

upon the nauplii of other species, it may have considerable ecological effect.

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Trout predation and the size composition of stream drift¹

Abstract—Nocturnal drift of stream invertebrates is examined as a predator avoidance adaptation via the hypothesis that those taxa or growth stages which are large, and thus subject to intense predation relative to smaller forms, should be most strongly constrained to nocturnal drift activity. Smaller taxa or stages may be aperiodic or day active. Data from an alpine stream document for the abundant and widespread mayfly *Baetis bicaudatus* that, on a continuum from small to large size, the risk of predation increases while the propensity to drift during the day decreases. There is supporting and some contrary evidence from the literature for the generality of this pattern.

Invertebrates living on or within the bottom of streams may be captured in large numbers drifting in the current (Müller 1954). Drift activity is much greater at night than during daylight hours (Tanaka 1970), often showing a strong peak immediately after nightfall. The governing influence of light on propensity to drift can be demonstrated readily by artificial shading or lighting (Müller 1974).

Several intriguing patterns of drift behavior are at present difficult to explain. While most taxa are night active, some are active by day and others are largely

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Table 1. Total numbers of invertebrates collected in benthos and drift on three sampling dates, as well as temperature and flow.

| Date* | Total invertebrates in benthos (per m ²) | Temp (°C) | | Total flow (m ³ ·s ⁻¹) | Flow through net (%) | Total invertebrates in drift (per 24 h) |
|--------|--|-----------|-----|---|----------------------|---|
| | | Min | Max | | | |
| 18 Jul | 1,456 | 4 | 17 | 0.68 | 7.93 | 1,296,810 |
| 2 Aug | 1,168 | 2 | 17 | 0.52 | 8.09 | 1,289,691 |
| 11 Sep | 1,321 | 3 | 16 | — | 8.01† | 395,605 |

* All benthic sampling took place 2 days after initiation of drift sampling.

† Because total flow was not measured on 11 September 1976, flow through net was estimated by averaging the two previous values.

aperiodic (*see* Waters 1972). Moonlight sometimes, but not always, depresses nocturnal drift. Large taxa may be relatively rare in the drift (Bishop and Hynes 1969) or disproportionately common (Elliott 1967), and larger specimens may be more abundant in drift at night than during the day (Anderson and Lehmkuhl 1968).

It seems reasonable that nocturnal activity is an adaptation to minimize mortality due to visually feeding vertebrate predators. An unequivocal test is difficult, however, because the behavior is now fixed and would not be expected to change in the short term absence of predators. Here I report on a testable hypothesis which stems from the fact that predation by visual predators (i.e. fish) falls disproportionately on large prey. Invertebrate taxa or growth stages which are large, and thus subject to intense predation relative to smaller taxa, should be most strongly constrained to nocturnal drift activity. Smaller taxa or stages may be aperiodic, or day active.

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The study was conducted in Cement

Creek, Gunnison County, Colorado, at an elevation of 3,000 m (*see* Allan 1975). Samples of insects were collected from the benthos and drift in mid-July, early August, and September of 1976. Each benthic collection consisted of 12 Surber samples (bottom area of one sample = 0.093 m², net mesh = 300 μ m) positioned as a 3 \times 4 grid across the stream. Drift was sampled using nets of 0.1 m² (300- μ m mesh) submerged for 1 h duration at 3-h intervals over 24 h. I measured total water flow and flow through the net to ascertain the proportion of total stream drift which the drift net sampled and also to determine that there was no loss of filtering efficiency due to clogging. All samples were sorted in their entirety, and head widths were measured on at least 50 individuals of several taxa.

The major vertebrate predator in Cement Creek is the trout, primarily brook trout *Salvelinus fontinalis* Mitchell in the area studied. Trout for stomach analysis were collected by electroshocking, also at 3-h intervals over 24 h, on 7 July, 5 August, and 8 September 1976. At each time I collected six trout representing small (<10 cm), medium (10–16 cm), and large sizes (>16 cm), for a total of 48 fish on each date. Head width was measured of all prey in the stomachs.

