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LIFE CYCLES AND HABITATS OF WISCONSIN HEPTAGENIIDAE (EPHEMEROPTERA)

R. W. FLOWERS & W. L. HILSENHOFF

Laboratory of Aquatic Entomology, Florida A & M University, Tallahassee, FL 32307; Department of Entomology, University of Wisconsin, Madison, WI 53706

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Abstract

Detailed studies were made of the life cycles of Heptageniidae known to occur in Wisconsin. 19 species had univoltine cycles while two and possibly a third had bivoltine cycles. Three univoltine species developed in late spring and early summer while the other univoltine species developed in fall, winter and early spring. For three of the univoltine species, eggs hatched both in fall and the following spring. Diagrams of the life cycles of 15 Wisconsin heptageniids are presented, illustrating the different types of life cycles. Also presented are observations on the food and habitats of the nymphs and flight periods of the adults.

Introduction

The successful use of insects to monitor water pollution requires a knowledge of the ecology and life histories of all important groups of aquatic insects. Mayflies of the family Heptageniidae (Ephemeroptera) are widespread in streams with abundant firm substrate, where they often form a high percentage of the invertebrate fauna. Taxonomic studies (Daggy, 1941; Burks, 1953; Leonard & Leonard, 1962; Lewis, 1974; Flowers & Hilsenhoff, 1975) contain brief notes on habitat and flight periods for many Wisconsin species. More detailed life history information about some of these species can be found in regional studies of the mayfly faunas of Michigan (Lyman, 1955), northern Wisconsin (Hilsenhoff & Walton, 1972) and eastern Canada (Clemens, 1915 a, b; Ide, 1935; Mackay, 1969; Coleman & Hynes, 1970). This paper presents data on the life cycles and habitat requirements of all species of Heptageniidae known to occur in Wisconsin.

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Methods

A sampling program was established to obtain a series of specimens from populations of each species over a one-year period. Sampling stations were chosen on the basis of previous collecting experience to provide data on all species, using as few sites as possible. Nineteen streams and two ponds in various parts of the state were selected for regular sampling (Fig. 1). Streams ranged from large rivers to small creeks and were located in both agricultural and forested areas. Stations are numbered on a north-south gradient with Station 1 being farthest north.

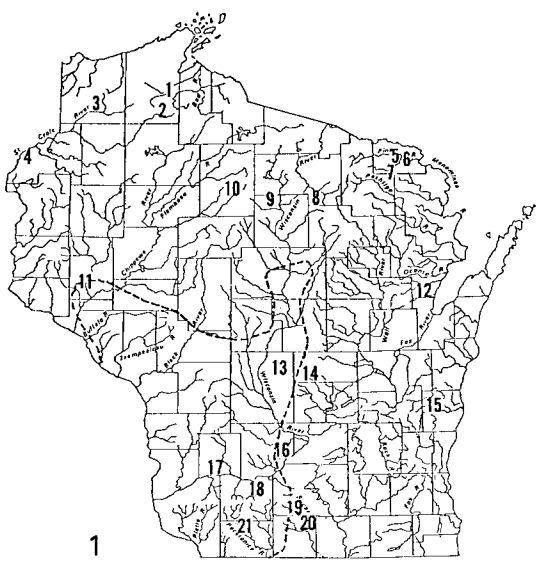


Fig. 1. Map of Wisconsin showing location of sampling sites. Numbers refer to Table 1. Dotted line marks boundary of 'driftless' area.

At each visit, water temperature (°C) was recorded and the current speed in each habitat where heptageniids were found was measured with a pigmy current meter held 2.5 cm above the substrate. More frequent measurements would have given a more precise idea of stream conditions but, because of the distance between sampling stations, this was not practical. Since most of the streams are heavily used for fishing and recreation, it was not feasible to leave recording devices in them. Sizes of the substrate rocks were classified according to the table in Cummins & Lauf (1969) by measuring a random sample of 10 rocks in each area sampled. The width of each stream and the depth of the areas sampled were measured during the low water months. The maximum temperature, maximum and minimum current speeds and types of substrate where heptageniids were found are summarized for each station in Table 1.

