Evidence of Diurnal Feeding Activity in Trichoptera Larvae

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INTRODUCTION

The literature of the aquatic insect order Trichoptera (caddisflies) is extensive. Ross (1944), Denning (1950a, 1950b, 1954, 1956), Banks (1944) and Betten (1934), among others, have been major contributors to the taxonomy and zoogeography of North American species.

Important studies of the general ecology of both adult and larval forms have been made by Lloyd (1921), Scott (1958), and Hynes (1961) but Mecom and Cummins (1964) have commented on the limited knowledge of the trophic relationships of Trichoptera. Hanna (1957), Jones (1950), Chapman and Demory (1963) studied the food ingested by Trichoptera larvae, but except for the very limited experiments of Smirnov (1962), there have been no efforts to determine diurnal feeding activity cycles of caddisflies.

It is the purpose of the present study to determine what cyclic or diurnal feeding behavior is present in five selected species and to correlate such activity with altitude and temperature.

MATERIALS AND METHODS

The larvae of five species of Trichoptera were hand-picked from the substrate of the St. Vrain River. The St. Vrain lies entirely within Boulder and Weld counties in northcentral Colorado at a latitude of approximately forty degrees North. The St. Vrain system arises from small glaciers and snow fields at elevations of 3400 to 3600m and flows eastward as three distinct streams fed by more than 30 permanent and semi-permanent creeks and brooks. Most of the water for the St. Vrain drainage basin comes from snow melt, and more than half of the annual discharge occurs in the late spring and early summer.

Summer water temperatures exceeding 20° are not uncommon at elevations below 1600 m, while July temperatures at 3200 m never rise above 9°. During the winter months the upper reaches of the stream are covered with ice which occasionally exceeds 25 cm in thickness. Often snowdrifts several meters deep are found along the shore and stream bed and only at elevations below 1750 m does the St. Vrain remain essentially free of ice throughout most of the winter.

The average decrease in elevation from west to east is 52 m per km and consequently the water velocity is uniformly high. The substrate of the St. Vrain is characteristic of this region and is composed primarily of coarse gravel, cobbles, and small boulders.

Larvae of five species of Trichoptera were collected from three sites in the St. Vrain River. The Hygiene site (Site H) is located one kilometer south of the town of Hygiene on Boulder County Highway 31 at an elevation of 1657 m (73N, R70W, S36). The stream width varies from 12 to 18 m and the depth of the water rarely exceeds 0.5 m. The substrate consists of small boulders, cobbles, and some coarse sand. The surrounding fields are cultivated and a small farm pond discharges into the stream 20 m upstream from the general collection area. The substrate is covered by a dense mat of *Myriophyllum*, *Elodea*, duckweed, and *Ulothrix*. Coleoptera, Hydracarina, Hirudinea, *Dugesia*, and *Physa* are abundant.

The Lyons site (Site L) is located at the mouth of the St. Vrain Canyon six kilometers southwest of Lyons on Colorado State Highway 7 at an elevation of 1750 m (T3N, R71W, S26). Stream width is less than 15 m, and the substrate consists of small boulders. Water velocity is high and there are no rooted aquatics.

The Canyon Site (Site C) is located in the St. Vrain Canyon nine kilometers from Lyons on Highway 7 at an elevation of 2050 m (T2N, R71W, S6). Stream width is less than five meters and water depth exceeds 1.4 m in several areas.

Larvae were collected at four hour intervals once a month from June, 1968, to May, 1969. The six diurnal collections per month were made at 7 a.m., 11 a.m., 3 p.m., 7 p.m., 11 p.m. and 3 a.m. MST. Water temperatures were taken with a field centigrade thermometer held one cm above the substrate. All organisms were sorted in 70 per cent alcohol until processed.

In order to determine whether cyclic feeding activity is present in Trichoptera larvae, two dissimilar methods were employed. One technique involved a visual examination of gut contents over a 24-hour period. The second technique consisted of determining the absolute weight of organic and inorganic material found in the gut during the same time period.

