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Diel epibenthic activity of mayfly nymphs, and its nonconcordance with behavioral drift[1]

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Abstract

Diel changes in the numbers and activity of mayfly (Ephemeroptera) nymphs on the substrate surface in a stony-bottom stream were determined by direct observations, to investigate the relationship between benthic activity and drift. Individuals were viewed through a glass box (0.1 m^2 area) at 2-h intervals for 24 h; dim red light was used during darkness. *Baetis* was relatively unaffected by the presence of the observer, whereas *Cinygmula* was very easily disturbed. The number of individuals in view, activity per individual, and total activity all were greatest by day and least during the night for both species. Each of these measures was significantly correlated with temperature, which varied 6°–8°C over the diel cycle. Drift activity, in contrast, was strongly nocturnal and generally peaked immediately after nightfall. Because of the clear lack of correspondence between drift and the activity of mayfly nymphs on stone tops, behavioral drift in this system cannot be explained as the passive consequence of foraging.

The downstream transport of organisms in rivers, termed drift, has been the subject of many studies (e.g. Waters 1969, 1972; Müller 1974). Particular attention has been focused on the pronounced diel rhythm in the drift activity of crustaceans and immature insects, which typically exhibit low daytime activity, a sharp increase in numbers drifting just after dark, and a high but variable level of drift during the hours of darkness. After the independent discovery in about 1960 of the diel periodicity of drift (Tanaka 1960; Waters 1962; Müller 1963), several investigators attempted to determine whether drifting individuals represented accidental, passive entry into the water or an active and purposeful entry. The passive explanation emphasizes the risks of dislodgement experienced by organisms living in running, often torrential waters, whereas the active model emphasizes purposeful movements between habitats. By about 1970, accumulating evidence seemed to strongly favor the passive model. Numbers drifting appeared to correlate well with changes in discharge but poorly with changes in benthic density, suggesting that physical risk of dislodgement mattered more than crowding (Elliott 1967). Laboratory studies of mayflies (Ephemeroptera), abundant in the drift, revealed a negative phototaxis and an endogenous rhythm of higher nocturnal activity (Elliott 1968). Thus, the tentative hypothesis emerged that insect larvae hid under stones by day, probably inactive but possibly feeding (e.g. Chapman and Demory 1963), and moved to stone tops to feed on attached algae, transported particles, etc. after dark. The observed nocturnal increase in numbers drifting is explained as the consequence of a nocturnal increase in densities on the substrate surface, together with accidental dislodgement (e.g. Elliott 1967, 1968; Bishop 1969; Bishop and Hynes 1969; Chaston 1972). This argument was supported by evidence from insect gut analysis, which indicated that insects fed more by night than by day (Chapman and Demory 1963; Meier and Bartholomae 1980; Ploskey and Brown 1980). Evidence that individuals that drift by day suffered greater risk of predation than individuals that drift by night was provided by Allan (1978) and Newman and Waters (1984). Thus, it seemed convincing that activity (i.e. feeding) on stone tops was restricted to hours of darkness to reduce the risk of accidental dislodgement during daytime when predation risk potentially would be much greater.

Although the passive model has some convincing support and appears to prevail in most reports, there are doubts as to the completeness of this explanation. Elliott (1968) pointed out that the nocturnal pat-

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tern of activity in the laboratory did not correspond precisely to drift, Chaston (1972) argued that the explanation of passive drift failed to establish whether organisms actively released from the substrate, and Waters (1972) remarked on the many apparent exceptions to these tentative generalizations. Some results from laboratory streams seemed most consistent with an active component to drift (Walton et al. 1977; Walton 1980; Corkum 1978; Corkum and Clifford 1980; Ciborowski 1983).

We undertook to determine the diel periodicity of insect activity on stone tops in order to examine its relationship to drift in a Rocky Mountain stream where drift was known to exhibit pronounced nocturnal periodicity (Allan unpubl. and below). If the passive drift model is correct, we would expect to find a corresponding increase in insect activity, numbers, or both on stone tops, because a positive relationship between activity on stone top surfaces and drift is the underlying basis of the passive drift model.