Each station was sampled monthly in 1973 and 1974 from April or May (after spring run-off) until late fall when ice formed. In addition, many stations were visited a second time in May and June to get more precise emergence data from the adults. One-minute kick samples were taken using a D-frame aquatic net (1 mm mesh). The mesh size of the net undoubtedly biased the sample against very young nymphs but these cannot be identified to species. At every station, each habitat suitable for Heptageniidae was sampled (pool. riffle, rock, submerged vegetation). Some stations had large rocks that could not be sampled efficiently by the kick method. In these areas, a sample was taken by lifting ten rocks in front of the net and rinsing off the attached animals. These two methods were roughly equivalent in terms of area of bottom sampled. All Heptageniidae found in each sample were preserved in 70% alcohol. During emergence periods, vegetation along the stream banks was swept with a long handled net to obtain adults. In the laboratory, samples were sorted, identified and counted. Adult emergence periods were established by dates when adults were collected and by the presence in a sample of mature nymphs with black wing pads. Laboratory rearing showed that such nymphs emerge within two days. To determine growth of nymphs, measurements of head capsules were taken using a microscope with an ocular micrometer. The head capsule was measured at its widest point, and larger nymphs were sexed. Life cycles were graphed as a series of monthly frequency histograms of head capsule width for each species except *Heptagenia flavescens, Heptagenia pulla, Pseudiron* sp. *Rhithrogena undulata, Spinadis* sp., *Stenonema integrum* and *Stenonema pulchellum,* which were not collected in sufficient numbers (Flowers, 1975). Table 2 shows the total numbers of heptageniid nymphs collected at each station.

Table 1. Sampling stations. Width was measured across stream at station; all other data refer to habitats where Heptageniidae were collected.

No.	Station	Max. Temp. °C	Current m/sec Max.	Current m/sec Min.	Width m	Depth cm	Principal Substrates
1.	White R.	19	.40	.12	10.7	17.5	sand and cobble
2.	18 Mile Cr.	16	.78	.30	2.1, 3	8.0	pebbles
3.	St. Croix R. (Douglas Co.)	24	.26	.10	20.2	40.0	cobble, boulders
4.	St. Croix R. (Burnett Co.)	25	.59	.05	61.0	107.0	cobble, boulders
5.	Pine R.	22	1.12	.13	37.5	8, 60	pebbles, gravel
6.	Pine R.	20	.30	.00	31.4	30.0	cobble
7.	Popple R.	22	.34	.06	21.3	4.5	pebbles, boulders
8.	N. Br. Pelican R. (temp. pool)	22				45.0	sedge stalks
9.	Big Somo R. (temp. pool)	22				15.0	grass
10.	Little Jump R.	24	.90	.08	4.6, 12.2	5, 32	gravel, pebbles
11.	Eau Galle R.	25	.53	.11	15.2	30, 35	sand, some rocks, submerged branches
12.	Little Suamico R.	28	.32	.07	30.5	15, 22	pebbles, rocks
13.	Big Roche a Cri Cr.	22	.36	.15	7.6	55.0	sand, rocks
14.	Mecan R.	20	.50	.13	5.2	38.0	gravel, pebbles, cobble
15.	Mullet R.	20	1.00	.13	5.7, 9.8	30, 45	pebbles, cobble
16.	Otter Cr. (Sauk Co.)	19	.45	.05	1.8	8, 30	cobble
17.	Wisconsin R.	26	.60	.10	122.0	105.0	cobble
18.	Otter Cr. (Iowa Co.)	22	.39	.06	6.1	45.0	sand, submerged wood
19.	Sugar R. (Dane Co.)	26	.60	.14	15.0	22.0	pebbles, cobble
20.	Sugar R. (Green Co.)	24	.32	.19	13.0	8, 30	boulders
21.	W. Br. Pecatonica R.	24	.80	.24	6.7	30.0	pebbles, cobble

Life Histories

Arthroplea bipunctata (McDunnough)

