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# Diel Periodicity of Emerging Mayflies (Insecta: Ephemeroptera) in a Laurentian Stream

by

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ABSTRACT

The diel periodicity of mayflies was investigated in a Laurentian stream in 1966. The peak period of emergence of mayflies was found to be between 13:00 and 16:00 h (Eastern Standard Time) during the first month of the season and the emergence was more dispersed during the rest of the summer due to the appearance of species emerging around sunset. Most species showed a definite diel pattern of emergence. Males and females of a given species emerged at the same time of the day in most cases, the emergence being perhaps a little more synchronous in females. They exhibited the same general pattern of diel periodicity throughout their seasonal emergence. In males of *Paraleptophlebia adoptiva* and *Leptophlebia cupida*, however, the peak period moved to an earlier time of day as the emergence season progressed and *Baetis pygmaeus* emerged in a slightly more dispersed fashion in mid-summer when days were longer and warmer. Notes on the diel periodicity of the reproduction are included and the possible factors determining the diel periodicity of emergence are briefly discussed.

## INTRODUCTION

Synchronization in the activities of adults of both sexes is important to ensure the fertilization of the female in ephemeral and fragile insects such as mayflies and this synchronization is brought about mainly by the restricted seasonal emergence (Tjønneland, 1960): it is also thought to be a mechanism for satiating predators (Edmunds and Edmunds, 1980). A close synchronization of the diel periodicity would further enhance the chances of a successful reproduction and thus ensure the survival of the species.

In a previous paper (Harper and Magnin, 1971), we described the seasonal occurrence of some species of mayflies during the summer of 1966 in a small stream in the Laurentian Highlands of Québec. The same data are now analyzed in regard to the diel periodicity of the species. Further studies in the same stretch of stream (Harper and Harper, 1982) enabled us to identify our material with more precision: *Ephemerella* sp. A and sp. B of the previous paper were both identified as *Eurylophella verisimilis, Centroptilum* sp. turned out to be *C. album, Cloeon* sp., *C. rubropictum* and *Paraleptophlebia* sp. C, *P. ontario;* the *Baetis* spp. have been sorted out and include *B. pygmaeus, B. flavistriga,* and *B. pluto. Heptagenia hebe* has in the meantime been transferred to a new genus, *Leucrocuta* (Flowers, 1980).

## METHODS

The collecting methods and the study area have been described in Harper and Magnin (1971). The six emergence traps (0.5 $m^2$) were visited five times a day from May 16th to June 25th, thus establishing five daily periods: 7:00 to 10:00 h (period 1), 10:00 to 13:00 h (period 2), 13:00 to 16:00 h (period 3), 16:00 to 19:00 h (period 4), and 19:00 to 7:00 h (period 5); and then twice a day from June 26th to August 24th, at 7:00 and 16:00 h (Eastern Standard Time). Collecting beyond August 24th was done only once a day. Additional data were obtained by emptying the traps at 4:00 h on May 20th, at 20:30 on May 26th, at 21:00 on June 7th, at 22:00 on June 19th and June 21st. Furthermore, on July 7th, traps were emptied 6 times, at 7:00, 10:00, 13:00, 16:00, 19:00 and 20:30 h (EST). We have no data for June 22nd.

Since the seasonal emergence patterns were similar in all emergence traps (Harper and Magnin, 1971), results from all traps have been pooled, but males and females have been considered separately as suggested by Corbet (1966) in a similar study on Trichoptera.

Diel patterns of emergence (as in Figs. 2 and 3) are illustrated by plotting the Williams means expressed as percentages (histograms) against each period. The Williams mean was defined by Haddow (1960) who discussed its advantages for this kind of data as

$$Mw = \text{antilog} \frac{\Sigma \log (n+1)}{N} - 1$$

in which n is an individual datum in a series of N data. The parts of the histograms covering the period from 19:00 to 7:00 (period 5) have been drawn in a broken line since the peak of emergence likely falls in a much more restricted lapse of time as can be inferred from the additional data and from the literature. From June 26th onwards, histograms of the Mw represent the emergence from 7:00 to 16:00 and from 16:00 to 7:00 h. In some instances, additional data have allowed us to pinpoint the exact time of emergence within this period; arrows on the graphs point to such periods. Corbet (1966) suggested recording the predictability of the patterns of diel periodicity by calculating the percentage of days when the maximum catch occurs in any given period of the day; the curve of predictability appears as a solid line on the graphs in Figures 2 and 3.