Some previous studies provide evidence that more insects are on stone tops by night than by day, but these efforts had concentrated on laboratory observations (Elliott 1968; Bailey 1981) and field observations were few and less convincing (*see discussion*). By testing the hypothesis that total numbers of insects and their amount of activity increase on stone surfaces at night, concordant with a nocturnal increase in drift, we directly test a fundamental assumption underlying the passive model.

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Methods

Activity on stone tops—All observations of insect activity were made through a glass box (30- × 30-cm viewing area) fastened to a platform made of wooden planks. On the night before observations were to begin, the viewing box was placed so that its bottom surface was about 10–15 cm above the substrate. Some trial and error were necessary to ensure that several suitably large stones were in clear view and that the presence of the viewing box did not cause scouring due to deflection of current.

Observations were made at 2-h intervals continuously for 24 h. The standard protocol was similar to that used by Elliott (1968) in laboratory observations of insect activity. We observed all individuals within the viewing area for 10 s, at 30-s intervals spaced over 10 min for a total of 20 successive observations. In each 10-s interval, we recorded the number of individuals in view. The number of nymphs moving also was recorded, with a single individual contributing a maximum of one movement per 10 s, regardless of whether it moved once or several times. Thus, each observation period resulted in 20 successive estimates of number of individuals in view and number of movements. These were combined to give single estimates, based on a 10-s period, of the number of individuals in view, the number of movements (activity units) per individual in view, and total number of movements (total activity). Because the 20 successive estimates were autocorrelated, we made no attempt to compute their variance. The rationale for making a series of observations over 10 min and then combining those values was to obtain a representative sample of activity for that observation period. The mayflies *Baetis* (probably *B. bicaudatus* Dodds) and *Cinygmula* (probably *C. mimus* Eaton) were the most abundant species and so contribute the only data reported here. All observations were preceded by a 5-min waiting period, which experience showed was necessary to allow animals to recover from the disturbance of our approach. At night, observations were made with a flashlight covered with red cellophane.

All data are from Cement Creek, a small, stony stream in Gunnison County, Colorado (*see* Allan 1975, 1982). The site is at 3,050 m in open meadow (site 2: Allan 1982), where the stream is about 4 m wide, 10–40 cm deep, and bordered by willows (*Salix* spp). Summer current speeds range from 20 to 60 cm s^{-1} in riffle regions and discharge ranges from 0.4 to ~1 m s^{-1}.

Drift—Drift collections from an earlier study were used for comparison between drift periodicity and activity on stone tops. Drift samples were obtained in the same section of Cement Creek between 1976 and 1978 with nets having a mouth area of 0.1 m^2, a length of ~2 m, and a mesh size of 0.3 mm. On each sampling date, eight samples were collected at 3-h intervals over 24 h. Further description of these samples is given elsewhere (Allan 1982; Allan and Russek 1985).

Results

Description of behavior—Baetis was the most easily observed species, as it showed very little sensitivity to the approach or presence of the observer. Movements generally consisted of very small shifts of the body forward or sideways. Animals appeared to feed steadily at one position for several minutes, although movement of mouthparts was not observable. The abdomen and tail often swung back and forth like a weather vane in individuals exposed to much current. No spacing behavior or reaction to contact with other mayflies was noticeable. *Cinygmula* was extremely sensitive to the presence of the observer and generally was not observed until after the observer had remained motionless for at least 5 min. Very slight movement by the observer was sufficient to cause *Cinygmula* to retreat under a stone. Undisturbed *Cinygmula* usually moved and fed continuously and conspicuously, as movements of the maxillary palps were easily observed. Contact with other mayflies was infrequent, and usually resulted in slight backward movement, then forward movement in a changed direction. We made occasional observations of *Rhithrogena robusta* Dodds, which behaved very much like *Cinygmula,* and of *Epeorus longimanus* Eaton, which moved little and appeared to be less easily disturbed than the other heptageniids. In about 60 h of observations, perlodid stoneflies were observed briefly on two occasions and caused dispersal of both *Baetis* and *Cinygmula.* On one occasion a brook trout (*Salvelinus fontinalis* Mitchell) was observed very briefly; the *Baetis* present did not respond.