This species is unique among Wisconsin Heptageniidae in its habitation of temporary ponds. While most Heptageniidae scrape their food from the substrate, *Arthroplea* has evolved a type of filter feeding. The nymphs sits lengthwise on a stalk of grass or sedge and rapidly sweeps its elongate maxillary palpi through the water alongside the head, Food is trapped by long hairs on the palpi and removed by drawing the maxillary palpi between the labial palpi (Froehlich, 1964). Gut analysis indicated that the food is a mixture of algae, detritus and animal remains of unknown origin. Live *Arthroplea* nymphs were collected from temporary ponds at the Pelican and Big Somo Rivers and reared in the laboratory. Animals from

Table 2. Total Heptageniidae collected at all sampling stations over 1973-1974.

Species \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Arthroplea bipunctata								58	38												
Epeorus vitreus			14	3	166	11	20			32											
Heptagenia diabasia											660						7	495	2	14	
H. flavescens				1							9						7			24	
H. hebe	43		107	5	54	141	68			185		4	1	38	922	338					
H. lucidipennis				7						52									86		4
H. pulla	74	17																			
Rhithrogena impersonata		406	1																		
R. jejuna					322																
R. pellucida	1	3			144																
Spinadis sp.																	4				
Stenacron interpunctatum	123		27	3	7	11	19			291	1	506	10	9	381	15	30	16	8	182	128
Stenonema bipunctatum			24	48			1														228
S. exiguum	14		134	54		5					15		105	40			18	49	6	106	17
S. fuscum	91		119	7	39	11	58			334	25	396	74	75	678	82			1		
S. integrum				1													43			8	3
S. mediopunctatum				8						12		19		2	147				34	10	519
S. pulchellum	11		3	31																	
S. rubrum	23		53	1	46		11			2			1	240	296						
S. terminatum											94	1					151	250	10	156	16
S. tripunctatum												108									
Total	390	426	489	169	778	179	177	58	38	908	804	1071	191	414	2424	435	256	810	145	500	915

the Pelican River were further developed than were those from the Big Somo. Nymphs were measured weekly and returned to their rearing pans. Those from the Pelican River matured and emerged successfully while those from the Big Somo River grew poorly and eventually died. Eggs hatched in early May and nymphs grew very rapidly until emergence at the end of May (Fig. 2).

Epeorus vitreus (Walker)

Small nymphs appear in September (Fig. 3). Growth begins at once, continues through the winter and adults emerge the following June and July. Ide (1935) believed that high summer temperatures killed both late developing nymphs and early hatching eggs.

The food of the nymphs is mostly detritus with some diatoms and filamentous algae (Shapas & Hilsenhoff, 1976).