In the visual technique a minimum of ten larvae each of *Leptocella* sp., *Hydropsyche occidentalis*, *Brachycentrus americanus*, and *Helicopsyche borealis* was selected at random from each of the six collections taken during a given month. Each group of ten was cleared in 10 per cent KOH from 12 to 24 hours (depending on the size of the

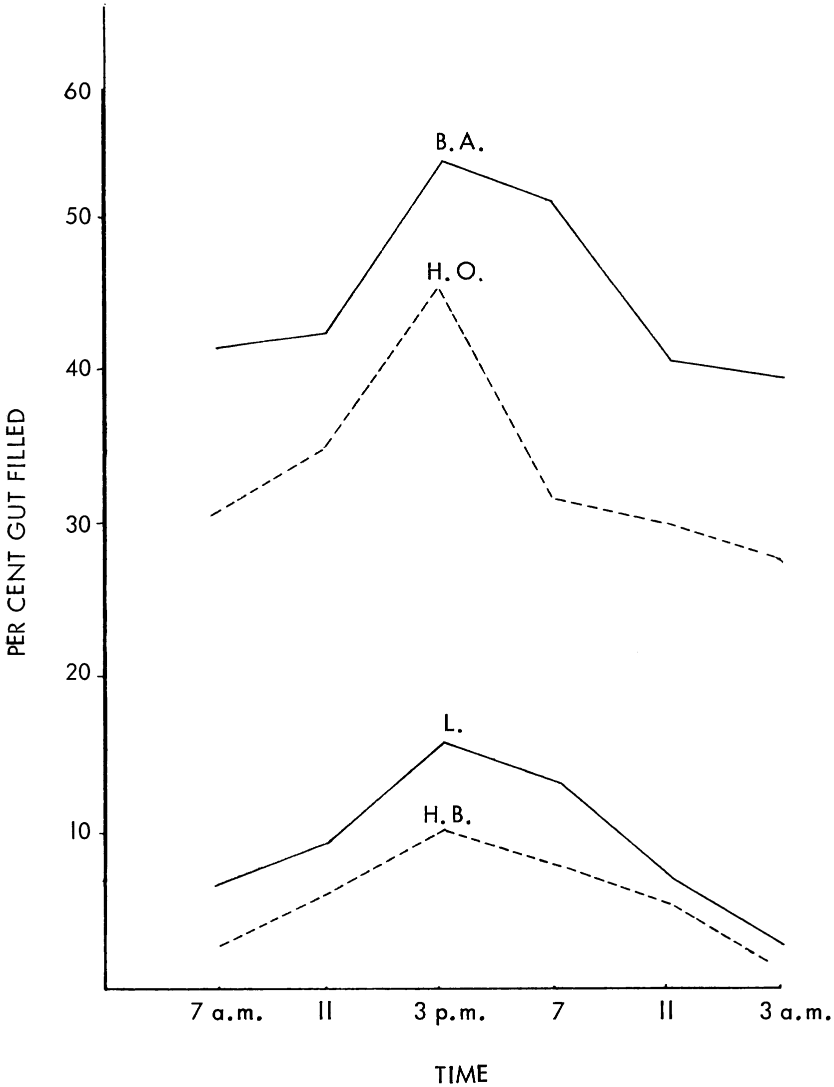

FIG. 1. The annual average per cent gut filled for each time interval of *Brachycentrus americanus* (BA), *Hydropsyche occidentalis* (HO), *Leptocella* sp. (L), and *Helicopsyche borealis* (HB). *Brachycentrus americanus* activity is based on data from June, 1968, to September, 1969.

larvae) and then neutralized in 3 per cent HCL for 20 minutes. After two washings with distilled water, the organisms were transferred to a 50 per cent solution of Gower's carmine which had been prepared from dried acidified carmine, alum, thymol, and distilled water. To prevent damage during solution transfer, the organisms were contained in modified plastic centrifuge tubes.

After staining was completed, the organism's gut appeared as a clearly defined dark brown or reddish mass easily visible through the transparent body wall. By viewing the organism both ventrally and laterally, it was possible to measure to the nearest 0.1 mm that portion of the gut filled with food and debris as compared to the total length of the digestive tract. In rare cases the gut volume appeared reduced and it was necessary to estimate the length occupied by ingested materials. If the gut or body wall was damaged during processing, the sample was discarded. After analysis, all larvae were stored in small screw-cap glass bottles containing two per cent formalin. All values derived from this procedure were expressed as "per cent gut filled" and represented an accurate indication of feeding activity throughout a 24-hour period.

In the gravimetric technique 150 larvae of *Hydropsyche* sp. were randomly selected from all diurnal periods and all months. The gut from the junction of the thorax and abdomen was carefully removed and placed intact into a crucible. The remaining abdominal tissue was placed in a separate preweighed crucible. Both samples were dried for 24 hours at 60° and weighed on a Speedigram analytical balance. After ignition in an electric furnace at 600°C, the crucibles were again weighed. It was computed that the gut and its contents represented an average of 37.9 per cent of the total weight of the abdomen from the thorax to the anus.