Virtually all observations were of mid–late instar nymphs; very early instars were observable when present, but were uncommon on stone tops.

Under red light, animals were easily, if dimly, observable. *Baetis* seemed undisturbed by our presence, as it showed no obvious response to the observer or to the red light. It is unclear whether *Baetis* could detect the observer under red light, but even under bright daylight it did not appear to respond to our presence. *Cinygmula* seemed somewhat less easily disturbed than in daylight, probably indicating that its ability to perceive the observer was reduced under dim light. However, we do have the impression that this species is able to detect red light, as the flashlight had to be held without movement.

Activity on stone tops—Complete 24-h observations of *Baetis* activity were made on four dates (9 and 30 August 1983, 11 July and 9 August 1984). For each of the two 1984 dates, replicate observations were made from two platforms located about 100 m apart, so a total of six data sets were obtained. Total activity (number of movements at each observation period) always was higher during the day than at night (Fig. 1). The general pattern was for activity to increase in late morning, reach a maximum in late afternoon (1500 hours), and decrease toward evening. Product-moment correlation coefficients between total activity and water temperature (Table 1) were significant for all dates except 9 August 1983, when the correlation was parallel but not significant ($0.05 < P < 0.10$). The similarity of the rank of total activity over time of day among the six data sets was evaluated by a test of concordance (Table 2). The index W varies from 0 to 1 (perfect concordance); for these data $W = 0.76$ indicating high similarity among the six data sets ($\chi^2 = 50.0$, $P < 0.001$).

Since total activity combines two variables, activity per individual and number of individuals, we analyzed these two measures separately to find out which contributed most to observed total activity. It

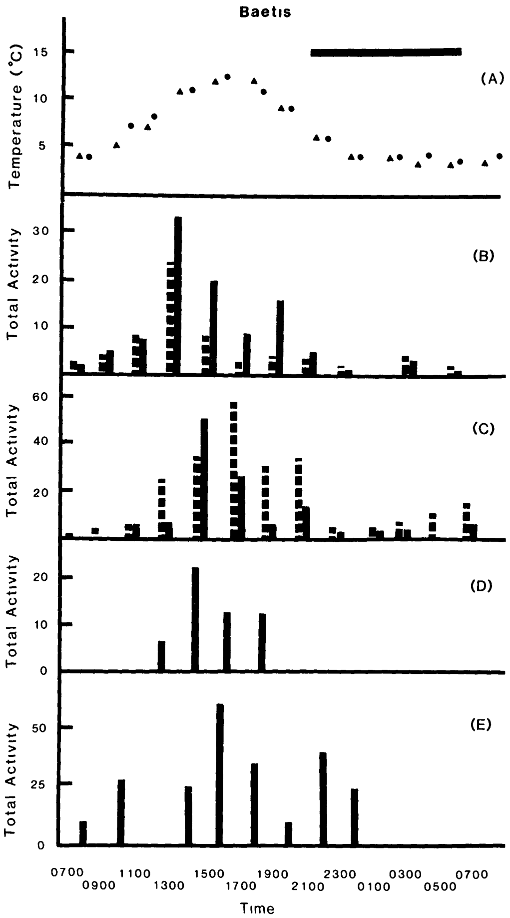

Fig. 1. Observations of the total activity of all *Baetis* nymphs in view on the tops of stones in a 0.1-m^2 area. A. Water temperature from 11–12 July 1984. Horizontal bar denotes darkness. Physical data from other dates were very similar. B. Activity data for 9–10 August 1984, two nearby sites. C. 11–12 July 1984, two nearby sites. D. 30–31 August 1983, one site only. E. 9–10 August 1983, one site only.

appears that both are correlated with temperature, but for any given data set one or the other may fail to show a significant relationship (Table 1). There is no obvious tendency for total activity to be influenced primarily by one or the other of its components.

