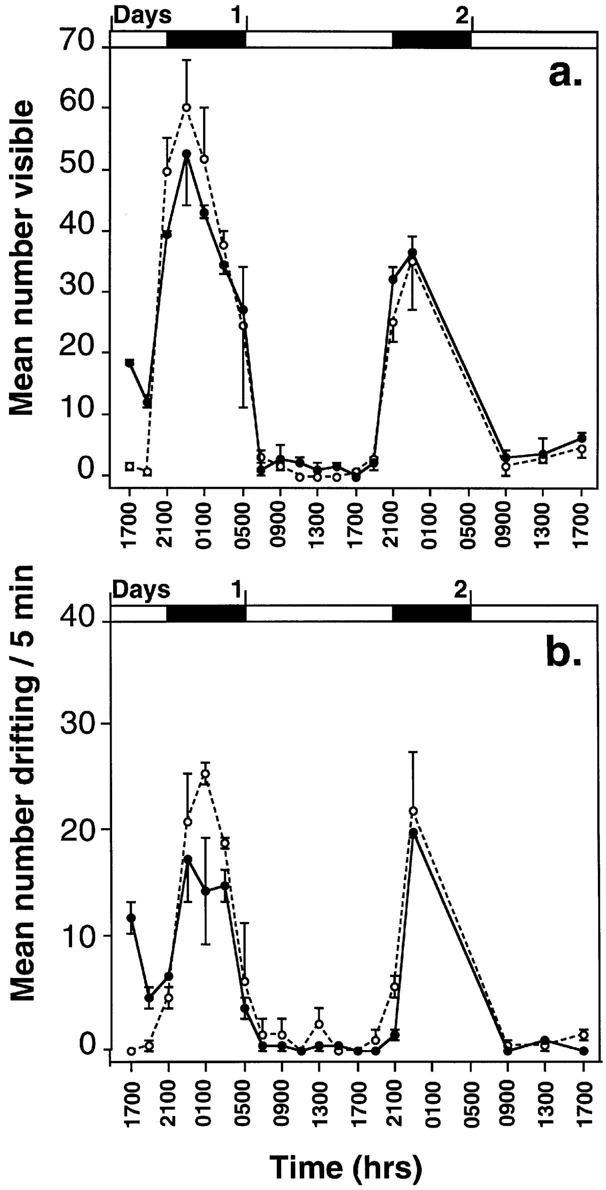

Fig. 3 Patterns of (a) the mean number of *Baetis* visible on stone surfaces, and (b) the mean number of *Baetis* drifting per 5 min over the course of the experiment with *Baetis* from the fishless stream in tanks with (○) and without (●) brook trout odour. The error bars indicate 1 SE and the horizontal black bars indicate times of darkness.

Fishless stream Baetis

Baetis from the fishless stream also displayed a diel periodicity in their positioning and drift (Fig. 3), as indicated by a significant between-subjects time effect in both cases (Table 2a and b). The significant within-subjects interaction between days, time and fish odour for positioning and the significant within-subjects days–fish interaction for drift indicate that the diel pattern of *B. bicaudatus* behaviour changed over time depending on the presence or absence of fish odour (Table 2a and b). Daytime behaviour was affected by our addition of trout odour on the first day, as we observed more mayflies on the tops of rocks and more mayflies in the drift in tanks without fish odour compared with those with fish odour (day 1, Fig. 3). However, on the second day this effect disappeared

Table 2 Repeated measures ANOVA table for (a) the number of fishless stream *Baetis* visible in tanks, and (b) the number of *Baetis* drifting per 5 min.

Source	df	MS	*F*	*P*
(a) Positioning				
Between subjects				
Time	1	1040.09	17.87	0.013
Fish	1	115.67	1.99	0.23
Time × fish	1	94.14	1.62	0.27
Error (subjects within groups)	4	58.20		
Within subjects				
Days	1	101.53	106.71	< 0.001
Days × time	1	132.61	139.37	< 0.001
Days × fish	1	126.67	133.13	< 0.001
Days × time × fish	1	117.67	123.67	< 0.001
Error (days × subjects within groups)	4	0.95		
(b) Drift				
Between subjects				
Time	1	355.10	18.97	0.012
Fish	1	56.79	3.03	0.16
Time × fish	1	63.72	3.40	0.14
Error (subjects within groups)		4	18.72	
Within subjects				
Days	1	22.13	3.83	0.12
Days × time	1	18.80	3.26	0.15
Days × Fish	1	50.04	8.67	0.042
Days × time × fish	1	43.79	7.58	0.051
Error (days × subjects within groups)	4	5.78		

and their behaviour was not affected by fish odour for the rest of the experiment (Fig. 3, days 2 and 3).