A minimum of ten *Hydropsyche* sp. larvae was selected from each diurnal collection and the length of the abdomen was measured in millimeters. The head, thorax, and limbs were separated from the abdomen with a microscalpel and discarded. The abdomens taken from each diurnal collection (six time periods per 24 hours) were placed in crucibles, dried and weighed, and then ignited and reweighed. Because of the various size classes represented in this species (the abdominal lengths of ten animals varied from 56 to 107 mm), the resulting weights of organic and inorganic material were converted to a base abdominal length of 50 mm for clarity. The quantitative values represent daily fluctuation in abdominal weight and are thus an indication of 24-hour feeding activity. Any errors inherent in such a procedure were probably the result of dissecting technique.

More than 2600 Trichoptera larvae of *Brachycentrus americanus, Hydropsyche occidentalis, Hydropsyche* sp., *Helicopsyche borealis* and *Leptocella* sp. were examined in an attempt to determine diurnal feeding activity. All *B. americanus* and *H. occidentalis* larvae were collected from sites L and C, while all of the remaining species were taken from the Hygiene site. Data are not complete on a full-year basis for *B. americanus, H. borealis,* and *Leptocella,* due to summer pupation or general reduction of winter populations. No diurnal analysis for any of the species was possible in May, 1969, because of heavy flooding.

The diurnal feeding cycle of the large *Hydropsyche* sp. was defined by the gravimetric technique while activity of the remaining four smaller species was investigated using the clearing and counterstaining technique.

RESULTS AND DISCUSSION

The literature concerning diurnal activity of both vertebrates and invertebrates is quite extensive, and the monograph by Harker (1964) is a comprehensive survey of diurnal physiology. Harker reviewed the various types of investigations carried out on a great variety of organisms, and it is apparent that diurnal activity of immature insects is very poorly known. Admittedly insects have been favorite subjects for some studies but most work has dealt with *Drosophila* emergence, cockroach running activity, and the physiological cycles in Coleoptera. The investigations of aquatic insect diurnal activity are almost totally restricted to adult stages.

Corbet (1960) reviewed the biting cycles of Culicidae, and the emergence and flight patterns of Odonates, Trichoptera, and *Simulium.* Harker (1953) completed one of the rare studies of rhythms in movement under various light and temperature conditions. Smirnov (1962) attempted to investigate diurnal cycles of Trichoptera larvae by mapping daily migratory movements, analyzing hourly changes in oxygen consumption, and counted fecal pellets to conclude that the genus *Phrygenea* exhibited no obvious diurnal behavior. Smirnov's results should not be considered particularly valid as fecal pellet counts are not truly significant unless a direct correlation between defecation and feeding can be made. In order to quantify oxygen consumption it was necessary to remove the animals from their natural cases. Smirnov's