Heptagenia Walsh

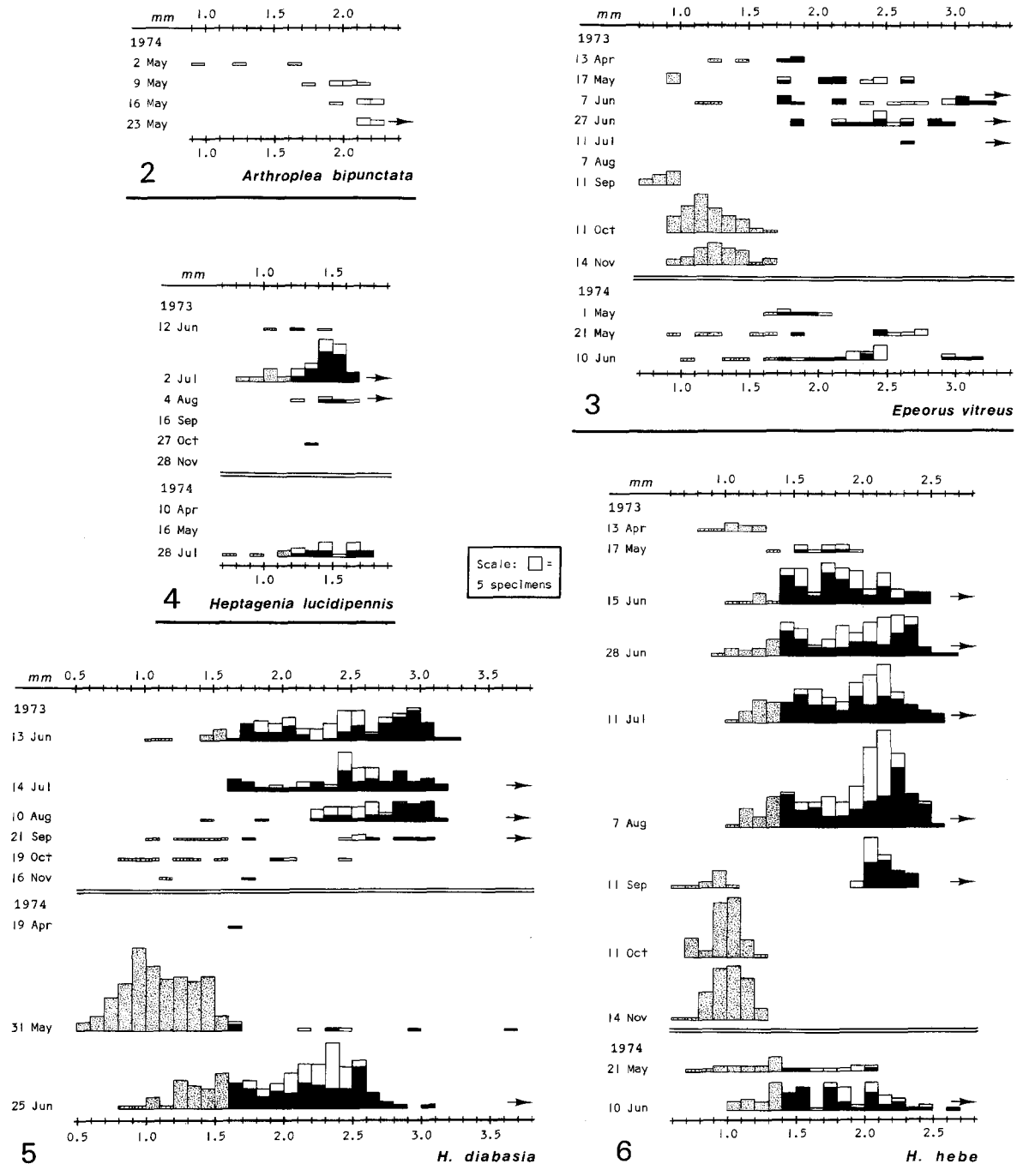
Heptagenia is widespread in Wisconsin, but does not seem quite as tolerant of slow, organically enriched water as *Stenonema* or *Stenacron*.

Detritus is the principal food of *Heptagenia*, although diatoms are an important food of *H. hebe*. Except for this case, detritus made up at least 75% of the gut contents of the specimens investigated (Shapas & Hilsenhoff, 1976).

Heptagenia diabasia Burks

H. diabasia is found mainly in the southwestern part of Wisconsin: the unglaciated or 'driftless' area. The streams here often have sandy beds with occasional log snags, submerged brush and grass, or rocks around bridge abutments providing the only firm substrates. In these limited areas, large populations of *H. diabasia* occur frequently. In Otter Creek (Iowa Co.) (Station 18) *H. diabasia* was common on submerged logs and, when the water was high, on grass.

In the Eau Galle River (Station 11) adults emerged from late June to early September (Fig. 5). Hatching of the nymphs apparently occurs both in fall and the following spring. Eggs laid by females emerging early in the flight period hatch the same year. Eggs of other females overwinter and hatch the following spring. This would explain the appearance of a few large and many tiny nymphs at the end of May, 1974. In Otter Creek the life cycle was similar to that of the Eau Galle River population but emergence took place in early June. Both large and small nymphs occurred in spring.