Discussion

The diel periodicities that we observed in the drift of *Baetis* from the trout stream are typical of the behaviour of mayflies from other streams with visually feeding fish (Malmqvist, 1988; Flecker, 1992; Douglas *et al.*, 1994; McIntosh & Townsend, 1994). These patterns of behaviour were altered by our manipulations of fish odour.

Mayflies from both streams changed their behaviour according to the presence or absence of brook trout odour. The reduction in night-time drift of *Baetis* from the trout stream when fish odour was present indicates that *Baetis* is sensitive to chemical cues related to the threat of predation. Mayflies from this stream maintained a nocturnal periodicity throughout the experiment regardless of the presence/absence of fish odour, but the magnitude of nocturnal drift was reduced when trout odour was present. Observations that mayfly diel drift periodicities are present in streams with visually feeding fish even when all predator cues are removed (e.g. Ciborowski *et al.*, 1977; Ciborowski, 1983; McIntosh & Townsend, 1994), indicate that the behaviour may be a fixed evolutionary response (Dill, 1987; Flecker, 1992). Our findings support the suggestion of Douglas *et al.* (1994) that responses to the level of light may regulate the timing of drift activity, but that proximate cues from predators may determine the level of activity. It is important to note that mayflies from the fishless stream did not show this response, so the experience of the prey population is also important. Other studies have shown that *Baetis* nymphs alter their behaviour in response to fish chemicals (Cowan & Peckarsky, 1994; Douglas *et al.*, 1994; Scrimgeour *et al.*, 1994). Gammarid amphipods also show reduced drift activity in response to chemical cues from fishes (Andersson *et al.*, 1986; Williams & Moore, 1985, 1989; Friberg *et al.*, 1994).

It is interesting that the drift behaviour of mayflies from the trout stream only changed according to the presence or absence of fish odour during the night, and their positioning was not affected by fish cues. The probability that a visually feeding fish will capture a prey item is higher during the day (Jenkins, 1969;

McIntosh & Townsend, 1995), but many workers have recorded that trout also feed during the night (Jenkins, 1969; Elliott, 1970; McIntosh & Townsend, 1995). Thus, reducing drift at night when fish are in the vicinity is likely to reduce the risk of predation. In contrast, being on the substratum surface during the night may not be as risky as moving in the water column because trout generally take most prey from the drift (Allan, 1981; McNicol, Scherer & Murkin, 1985; Glova & Sagar, 1991; Glova, Sagar & Näslund, 1992). During the day, when risk of predation by fish is highest, relying on chemicals to determine behaviour may be very risky, as it is impossible to detect fish downstream and trout have a much greater reaction distance during the day (Ware, 1973; O'Brien, 1979; Henderson & Northcote, 1985). An inflexible avoidance strategy, such as that used by *Baetis*, may be the most effective in these situations if the risk of accurately detecting variations in the predation threat is too great (Sih, 1987; McIntosh & Townsend, 1994).

We observed less dramatic drift and positioning periodicities in the fishless stream mayflies, but it is impossible to determine whether these were due to the differences in the numbers of mayflies present in that experiment, or to behavioural differences between populations. We expected the behaviour of mayflies from the fishless stream to be aperiodic, as has been reported for mayfly populations from fishless streams elsewhere (Malmqvist, 1988; McIntosh & Townsend, 1994; Douglas *et al.*, 1994). Cowan & Peckarsky (1994) have previously shown that the Benthette Brook population of *Baetis* was largely aperiodic in their feeding and positioning in the field and in laboratory channels. The differences in our results may be explained by a number of factors. Our experiment was run over a longer period than most investigations using laboratory or stream channel systems. Previous experimental examinations of fishless stream populations reporting aperiodic behaviour have lasted for 24 h or less (Cowan & Peckarsky, 1994; McIntosh & Townsend, 1994). Thus, removing mayflies from streams where they show an aperiodic pattern of behaviour may change some factor affecting their behaviour.

Our results raise an important point concerning the effect of visually feeding fish on mayfly behaviour in streams. If mayflies change their drift behaviour according to spatial variations in chemical cues from fish, variations in the abundance or patchiness in fish populations in a stream may result in spatial variations in mayfly drift. This study shows that mayflies do alter their behaviour according to the presence or absence of fish odour, but that alterations depend on the experience of the mayfly population and the time of day.

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