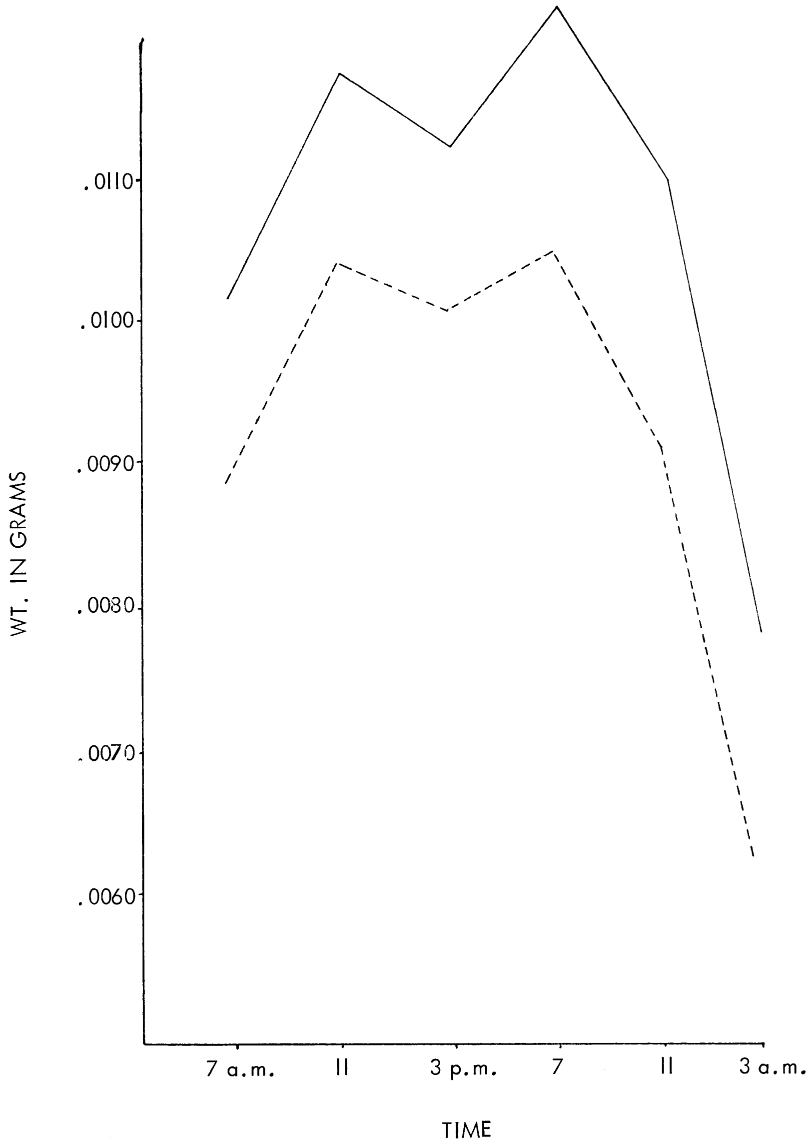

FIG. 2. The yearly composite diurnal feeding activity of *Hydropsyche* No. I (site H). The solid line represents total weight of 50 mm of abdomen. The broken line represents organic weight.

sample was very small (27 larvae) and he made little effort to duplicate natural parameters of photoperiod and temperature.

There is no question that *Brachycentrus americanus, Hydropsyche* sp., *Hydropsyche occidentalis, Helicopsyche borealis,* and *Leptocella* sp. exhibit a clearly defined diurnal feeding cycle. Figure 1 presents a composite (average monthly per cent gut filled during each time sequence) yearly diurnal activity cycle in *Leptocella, Helicopsyche borealis, Hydropsyche occidentalis* and *Brachycentrus americanus.* It is apparent that maximum gut-length filled and presumably greatest feeding activity occurs in mid-afternoon in all four of these species. Minimum feeding takes place in the early morning hours from 3:00 to 7:00 a.m. These data were derived from collections made at all three sites.

The yearly composite activity cycle of *Hydropsyche* sp. (Site H) is shown in figure 2. It should be noted that two feeding peaks occur, one in the forenoon and one in late evening. It is not known whether these maxima are a true indication of increased activity at 11:00 a.m. and 7:00 p.m. or are instead caused by some experimental error. Only in June, 1968, August, 1968, and April, 1969, was feeding activity highest at 3:00 p.m. MST. In all other months there was increased feeding both before and after the 3:00 p.m. maximum found in the four other species. The minimum activity of *Hydropsyche* sp. always occurred in the early morning hours.

There was little variation in the basic configuration of the diurnal curve with altitude or species. Figure 3 shows the diurnal feeding activity of *Hydropsyche occidentalis* at site L (1750 m) and site C (2050 m). In November and March the activity curve appeared reduced in per cent gut filled at the higher site (C) as compared to the lower site (L), but during July the reverse was true. A comparison of diurnal rhythms of *Helicopsyche borealis* and *Leptocella* sp. is seen in Figure 6 for the late fall, winter and spring; and it is apparent that both of these species exhibit the same fundamental cycle at a given site. Harker (1953) reported that in *Ecdyonurus* (Ephemeroptera) nymphs, diurnal migratory activity was only partially related to temperature. She found that general activity increased with higher temperatures, but explained that the basic configuration of the cycle was not altered. Figure 4 shows the generally high per cent gut filled of *Brachycentrus americanus* during the summer months, and Figure 3 shows the same rise in activity of *Hydropsyche occidentalis.* The increased gut weight of *Hydropsyche* sp. in Figure 5 was due primarily