## RESULTS AND DISCUSSION

The species (Fig. 1) emerged in the same order in 1966 as they were to in 1972 and 1973 in the same stream (Harper and Harper, 1982) except for the much later appearance of *Heptagenia pulla* in 1966. Moreover *Baetis propinquus* was not found in 1966 and *Tricorythodes atratus* was not found in 1972 or 1973.

Total catches of males and females at each period of the day appear in Table 1; days when one or more data are missing have not been included in the totals.

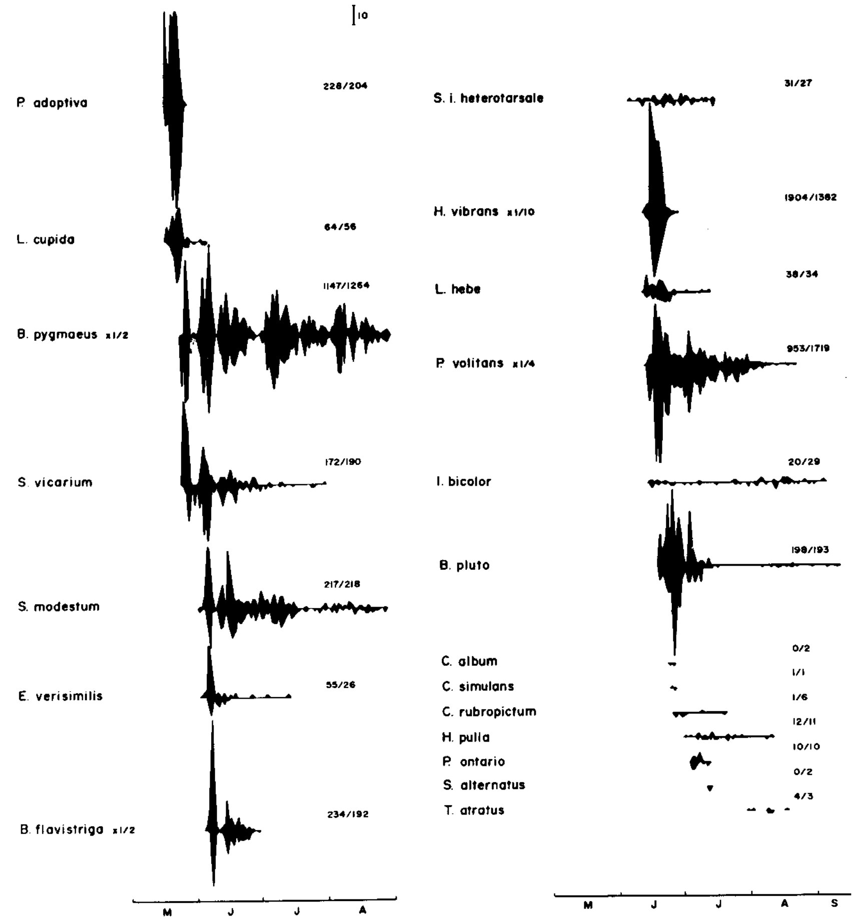



Fig. 1. Seasonal succession of Ephemeroptera collected in six emergence traps during the summer of 1966. The upper part of each diagram represents the emergence of males and the lower part, the emergence of females. Total numbers of males/females appear for each species.