Figs. 2-6. Life cycles of *Arthroplea, Epeorus* and *Heptagenia* as represented by width of nymphal head capsules: 2, *Arthroplea bipunctata* from Stn. 8; 3, *Epeorus vitreus* from Stn. 5; 4, *Heptagenia lucidipennis* from Stn. 19; 5, *H. diabasia* from Stn. 11; 6, *H. hebe* from Stn. 15. Solid, open, and stippled bars represent female, male, and unsexed nymphs respectively; arrows indicate presence of emerging adults.

Heptagenia flavescens (Walsh)
Like *H. diabasia,* this species is most common in southwestern Wisconsin in larger streams where the nymphs live under large rocks. Specimens were found only occasionally in medium sized streams (Eau Galle River) or in large rivers (St. Croix, Wisconsin, Sugar Rivers), only a few being obtained on each visit. The most complete series came from the Sugar River (Green Co., Station 20) but too few were found to construct a meaningful life cycle. Based on adult captures at the Sugar River and at lights in Madison, they emerge in June. A mature nymph ready to emerge was also taken in late August. Two generations a year is a possibility, but further collecting, especially in deep areas of rivers such as the Wisconsin River, is needed for confirmation.

Heptagenia hebe McDunnough
H. hebe is the most ubiquitous of Wisconsin's *Heptagenia.* Found on rocky substrates from gravel to boulders, it occurs in a wide range of current speeds but appears more abundant in moderate riffles than in either very fast riffles or quiet water. The life cycle (Fig. 6) in the Mullet River (Station 15) follows a univoltine pattern with an extended emergence (June to August and early September). The presence of small nymphs in both fall and spring suggests that hatching occurs in both seasons. The many small nymphs present throughout the summer may have been part of the spring brood prevented from maturing by high water temperatures. In Otter Creek, Sauk Co. (Station 16), a colder stream, fewer small nymphs were found in summer samples.

Heptagenia lucidipennis (Clemens)
This species is unusual among Wisconsin heptageniids in that all nymphs apparently overwinter as eggs. The first small nymphs appeared in June at the Sugar River (Station 19) (Fig. 4). Growth was rapid and adults appeared in July and early August. The nymphs lived on pebbles and cobble in slower currents. In the Little Jump River (Station 10), the life cycle was similar to the Sugar River population, except that emergence occurred in late June and early July. Nymphs about to emerge were found at the water's edge while immature nymphs occurred in deeper water. Since the Sugar River is south of the Little Jump River, Sugar River adults would normally be expected to emerge earlier.

The scattered records of this species in Wisconsin are due partly to confusion in earlier surveys between nymphs of this species and those of *H. hebe.* A short life cycle makes *H. lucidipennis* an easy species to miss in monthly or irregular surveys.

Heptagenia pulla (Clemens)
In Bayfield Co. this species commonly occurs in streams running through sandstone formations in old lake basin areas. Nymphs were found under cobble and among pebbles. This species has also been found in Green Bay and Lake Superior.

Not enough specimens were found to classify the life cycle. Nymphs with black wingpads occurred in late May, June and late July at the White River (Station 1). This could represent either two generations or one extended emergence period. Ide (1935) found two flight periods for *H. pulla* at some sites on a river, while at other places on the same river there was only one flight period. He concluded that temperature was responsible for the differences.