Finally, because activity sometimes seemed to lag behind temperature, the correlations were reanalyzed introducing a one-step time lag. In a few instances (11 July 1984) a lag improved the correlation, but this did not appear to be generally true (Table 1).

Four complete data sets for *Cinygmula* were obtained (9 and 30 August 1983, and two sets from 9 August 1984). Results were similar to those for *Baetis,* except that the daytime maximum in activity was even more pronounced (Fig. 2). Again, the correlation of total activity with temperature was significant (Table 1). Both activity per individual and number of individuals also correlated with temperature, except at one location on 9 August 1984, when activity per individual was not significant ($0.05 < P < 0.10$). In general, a time lag did not improve the correlations with temperature.

Concordance among the four data sets was again significant ($\chi^2 = 23.6$, $P < 0.001$), and $W = 0.54$ (Table 3).

Drift activity—Drift collections (three sites per date) from 10 dates between 1976 and 1978, and ranging from June to September, invariably showed a nocturnal increase in drift density for both *Baetis* and *Cinygmula.* The typical pattern was for low and apparently constant drift densities during the day and much higher values at night, with the maximum usually observed to be the first nighttime collection (Fig. 3).

Discussion

Clearly, the principal result of this study is the pronounced difference in timing between peak drift and the activity of these mayfly nymphs on stone tops. As is generally observed, drift collections from Cement Creek exhibited nocturnal increases, while daytime drift was low and relatively constant. However, direct observations of the substrate surface revealed that numbers of nymphs and activity per individual always were lowest by night. Daytime activity was markedly higher and seemed to follow the diel temperature curve, presumably because of the influence of temperature on metabolic activity. However, the afternoon decline in activity may also have been influenced by falling light levels. These data represent one of the first attempts to directly observe insect activity on stone tops in the field, in detail and over several 24-h cycles. The obvious conclusion is that our results

Table 1. The relationship between temperature and three measures of insect activity on stone tops, determined by direct observation. Product-moment correlations (*r*) and probabilities (*P*) are for 12 observation periods (10 df) over 24 h in every instance. Note that in 1984, two replicate data sets were collected on each date.

	Activity per individual		No. of individuals		Total activity	
	r	*P*	*r*	*P*	*r*	*P*
			Baetis			
9 Aug 83	0.61	<0.05	0.50	<0.10	0.54	<0.10
30 Aug 83	0.91	<0.01	0.81	<0.01	0.85	<0.01
11 July 84–1	0.41*	n.s.	0.64*	<0.05	0.72	<0.01
11 July 84–2	0.77	<0.01	0.34*	n.s.	0.80*	<0.01
9 Aug 84–1	0.27	n.s.	0.76	<0.01	0.63	<0.05
9 Aug 84–2	0.72	<0.01	0.78	<0.01	0.84	<0.01
			Cinygmula			
9 Aug 83	0.71	<0.01	0.64	<0.05	0.64	<0.05
30 Aug 83	0.79	<0.01	0.69*	<0.05	0.87	<0.01
9 Aug 84–1	0.51	<0.10	0.79	<0.01	0.80	<0.01
9 Aug 84–2	0.77	<0.01	0.82	<0.01	0.84	<0.01

* Correlation improved by lag of one time unit.

decisively reject a fundamental premise of the passive drift model, namely that these mayflies are night-active on the substrate surface.

In fact, several lines of evidence from previous investigations cast doubt on the universal applicability of the passive drift model. Elliott (1968) noted that drift periodicity did not correspond exactly in timing to laboratory measures of activity of mayfly nymphs and in addition that the former was much more variable than the latter. In Bailey's (1981) study of the mayfly *Atalophlebioides,* both drift and laboratory activity were nocturnal but the correspondence was far from exact. Bohle (1978) examined drift of *Baetis rhodani* in a laboratory stream under varying conditions of food supply. Abundant food resulted in local concentration of individuals and lack of drift, while drifting only occurred some hours after food became unavailable. No diel periodicity was observed in larval distribution between illuminated and shaded locations or in feeding periodicity.