Table 1. Total numbers of Ephemeroptera emerged per time period during the season (males : females). Days when some data are missing have been omitted from the totals.

| Species | Total numbers per period May 18th to June 25th | | | | | Total numbers per period June 26th to August 24th | |
|---|---|---|---|---|---|---|---|
| | 7h-10h | 10h-13h | 13h-16h | 16h-19h | 19h-7h | 7h-16h | 16h-7h |
| *Paraleptophlebia adoptiva* (McD.) | 64:29 | 71:96 | 81:64 | 9:15 | 3:0 | — | — |
| *Leptophlebia cupida* (Say) | 11:2 | 40:46 | 11:8 | 2:0 | 0:0 | — | — |
| *Baetis pygmaeus* (Hagen) | 5:19 | 191:165 | 300:330 | 28:48 | 11:22 | 457:470 | 104:143 |
| *Stenonema vicarium* (Walker) | 37:37 | 26:29 | 34:40 | 14:18 | 48:41 | 1:2 | 9:16 |
| *Stenonema modestum* (Banks) | 15:9 | 10:3 | 7:1 | 7:10 | 81:67 | 8:14 | 68:83 |
| *Eurylophella verisimilis* (McD.) | 11:2 | 16:24 | 24:8 | 0:1 | 1:0 | 2:1 | 0:0 |
| *Baetis flavistriga* McD. | 40:32 | 47:43 | 75:47 | 53:49 | 6:6 | 1:1 | 0:0 |
| *Stenacron interpunctatum heterotarsale* (McD.) | 4:1 | 0:0 | 1:0 | 0:0 | 7:6 | 3:3 | 12:13 |
| *Habrophlebia vibrans* Needham | 27:20 | 473:35 | 944:907 | 97:94 | 44:29 | 22:32 | 4:2 |
| *Leucrocuta hebe* (McD.) | 6:5 | 1:0 | 2:1 | 0:0 | 16:13 | 2:1 | 2:5 |
| *Paraleptophlebia volitans* (McD.) | 39:74 | 30:29 | 10:44 | 42:35 | 183:347 | 132:216 | 367:707 |
| *Isonychia bicolor* (Walker) | 0:0 | 0:0 | 1:1 | 0:1 | 3:0 | 6:11 | 7:11 |
| *Baetis pluto* McD. | 16:7 | 21:13 | 5:0 | 0:0 | 0:0 | 112:130 | 6:6 |
| *Centroptilum album* McD. | 0:0 | 0:1 | 0:0 | 0:0 | 0:0 | 0:1 | 0:0 |
| *Caenis simulans* McD. | 0:0 | 1:0 | 0:0 | 0:0 | 0:0 | 0:1 | 0:0 |
| *Cloeon rubropictum* McD. | — | — | — | — | — | 2:0 | 0:6 |
| *Heptagenia pulla* (Clemens) | — | — | — | — | — | 6:3 | 5:8 |
| *Paraleptophlebia ontario* (McD.) | — | — | — | — | — | 8:10 | 2:0 |
| *Siphlonurus alternatus* (Say) | — | — | — | — | — | 0:0 | 0:2 |
| *Tricorythodes atratus* McD. | — | — | — | — | — | 3:2 | 1:1 |
| Totals | 512 | 1401 | 2946 | 523 | 934 | 1663 | 1590 |
| | | 4859 | | 1457 | | | |

Figures 2 and 3 illustrate the diel periodicity of emergence of the more abundant species.

It is clear that most species show a definite diel periodicity of emergence. *Paraleptophlebia adoptiva, L. cupida, E. verisimilis, B. flavistriga, B. pygmaeus, H. vibrans, B. pluto,* and *P. ontario* are almost exclusively daytime emerging species in our stream; *C. album, C. stimulans, C. rubropictum,* and *T. atratus* (Table I) would also seem to fit into this category although few data were obtained.