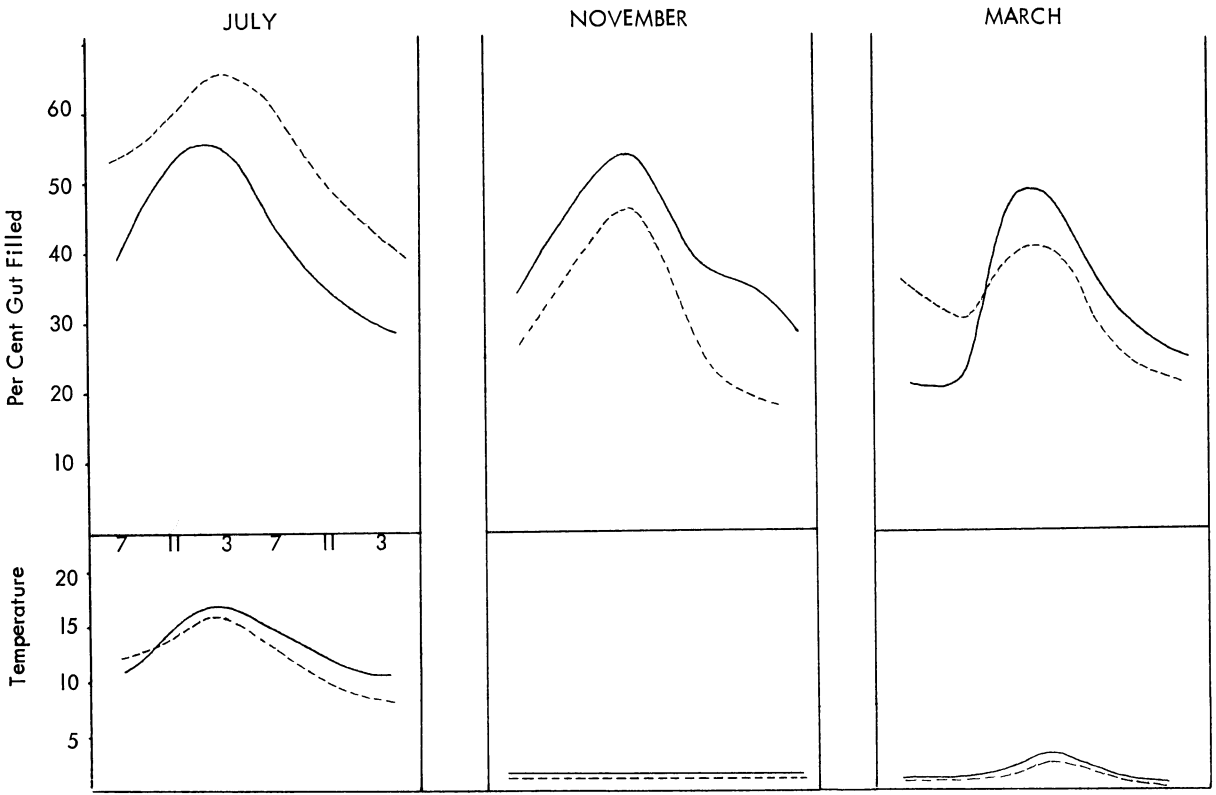

FIG. 3. The diurnal feeding of *Hydropsyche occidentalis* in July, 1968, November, 1968, and March, 1969. The solid line represents site L and the broken line site C.

to an increase in organism size in April and not directly related to temperature. It can be seen that the structure of the diurnal feeding cycle was not radically different whether the temperature varied 15 to 18 degrees in summer or remained near zero for many weeks at a time in winter.

Harger (1953) found that mayfly nymphs reared from eggs in continuous light do not possess a discernible rhythm, but when the same organisms were exposed to natural light-dark periodicity, diurnal activity appeared in full form in less than 24 hours. She stated that once the rhythm was established it could not be altered by light "reversal" or by periods of continuous light or continuous darkness. Corbet (1960) also supported such a view but stated that light controlled diurnal activity could be expressed only under optimum temperature conditions.

Unfortunately there are no data available concerning the direct effects of light exposure on Trichoptera. The more rapid increase in early morning feeding activity in the St. Vrain in summer when light intensities are greater than comparable winter periods might be an example of the direct effects of light, but generally higher summer temperatures could also elicit the same response.

Table 1 shows the abnormal diurnal cycles during periods of reduced light intensity. The collection of February 20 to 21, 1969 was made during a moderate snow storm in which cloud cover was continuous for over 60 hours. The diurnal data for *Hydropsyche occidentalis* were highly irregular at Site L, while the diurnal cycles of *Lep-*

TABLE I

The abnormal diurnal feeding cycles of *Hydropsyche* sp. (HI), *Helicopsyche borealis* (HB), *Leptocella* sp. (L), *Hydropsyche occidentalis* (HO), and *Brachycentrus americanus* (BA) during periods of reduced light intensity in February, 1969, (moderate snowstorm) and August, 1968, (hailstorm). Diurnal activity is expressed as organic and inorganic abdominal weight (HI) or per cent gut filled (BA, HB, HO, and L).