It has been reasoned by several investigators that, if the passive model is correct, benthic collections ought to reveal greater abundances on stone tops by night than by day. Repeated efforts have failed to corroborate this. Clifford (1972) sampled the benthos of a Canadian river by day and by night and found no differences in abundances. Kovalak (1978) sampled stones and artificial substrates (bricks) in two Michigan streams with similar results. Wiley and Kohler (1981) monitored *Baetis* numbers on stone tops with cinematography and found

Table 2. Test of concordance among rank order of total activity of *Baetis* over 24 h.

	0700	0900	1100	1300	1500	1700	1900	2100	2300	0100	0300	0500
9 Aug 83*	7.5	4	10.5	5.5	1	3	7.5	2	5.5	10.5	10.5	10.5
30 Aug 83†	8.5	8.5	8.5	4	1	2.5	2.5	8.5	8.5	8.5	8.5	8.5
11 July 84–1	10.5	10.5	4	5.5	1	2	5.5	3	10.5	7	8	10.5
11 July 84–2	12	11	7	5	2	1	4	3	10	9	8	6
9 Aug 84–1	8.5	7	2.5	1	2.5	8.5	5	5	10.5	12	5	10.5
9 Aug 84–2	9	6.5	5	1	2	4	3	6.5	11	11	8	11
Sum of ranks	56.0	47.5	37.5	22.0	9.5	21.0	27.5	28.0	56.0	58.0	48.0	57.0

$W = 0.76$, $\chi^2 = 50.0$ (11 df), $P < 0.001$

* Observations began at 1300 hours.

† Observations began at 0900 hours.

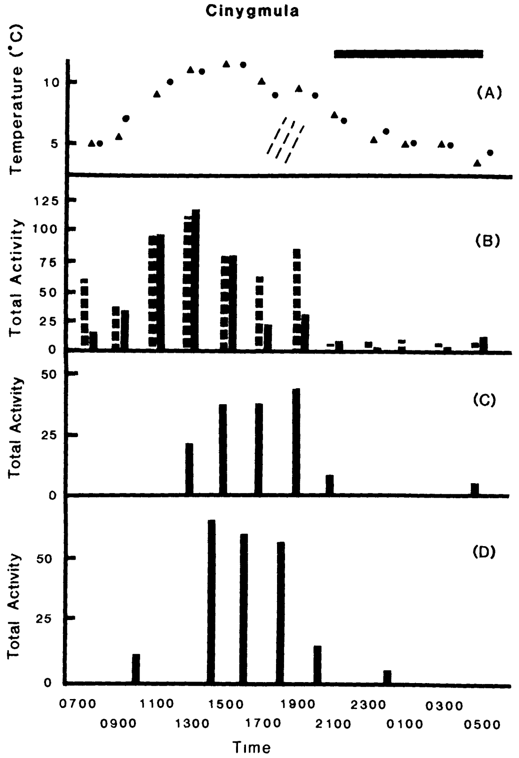

Fig. 2. As Fig. 1, but of *Cinygmula*. A. Water temperature from 9–10 August 1984. Dashed lines indicate rain. Horizontal bar denotes darkness. Physical data from other dates were very similar. B. Activity data for 9–10 August 1984, two nearby sites. C. 30–31 August 1983, one site only. D. 9–10 August 1983, one site only.