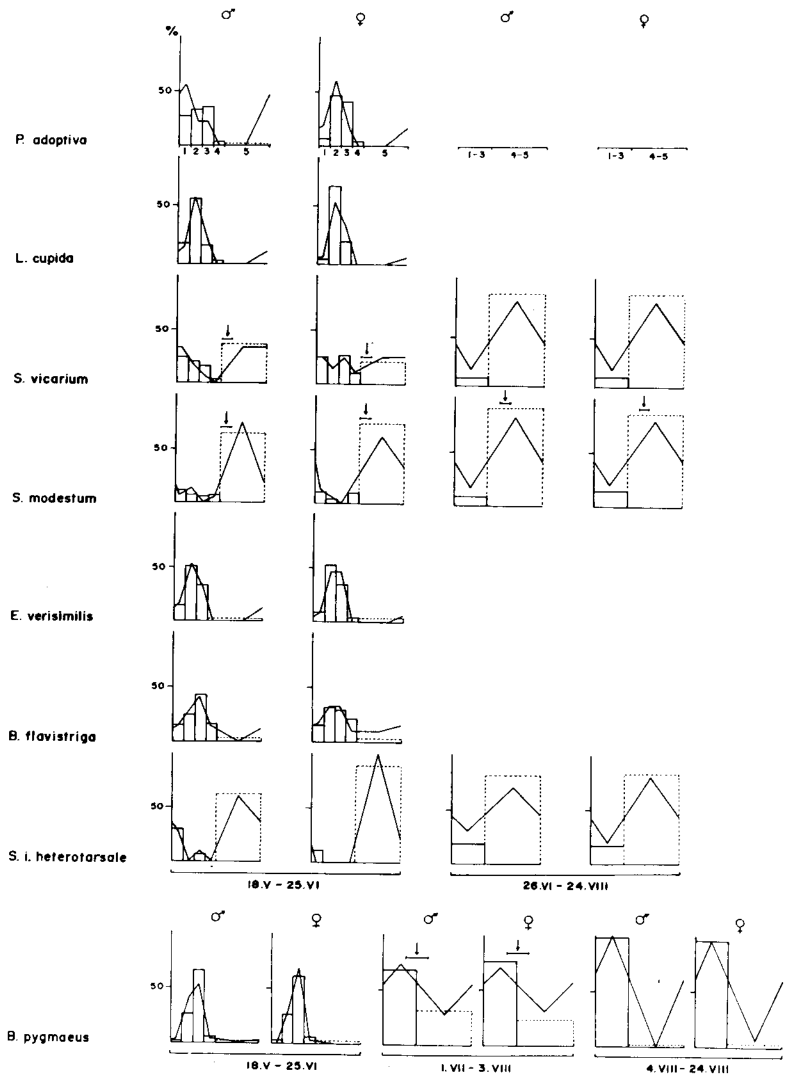
*Stenonema modestum* (Fig. 2) and *P. volitans* (Fig. 3) emerged around sunset, mostly around 21:00 h. *Stenacron interpunctatum heterotarsale* (Fig. 2) and *L. hebe* (Fig. 3) emerged sometime between 19:00 and 7:00 h but no data are available to pinpoint the exact moment of emergence. Sprules (1947) however established the time of emergence of *S. i. heterotarsale* as being between 22:00 and 23:00 h at the same latitude and Friesen et al. (1980) in Manitoba caught all their specimens of *L. hebe* between 18:00 and 22:00 h. The two females of *S. alternatus* and all the females of *C. rubropictum* (Table 1) also emerged during period 5. Females of *C. rubropictum* in Manitoba emerge between 20:00 and 24:00 h (Friesen et al., 1980).

In *Stenonema vicarium* (Fig. 2) and *I. bicolor* (Fig. 3), the emergence was more dispersed over the day, although *S. vicarium* seems to have become an evening emerger in the last month of its emergence season. Clemens (1917) established the time of emergence of *I. bicolor* in late afternoon and early evening in New York and Sprules (1947), between 19:00 and 21:00 h in Ontario, but the latter also saw the emergence take place between 7:00 and 9:00 h.