Large numbers of invertebrates, including representatives of about 30 taxa, were collected in the benthos and the drift (Table 1). The results following concentrate on one species only, *Baetis bicaudatus* Dodds. Unlike most species in Cement Creek, *B. bicaudatus* is bivoltine; hence it often is represented by a wide range of sizes at any one time. In

Table 2. Percent by numbers of total assemblage that is *Baetis bicaudatus*.

| Date | Drift | | Benthos | Trout stomachs* |
|--------|-------|-------|---------|-----------------|
| | Day | Night | | |
| 18 Jul | 36 | 73 | 30 | 37.5 |
| 2 Aug | 43 | 65 | 34 | 12.3 |
| 11 Sep | 12 | 40 | 11 | 16.0 |

* Collection dates: 7 July, 5 August, and 8 September.

SIZE COMPOSITION OF NYMPHS IN BENTHOS (▨), DAY DRIFT (□), AND NIGHT DRIFT (■)

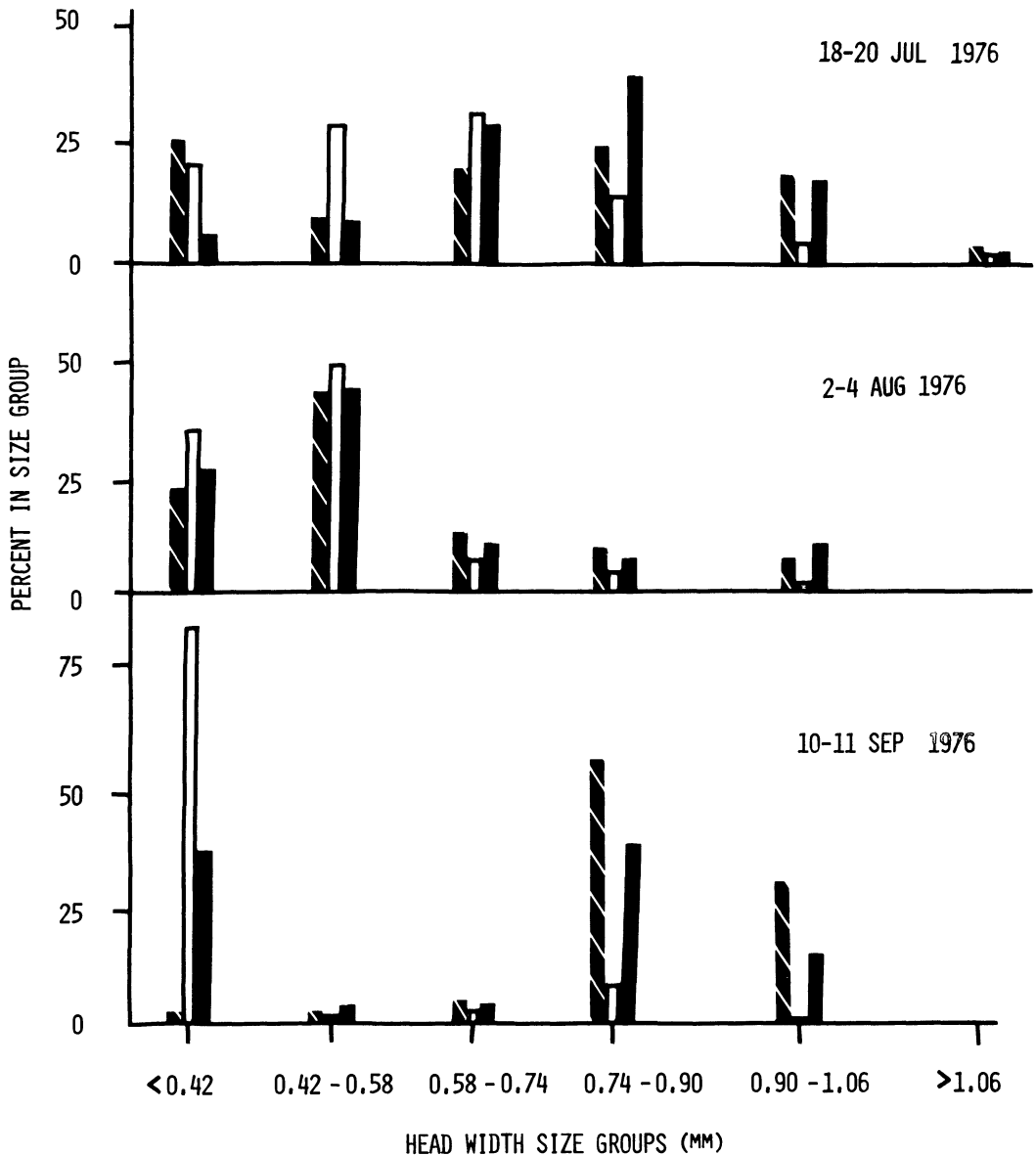


Fig. 1. Frequency of nymphs of *Baetis bicaudatus* in various size classes as determined by head width measurements. Note that small nymphs constitute a greater proportion of drift during day, while reverse occurs at night.

addition, *B. bicaudatus* typically is the most abundant species in the assemblage, ranging from 11-75% of total numbers depending on season and sampling

method (Table 2). Since the next most abundant taxa were smaller dipterans, conversion of numbers to biomass should not affect this statement.