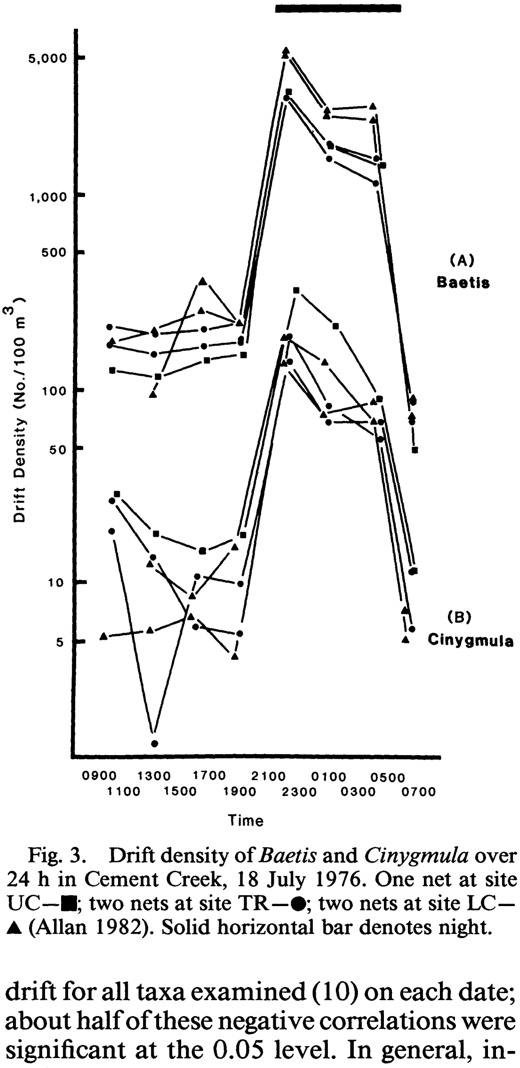

Fig. 3. Drift density of *Baetis* and *Cinygmula* over 24 h in Cement Creek, 18 July 1976. One net at site UC—■; two nets at site TR—●; two nets at site LC—▲ (Allan 1982). Solid horizontal bar denotes night.

differences in densities between successive days, but not between day and night. Graesser and Lake (1984) compared diel drift collections to benthic collections obtained by scrubbing the surface of natural stones in an Australian stream on three dates. They observed a negative correlation between numbers on stone tops and numbers in the drift for all taxa examined (10) on each date; about half of these negative correlations were significant at the 0.05 level. In general, individuals were more numerous on stone tops by day and in drift samples by night, leading the investigators to suggest that the nighttime reduction in numbers on stone tops was due to the presence of these individuals

Table 3. As Table 2, but of *Cinygmula*.

	0700	0900	1100	1300	1500	1700	1900	2100	2300	0100	0300	0500
9 Aug 83*	9.5	5	9.5	1	2	3	4	9.5	6	9.5	9.5	9.5
30 Aug 83†	9.5	9.5	9.5	3	2.5	2.5	1	4	9.5	9.5	9.5	5
9 Aug 84–1	6	7	2	1	4	5	3	12	9	8	10.5	10.5
9 Aug 84–2	7	4	2	1	3	6	5	9	11.5	11.5	10	8
Sum of ranks	32	25.5	23	6	11.5	16.5	13	34.5	36	37.5	39.5	33

$W = 0.54$, $\chi^2 = 23.6$ (11 df), $P < 0.001$

* Observations began at 1300 hours.
† Observations began at 0900 hours.

in the drift. However, several workers (Elliott 1967; Bishop and Hynes 1969) have estimated that the proportion of the benthos in the drift at any one time is very low, and this casts doubt on the plausibility of Graesser and Lake's interpretation.

Finally, Kohler (1983) compared diel changes in drift to numbers on the tops and the bottoms of tiles that were left to be colonized with mayfly nymphs in a Michigan stream. Although drift usually exhibited nocturnal peaks, no significant differences in position (top vs. bottom of tile) was observed for any of several taxa on each of two dates. *Baetis* tended to be more common on the tops of tiles by day and by night. Other taxa (*Paraleptophlebia mollis,* early instars of two *Ephemerella* species, and several *Stenonema* species) tended to be more common on the bottom of tiles both by day and by night. In contrast to the findings of Graesser and Lake (1984), all correlations between diel densities of drift and on stone tops were positive, but only 2 of 13 were significant, and in one of these, drift did not show a nocturnal peak. Kohler (1983) doubted that positioning changes between the top and underside of stones were a contributing factor to drift periodicty in his study.