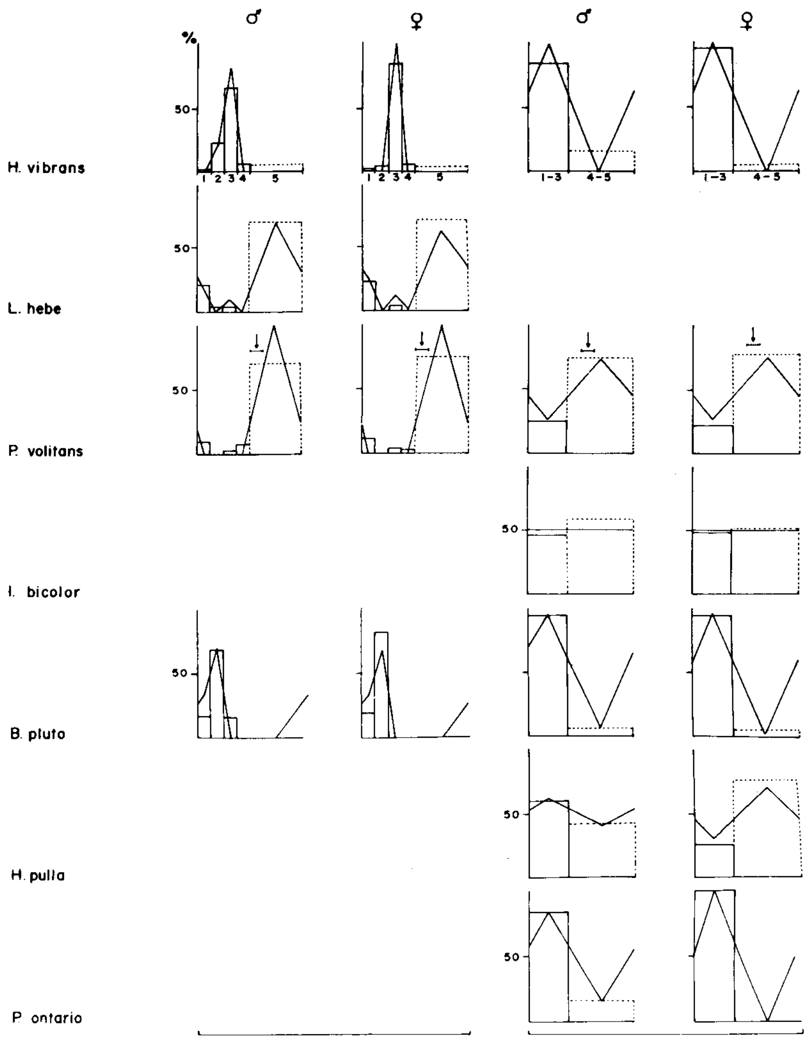
For the two most precocious species, *P. adoptiva* and *L. cupida,* the calculation of the Williams mean obscures the fact that the peak period of emergence moved to an earlier hour of the day in the males from day 1 to day 6 (Fig. 4), concurrently with an increase in mean daily temperature and a decrease in relative humidity (Fig. 4). In both these species, emerging during the daytime probably ensures suitable conditions for their flight activity in a period when the dark hours of the day are still fairly cold (Flannagan, 1978).

In *H. pulla,* males seem to emerge in a dispersed manner throughout the day and females mostly between 16:00 and 7:00 h (Fig. 3). All females of *C. rubropictum* emerged between 16:00 and 7:00 h and both males were caught in the daytime. This species shows the same particularity in Manitoba, all males being caught during the day and the females emerging between 22:00 and 24:00 h (Friesen et al., 1980). A similar phenomenon is reported in *T. atratus* by Hall et al. (1975). In other species, males and females have similar patterns and this is a general feature in mayflies (Boerger and Clifford, 1975; Friesen et al., 1980; Brittain, 1982). The emergence of females may be a little more synchronous than that of the males in certain species viz. *P. adoptiva, L. cupida, H. vibrans,* the early *S. i. heterotarsale* and perhaps *H. pulla* and *B. pluto* (Figs. 2 and 3).

The data on *B. pygmaeus* were treated in a slightly different manner in view of its particular seasonal pattern of emergence (Fig. 1). There are three distinct emergence periods and each has been dealt with separately since it may represent a different cohort or generation (Fig. 1). The emergence takes place mostly in the daytime throughout the summer with males and females behaving in a similar manner.