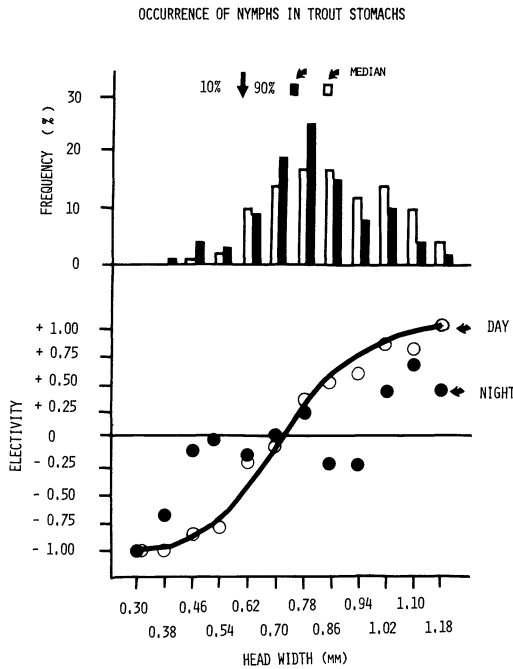


Fig. 2. Occurrence of nymphs of *Baetis bicaudatus* in trout stomachs compared to frequency in drift. Top panel—size frequency of nymphs in stomachs of trout feeding by day (open bars) and by night (solid bars). Of nymphs consumed, 90% had >0.60-mm head width (arrow). Median size of nymphs consumed was greater during day (small squares). Bottom panel—electivity index based on diet of day-feeding brook trout compared to day drift (open circles) and on diet of night-feeding brook trout compared to night drift (solid circles). Line fit visually.

The drift rate of *B. bicaudatus*, per hour, was estimated for each of eight sampling intervals over the 24-h cycle and separated into six size categories

based on nymphal head width. The five samples collected during daylight hours were sufficiently similar that these data were pooled, as were the three samples collected during the dark. As a result, the proportional representation of individuals among size classes was based on measurement of 200–300 individuals in each instance. In all size classes on all dates, nocturnal drift exceeded day drift (Table 3). However, when the day drift is expressed as a proportion of the night drift, it is apparent that this ratio decreases with increasing prey size. For the smallest nymphs, day drift ranged from 18–94% of night drift, while for the largest nymphs the corresponding values are 0–9%.

These data are presented graphically in Fig. 1 along with the proportional representation of size groups in the benthos. In July, benthic samples show a wide range of sizes, apparently due to the presence of late instars of slow maturing individuals from the winter generation and early instar offspring of already emerged adults of that winter generation (Fig. 1: hatched bars, top panel). Growth of these early instar nymphs results in a high frequency of the second smallest size group in samples collected 2 weeks later (middle panel), and, after an additional 5 weeks, most of these individuals had grown into the largest size class (bottom panel) as the summer generation neared maturity.

The proportional representation of size groups in drift samples often differed from that observed in the benthos (Fig.

Table 3. Rate of drift of nymphs of *Baetis bicaudatus*, per hour, past sampling site. In each size class, average day drift is expressed as a ratio by dividing by average night drift. Although all size classes tend to be active by night, pattern is more pronounced in larger nymphs.