The common denominator of the above four studies, in different geographic areas and with somewhat different techniques, is the absence of a nocturnal increase of insect nymphs on the tops of stones, even though drift was observed to increase greatly at night. These results cast serious doubt on the passive drift model for the systems described, although Graesser and Lake (1984) attempted to reconcile their observations with this model by suggesting that animals are sparse on stone tops simply because they are drifting at that moment. In addition, these results do not corroborate our finding of significantly greater activity on stone tops by day, except for the study by Graesser and Lake (1984) and Kohler's (1983) data for *Baetis.*

It may be that differences in methodology substantially account for this discrepancy. None of these studies included systematic observations, but instead required the investigators to enter the stream and either scrape the substrate surface or remove the substrate. Our observations indicate that whereas *Baetis* does not appear to be readily disturbed by an observer on a platform above the stream, it was disturbed by walking in the stream or reaching one's hand to the stone. Even slight movements by an observer watching under dim red light through an observation box were sufficient to send the heptageniid *Cinygmula* rapidly running to the underside of the stone, and it could take several minutes for an individual to return to the stone top. For any animals that exhibit such escape behavior, it seems plausible that removal of a stone or tile by the investigator would cause most individuals to be found on the underside. Moreover, because we also observed that *Cinygmula* was somewhat less easily disturbed under dim red light than in full daylight, it is possible that an investigator scraping the tops of stones, as did Graesser and Lake (1984), will catch relatively more such individuals by night than by day. In any event, we suggest that direct observations by an investigator on a platform above the stream may provide more useful information than the removal or scraping of stones. In Cement Creek, we also made diel collections at 3-h intervals on three dates, in which we brushed the tops of stones while holding a net at the downstream edge. No significant changes in abundances were found between day and night (unpubl. results), in contrast to our observational data, and we are skeptical about the presumption that the animals so obtained come directly from the brushed surface rather than the general region upstream of the collector.

The literature on drift is rich with speculative arguments over the accidental vs. purposeful entry of invertebrates into the drift and is not without seemingly contradictory data (cf. Waters 1972). *Baetis rhodani* has been shown in one laboratory study to be negatively phototactic and to possess an endogenous rhythm of nocturnal activity (Elliott 1968). Yet in another laboratory study (Bohle 1978), it exhibited no nocturnal periodicity in feeding or occupation of the tops of tiles, but was nocturnal in its drift and also varied in drift propensity in response to food shortages. Direct, in-stream observations by a light amplification technique indicated that several species of *Baetis* (primarly *Baetis buceratus*) occupied stone tops by day and were not present at night, similar to our results (Statzner and Mogel 1984). Such contradictory results for the same genus are difficult to explain and may reflect differences in methodology, geographic variation in behavior, or a poorly understood heirarchy of controlling variables. Ultimately, we may arrive at a mixed model in which the relative importance of purposeful vs. accidental entry into the drift is well defined (cf. Wiley and Kohler 1984).

In conclusion, we argue that the timing of drift in the mayflies *Baetis* and *Cinygmula* in our study does not reflect their activity on stone tops, but instead is presumed to be due to active entry. On the basis of our observations that animals were actively feeding by day and the findings of others that *Baetis* feeds efficiently in high food patches while drifting after food is exhausted (Bohle 1978; Kohler 1985), we suggest that nocturnal drift represents active dispersal in search of new feeding sites. The possibility exists that encounters with predaceous stoneflies initiate drift (Corkum and Clifford 1980), but such encounters appear to be too infrequent in this study system to play an important role. The nocturnal timing of drift is hypothesized to be an evolved response to risk of predation from drift-feeding fish, which is a particularly strong selective pressure acting on larger nymphs (Allan 1978). The sharp peak in drift activity immediately after dark then would not represent the fact that animals have been awaiting darkness to begin feeding, but instead represents a saltatorial search for new habitat. Under this explanation, the pattern of drift throughout the night would not represent successive feeding bouts, as suggested by (e.g.) Bishop (1969) but, presumably, the extent of habitat search. However, little is known about these movements at present, and further laboratory and field investigations clearly are called for, under a variety of conditions, before we can claim even a rudimentary understanding of this most unique phenomenon of running waters.

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