Figs. 2 and 3. Diel patterns of emergence of the most abundant species. The histograms represent the Williams mean expressed as % for each period of the day. The two diagrams on the left illustrate the diel periodicity of males and females respectively from May 18th to June 25th and the two diagrams on the right illustrate the diel periodicity of males and females between June 25th and August 24th. Periods 1, 2, 3, 4, and 5 are respectively from 7:00 to 10:00, 10:00 to 13:00, 13:00 to 16:00, 16:00 to 19:00 and 19:00 to 7:00. Period 5 covering a much grater lapse of time is illustrated in a broken line. Arrows point to the peak moment of emergence during period 5, when it was possible to evaluate it.




However, during the second peak, the emergence is more dispersed (Fig. 2); Friesen et al. (1980) also report a less rigid periodicity in July as compared to that of June or August in *Baetis intercalaris* and relate this shift to illumination. In the case of *B. pygmaeus* in our stream, the diel periodicity would seem to be more temperature dependent than light dependent since the emergence period is confined to daylight hours when illumination is fairly stable throughout the day. The data recorded by Friesen et al. (1980) on *B. pygmaeus* seem to indicate that in Manitoba the species emerges a little later in the day in July (between 18:00 and 22:00 h) and is a little more dispersed in August.

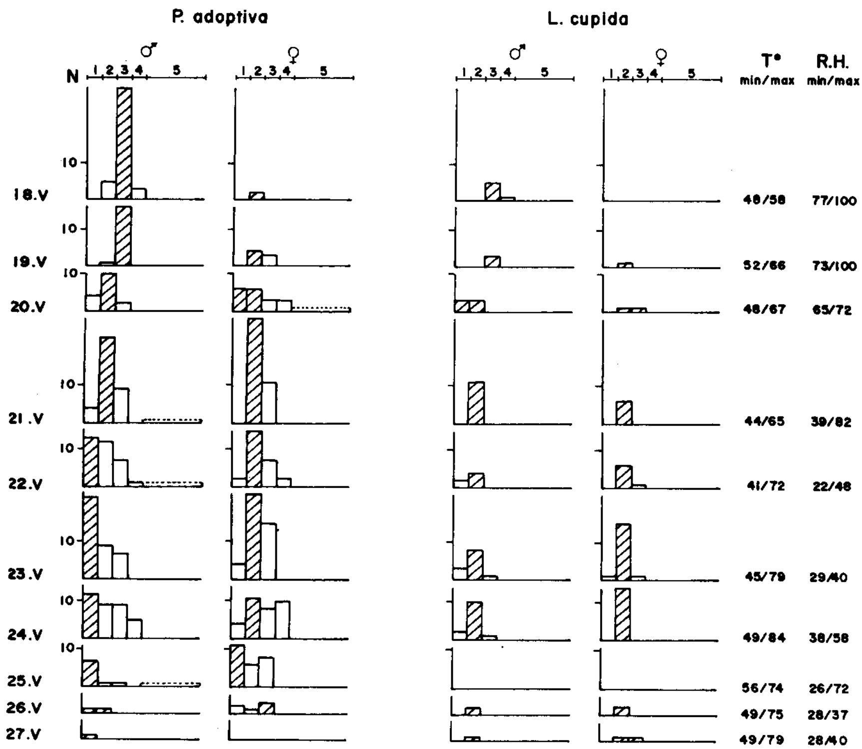



Fig. 4. Diel periodicity of males and females of *P. adoptiva* and *L. cupida* from May 18th to May 27th. The striped histogram represents the peak period of emergence each day. Data on temperature and relative humidity appear for each day.

With very few exceptions, the species follow the same diel strategy throughout their seasonal emergence.