| Size (mm) | 18–19 Jul | | | 2–3 Aug | | | 11–12 Sep | | |
|----------------------------|-----------|---------|-------|---------|--------|-------|-----------|-------|-------|
| | Day | Night | D:N | Day | Night | D:N | Day | Night | D:N |
| <0.42 | 2,668 | 7,375 | 0.362 | 1,251 | 6,918 | 0.181 | 743 | 795 | 0.935 |
| 0.42–0.58 | 3,684 | 9,833 | 0.375 | 1,742 | 11,311 | 0.154 | 21 | 95 | 0.221 |
| 0.58–0.74 | 3,938 | 35,646 | 0.111 | 283 | 2,745 | 0.103 | 30 | 95 | 0.316 |
| 0.74–0.90 | 1,779 | 47,938 | 0.037 | 179 | 1,977 | 0.091 | 74 | 816 | 0.091 |
| 0.90–1.06 | 508 | 20,896 | 0.024 | 104 | 2,745 | 0.038 | 16 | 331 | 0.048 |
| >1.06 | 127 | 1,475 | 0.086 | 0 | 220 | 0 | 0 | 0 | — |
| Total · 24 h ⁻¹ | 38,112 | 369,489 | 0.103 | 10,677 | 77,748 | 0.137 | 2,652 | 6,396 | 0.415 |

1). In addition, day and night drift of *B. bicaudatus* revealed different size frequency patterns: small nymphs were disproportionately abundant during the day compared to nighttime samples. This pattern is quite striking in samples collected in July and September and present, but less pronounced, in samples collected in August. A comparison of numbers drifting by day vs. by night in each size class was made by *G*-test (Sokal and Rohlf 1969) with $P < 0.005$ in each of the July, August, and September samples. In August large nymphs were relatively uncommon, because the winter generation had emerged and the summer generation had not yet attained large size. Hence in this instance, differences in the size composition of drift between day and night might be expected to be less obvious.

In summary, a change in drift behavior seems to occur in nymphs of *B. bicaudatus* as they increase in size (Table 3, Fig. 1). Larger nymphs are strongly nocturnal; smaller nymphs are proportionately more common in daytime.

The stomachs of trout collected on 7–8 July, 8–9 August, and 8–9 September 1976 were analyzed for prey composition and size. All samples collected throughout the day were pooled, as were all samples collected throughout the night. Trout stomach samples used for analysis were collected at least 3–4 h after dawn or dusk to reduce the possibility that (say) prey in the stomachs collected at night derived from feeding during the day. However, this source of error cannot be eliminated completely.

Trout collected 7–8 July had been feeding heavily on nymphs of *B. bicaudatus*. Trout collected in early August consumed few *B. bicaudatus*, evidently because only small nymphs were abundant at that time (Table 3, Fig. 1). Trout collected 8–9 September also consumed few nymphs of *B. bicaudatus*, despite the presence of larger instars (Fig. 1). Possibly this was because nymphs were less abundant overall (Table 3). In addition, the stonefly *Zapada haysi* (Nemouridae) exceeded *B. bicaudatus* in body

size by September and became the preferred prey (Allan unpubl.). As a result the analysis of prey selection by trout is based on nymphs observed in the July collection ($n = 472$). Data from August and September were consistent with the July data but too few for separate analysis.

Of the *B. bicaudatus* nymphs consumed, 90% were > 0.60 mm (Fig. 2: arrow). This suggests a strong preference for larger prey. Inspection of prey size in the stomachs of various size groupings of trout revealed no difference in selectivity based on trout size. When the diets of trout which had been feeding primarily at night (prey $n = 216$) are compared to those feeding during the day (prey $n = 256$), it is apparent that the bias for large prey is even stronger in day-feeding trout (cf. open bars to solid bars, top panel: $P < 0.01$ by *G*-test of independence). The median head width of nymphs consumed at night was 0.75 mm and of nymphs consumed in daylight was 0.83 mm.

The size composition of trout diet may be explicitly compared to the size composition of the drift by Ivlev's (1961) electivity index. This comparison makes the implicit assumption that trout are feeding exclusively from the drift. The index varies from -1 (complete avoidance) to $+1$ (complete selection), with values of zero indicating that feeding is proportional to prey abundance. For trout feeding during the daytime (Fig. 2: bottom panel), the electivity index shows avoidance of prey with heads < 0.70 mm wide and selection of larger prey. A strong and consistent relationship between prey size and prey choice by trout is suggested by the data. In contrast, trout feeding at night showed a less consistent relationship. The smallest prey were avoided and the largest prey were positively selected. Over a wide range of intermediate sizes, prey selection did not appear to be operating. Possibly this weaker selection is the result of reduced visual acuity under low light conditions.

Selection for larger prey by fish feeding on invertebrates has been document-

ed extensively. Studies of rainbow trout (*Salmo gairdneri*) have demonstrated that reaction distance increases with prey size (Ware 1972) and that larger insects in the surface drift are taken in preference to smaller insects (Metz 1974). My study extends this pattern to brook trout (*S. fontinalis*) feeding on drifting insect nymphs.