			February 20, 1969 (site H)				
Species	*7 a.m.*	*11 a.m.*	*3 p.m.*	*7 p.m.*	*11 p.m.*	*3 a.m.*	
HI	.0108	.0112	.0113	.0135	.0124	.0015	(org. dry wt.)
	.0018	.0012	.0012	.0013	.0013	.0012	(inorg. dry wt.)
HB	.01	6.58	12.28	11.76	9.52	6.41	(% gut filled)
L	1.52	5.73	8.67	8.91	7.86	3.61	
HO	25.72	30.82	33.54	15.80	25.93	23.83	
		August 17, 1968 (site C)			* hailstorm		
HO	45.06	41.68	50.27	30.64*	38.39	33.24	(% gut filled)
BA	49.01	52.39	57.36	45.21*	51.48	42.64	

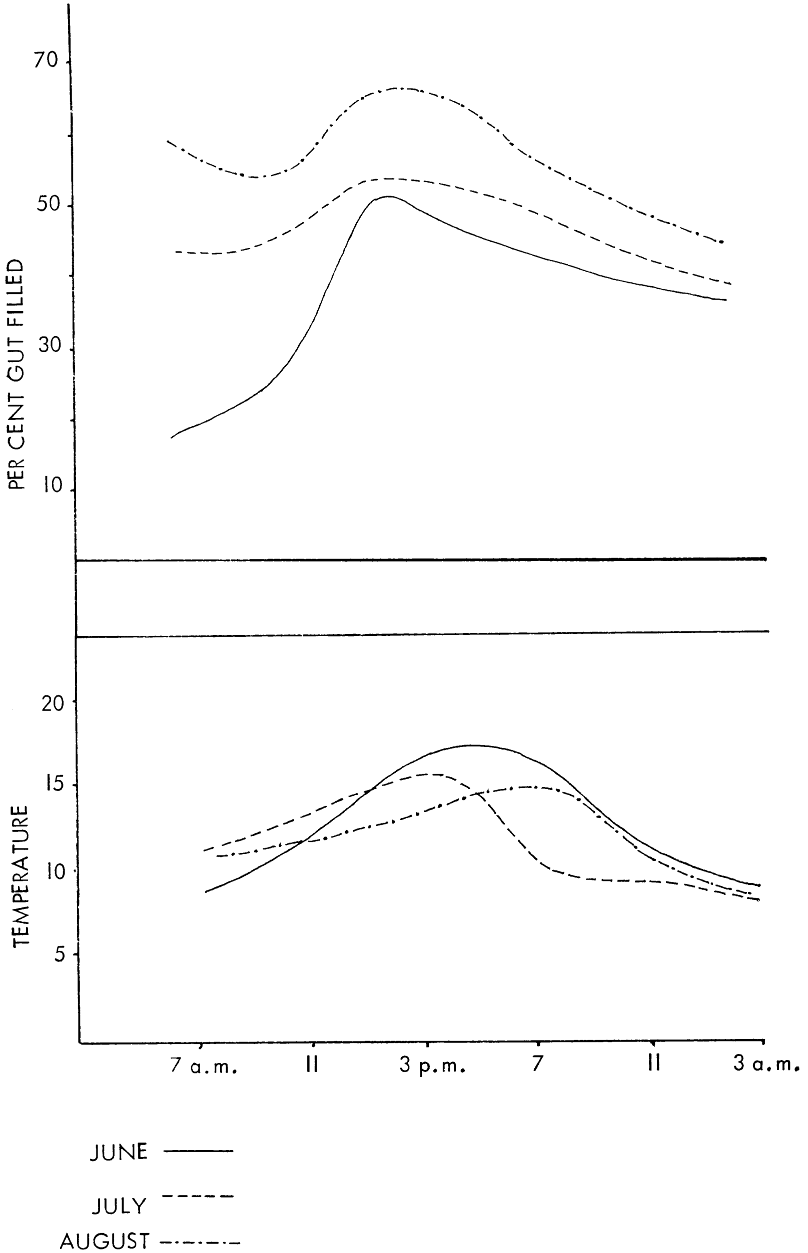

FIG. 4. The diurnal feeding activity of *Brachycentrus americanus* (site C) in June, July, and August, 1968.