Friesen et al. (1980) found that the peak period of emergence of mayflies as a group in Manitoba took place at dusk; Edmunds and Edmunds (1980) indicate that "the most common time of emergence for most temperate species is from late afternoon through the first hours of darkness" and Brittain (1982) notes that "in temperate regions the crepuscular emergence of mayflies is well known". By contrast, Elliott (1967) noted a maximum in daylight hours and similarly our results show a maximum between the hours 13:00 and 16:00, at least in the early summer months (Table 1). Seventy-six percent of the mayflies emerged between 7:00 and 16:00 h before June 25th. Later in the season, this pattern is modified by the appearance of species emerging afound sunset (51% from 7:00 to 16:00 and 49% between 16:00 and 7:00 h). The fact that the diurnal catches are made up of abundant species of small to medium size (with the exception of *L. cupida* whose diurnal emergence is related to its early appearance in the season) accounts for the peak period occurring around mid-day rather than at dusk. These smaller species can afford to emerge during the day since their smaller size and their greater abundance protect them against decimation by eventual predators. The larger heptageniids and *P. volitans* find their advantage in emerging in the evening. The case of *I. bicolor,* the largest species in our traps, remains to be explained since in spite of its size it seems to emerge at all times of day or evening.

The reproductive activity of some species has been observed on various occasions and its diel periodicity can be compared to that of emergence. *Isonychia bicolor* which does not follow a distinct diel pattern of emergence has been seen laying eggs on a few occasions between 16:00 and 19:30 h. *Paraleptophlebia volitans* is essentially an evening emerger, but swarms have been observed on several occasions in the morning between 7:00 and 10:00 h and once at 16:00 h. *Callibaetis floridanus* (Trost and Berner, 1963) is also known to exhibit different diel periodicities of emergence and reproductive activity. However, in most of our species, namely *P. adoptiva, L. cupida, S. vicarium, S. rubromaculatum, S. i. heterotarsale, H. vibrans,* and *H. pulla,* the diel periodicity of mating and oviposition does seem to follow the diel periodicity of emergence. In Trichoptera, Corbet (1966) recorded that the periodicity of oviposition followed that of emergence in both afternoon and evening emergers.

If the periodicity of a species is maintained throughout its adult life, the logical question that arises is whether this periodicity is a sequel of a larval rhythm. Hartland-Rowe (1958) found a lunar rhythm of emergence in the tropical *Povilla adusta* Navas and he suggested that the variations in the light intensity of the moon light might induce a rhythm in the larvae, this rhythm being carried on in the emergence activity when the larvae are mature. In northern latitudes, a similar mechanism seems to be involved, even though the stimulus might be different: a rhythm was found in the larvae of two European lake species of *Leptophlebia,* this rhythm shifting from nocturnal to predominantly diurnal prior to emergence. In these species, the nocturnal activity is related to the search for food, while the diurnal rhythm is related to emergence. The diurnal rhythm is more pronounced when the weather conditions are favorable for emergence, which seems to indicate a certain flexibility of rhythm according to the climatic conditions (Solem, 1973). In running waters, the locomotor activity and drifting of mayflies are known to be clearly nocturnal during most of the year (Elliott, 1967) except in the polar midsummer when activity becomes arhythmic (Solem, 1973). In some species, a shift from day to night activity occurs with increasing size (Steine, 1972). It would thus seem that the emergence rhythm in mayflies may be different from that of the larvae, though the mechanisms involved in this shift are not known.

The hypothesis of an intrinsic factor or biological clock controlling the periodicity (Tjønneland, 1960; Brittain, 1982) has not been corroborated in the adults and has been disproved in many larvae (Müller, 1974). Among extrinsic factors, Tjønneland emphasizes the great importance of light; in more temperate climates, the role of temperature in the emergence of aquatic insects is certainly very important (Ide, 1940; Sprules, 1947; Humpesch, 1971; Flannagan, 1978; Flannagan and Lawler, 1972; Friesen et al., 1980).

Finally, a correlation can be established between the diel periodicity and the type of seasonal emergence (as described by Harper and Magnin, 1971); all species of type 1 emergence (synchronous) emerge during the day and most species of type 2 emergence (dispersed) emerge in the evening. This correlation may however be purely coincidental, but if it were to reappear in other similar studies, its significance should be investigated.

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