As prey size increases, the increasing risk of predation, especially during the day (Fig. 2), is closely paralleled by a decreasing propensity to drift during the day (Table 3). This lends strong support to the hypothesis under consideration for nymphs of *B. bicaudatus*.

It is extremely unlikely that the rarity of larger nymphs drifting by day is due solely to their depletion by trout. The absolute numbers drifting (Table 3) almost certainly exceed the number which the existing trout population could remove (Allan unpubl.; see also Mundie 1974). However, any individual nymph of large size would suffer greater risk of mortality by drifting during the day, and natural selection should act to suppress such behavior. I conclude that a change occurs in propensity to drift during the day as nymphs of *B. bicaudatus* mature.

If the hypothesis under consideration has generality, smaller taxa should be less strongly constrained to drift by night than should larger taxa, and other species in addition to *B. bicaudatus* should show a decreasing propensity to drift by day as they mature.

Water mites (Hydrachnae) tend to drift by day (Elliott and Minshall 1968; Bishop and Hynes 1969). Mites are small, and I have rarely found them in the stomachs of trout. Midges (Chironomidae) also are small and tend to show little diel periodicity (Waters 1972); they are preyed on mostly by very young salmonids (Allan unpubl.; Allen 1941). Although neither of these taxa is immune from predation, they appear to suffer markedly lower predation pressure than do larger invertebrates. In an intriguing study of a subtropical stream in Florida, Cowell and Carew (1976) found a shift from no periodicity to nocturnal drifting in *Polypedic-*

lum haterale when late instars predominated.

Anderson and Lehmkuhl (1968) found the mean weight of drifting individuals in four groups (Chironomidae, *Baetis*, *Paraleptophlebia*, *Capnia*) to be greater by night than by day. A shift from daytime to nighttime drifting within a taxon has been reported for *B. bicaudatus* (this study), *P. haterale* cited above, *Deleatidium* sp. (Ephemeroptera) (Devonport and Winterbourn 1976), *Amiocentrus aspilus* (Trichoptera) (Anderson 1967), *Helicopsyche borealis* and some Limnephilidae (Bishop and Hynes 1969).

Finally, in a well documented study Anderson (1966) demonstrated that moonlight suppressed nocturnal drift of larger specimens of several taxa more than it suppressed nocturnal drift of smaller individuals and speculated that this response was an adaptation to fish predation.

There is some contrary evidence, however. The pattern reported for *B. bicaudatus* was not apparent in other taxa observed in Cement Creek. This may be due in part to inadequate data for rarer taxa, and especially to the fact that univoltine species typically are represented by a narrow range of sizes at any one time, rendering such comparisons less fruitful. In addition, several species of *Baetis* are especially prone to drift, relative to other taxa (Lehmkuhl and Anderson 1972). Nevertheless, a size difference between day and night drifting specimens was not general in the stream I studied.

Species that drift by day should not be ones that are readily fed upon by fish. However, the limnephilid caddisfly *Oligophlebodes sigma* is an abundant day drifter (Pearson and Kramer 1972) and suffers at least some predation by trout (Pearson pers. comm.).

Elliott (1968, 1970) observed the diel activity and position on stones (top or bottom) of five mayflies and four caddisflies under controlled conditions. This included taxa and instars which differed in size. His results indicated a strong nocturnal periodicity in all but one caddisfly,

with no differences related to size. However, he did not use the very smallest instars of any species, and when instars of different sizes were used it was at different times of year when other factors such as temperature and perhaps predation would also differ.

My results and those of several other studies support the hypothesis that smaller instars or taxa are less constrained than larger forms to drift only at night, because the smaller forms suffer less risk from fish predators. By implication these data support the argument that the nocturnal periodicity of drift is an adaptation to avoid predation. However, the generality of the pattern observed in *B. bicaudatus* is far from being established, and other factors may complicate the story. Body size is a function at least of the season, the species, and the life cycle. For various univoltine species, large size will be attained only at particular times of the year; differences in temperature which can affect activity, in predation intensity, and perhaps even the availability of alternate prey may play a role. Activity patterns of younger and more mature instars may differ depending upon periods of rapid growth, and certainly will differ due to pre-emergence or pre-pupation events. Relatively few studies of drift have included detailed size data; until more such data are available some of these complexities will remain unresolved.

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