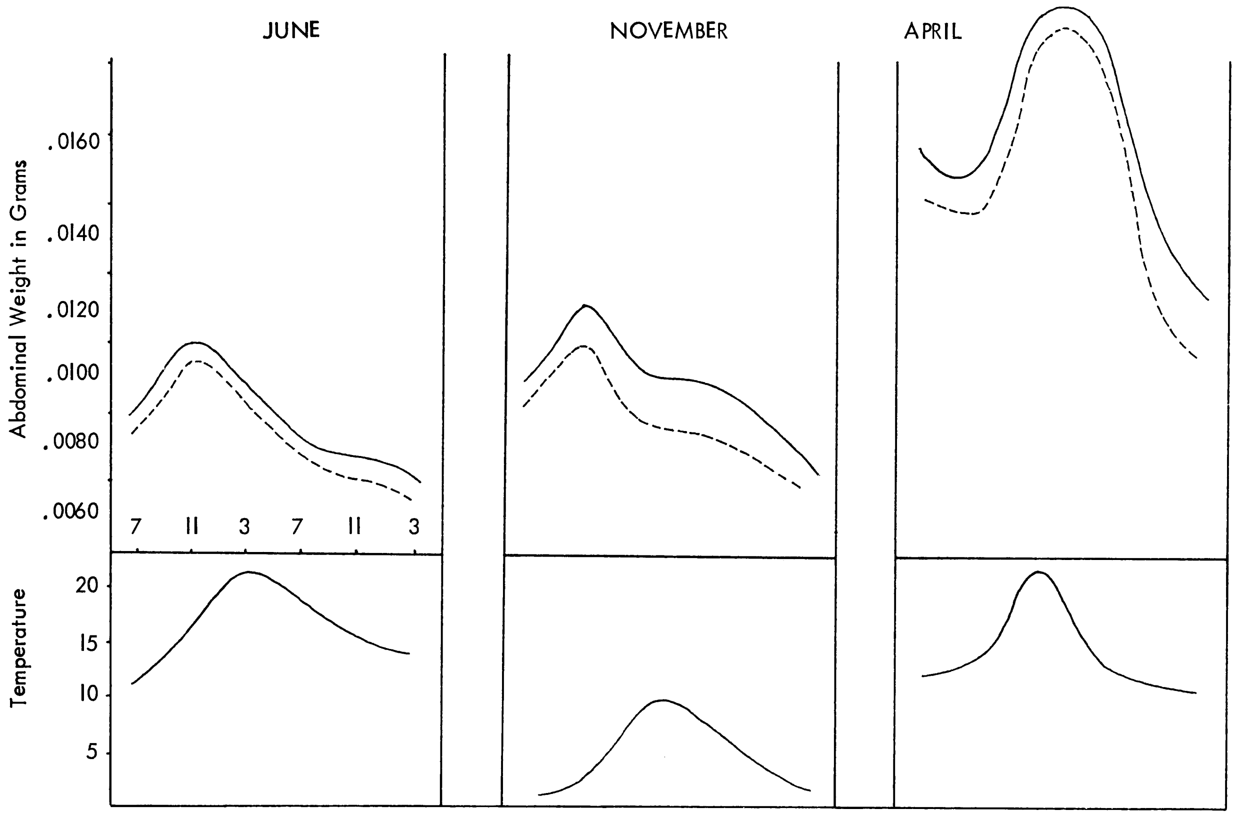

FIG. 5. The diurnal feeding activity of Hydropsyche No. 1 in June, 1968, November, 1968, and April, 1969 (site H). Solid line is total dry weight per 50 mm of abdomen. Broken line is total organic weight per 50 mm of abdomen.

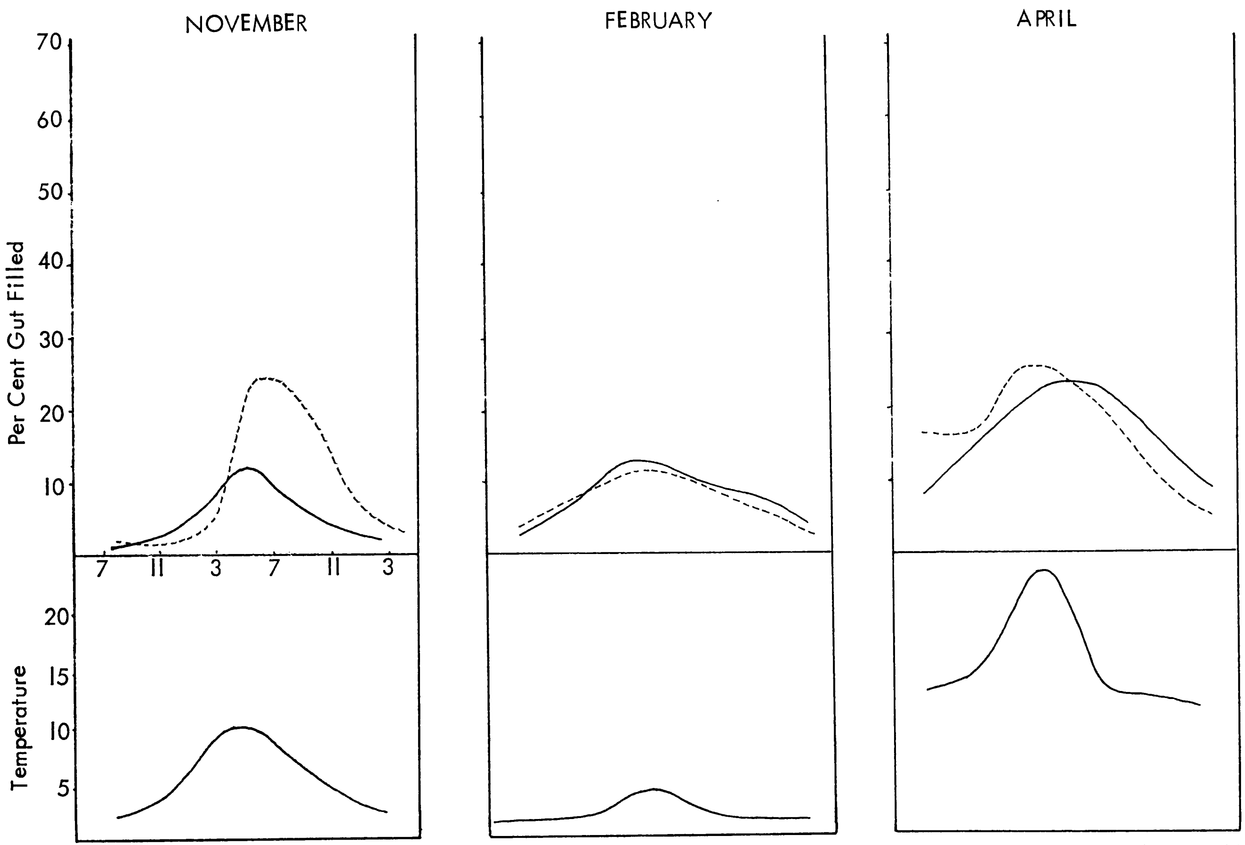

FIG. 6. The diurnal feeding activity of *Helicopsyche borealis* and *Leptocella* (Site H) during November, 1968. February, 1969, and April, 1969. *Leptocella* is represented by the broken line and *Helicopsyche borealis* by a solid line.

tocella sp., *Helicopsyche borealis,* and *Hydropsyche* sp. were unaffected during the same period. In August, 1968, at site C the 7:00 p.m. feeding activity of *H. occidentalis* and *Brachycentrus americanus* was sharply reduced during a severe two-hour rain and hailstorm.

Other variables could also play important roles in determining the diurnal cycle of Trichoptera larvae. It is common knowledge that photosynthetic productivity is highest at mid-day and that more algae are released from the substrate during daylight hours. Daily variation in available food thus could possibly effect diurnal feeding activity to a small degree.

Daily variations in stream discharge resulting in greater delivery of floating food debris to the larvae could not affect diurnal feeding activity to a major degree. Flow was completely stable during the winter months, and the greatest variation occurred during rare thundershowers or because of alternate freezing and thawing in autumn and spring.

In summary it can be concluded that Trichoptera larvae exhibit a clearly defined diurnal feeding cycle in the St. Vrain River. Temperature apparently affects this cycle only by generally increasing or decreasing food consumption in a 24-hour period but does not alter the essential configuration of the basic cycle. Light intensity possibly is a primary controlling factor but may serve only to set or release the innate circadian rhythm. There is no definite evidence that increased primary production or variation in daily discharge affect diurnal activity significantly.

ACKNOWLEDGMENTS

I am especially indebted to Dr. Robert W. Pennak and Dr. John Windell for critical review of the manuscript. Dr. Kenneth W. Cummins (Michigan State University), Dr. H. H. Ross (University of Georgia), Dr. Glenn Wiggins (University of Toronto), and Mr. James Haddock (University of California) were kind enough to aid in the identification of difficult species.

This research is Contribution No. 57 of the University of Colorado Limnological Laboratory and was supported in part by the Kathy Lichty Memorial Fund and a National Science Foundation Pre-Doctoral Summer Traineeship.

Final preparation of the manuscript was made through the facilities of Southern Methodist University.

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