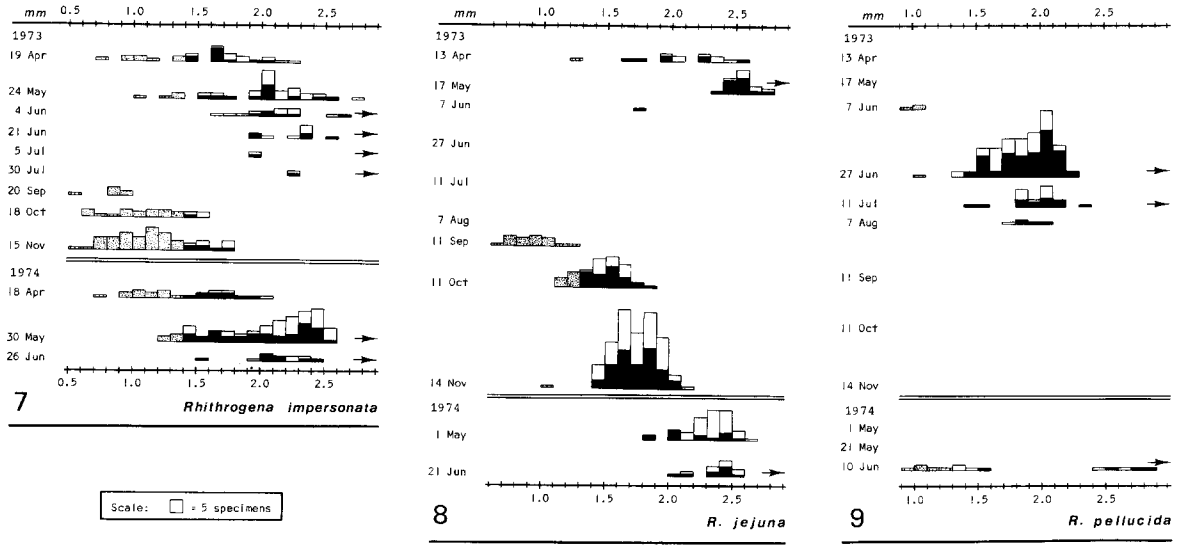
Pseudiron McDunnough
This genus is known in Wisconsin only from two nymphal exuviae collected on July 1, 1976 from the Wisconsin River (Columbia Co.). The species, probably *P. centralis* McD., occurs in a large, deep section of the Wisconsin River. Members of this genus are predaceous (Edmunds, Jensen & Berner, 1976).

Rhithrogena Eaton
We have found these nymphs in large numbers only in clean swift water with substrate of smooth rounded pebbles less than 7.5 cm in diameter. Despite the enlarged gills, the nymphs are active and, when disturbed, move quickly to cover. The food consists of approximately three-fourths detritus and one-fourth diatoms (Shapas and Hilsenhoff, 1976).

Rhithrogena impersonata (McDunnough)
This species includes both typical *R. impersonata* and *R. i. sanguinea* which we have recently synonymized (Flowers & Hilsenhoff, 1976).

Both forms hatched in September (Fig. 7), grew through the fall and winter, and emerged the following spring, beginning in late May or June and continuing through July.

Rhithrogena jejuna Eaton
The eggs hatched in September, nymphs grew rapidly through the winter and adults emerged the following May (Fig. 8). In the Pine River (Station 5), *R. jejuna* was abun-



Figs. 7-9. Life cycles of *Rhithrogena* as represented by width of nymphal head capsules: 7, *R. impersonata* from Stn. 2; 8, *R. jejuna* from Stn. 5; 9, *R. pellucida* from Stn. 5. Solid, open, and stippled bars represent female, male, and unsexed nymphs respectively; arrows indicate presence of emerging adults.

dant in a swift shallow riffle but not in deeper water, although the gravel substrate was similar.

Rhithrogena pellucida Daggy

Like *Heptagenia lucidipennis,* this species apparently spends the winter in the egg stage. Nymphs appeared in June. Growth was very rapid with emergence taking place at the end of June. By early August, nymphs disappeared from the stream (Fig. 9). Although *R. pellucida* shared the same riffle with *R. jejuna* in the Pine River, there was no temporal overlap and hence no competition.

R. pellucida has the widest range of any species of *Rhithrogena* in Wisconsin. It has been found as far south as the Mecan River (Station 14) where occasional specimens have been collected from pebble substrate. Here, mature nymphs have been found as late as August. Evidently, *R. pellucida* can tolerate higher temperatures than other Wisconsin *Rhithrogena.*

Rhithrogena undulata (Banks)

This species was not recognized in time to make a detailed life history study. Adults emerge in early June; presumably the rest of the life cycle resembles that of *R. impersonata.*

Spinadis sp.

Of the five nymphs found to date, one, collected from the Wisconsin River (Station 17) on June 26, 1974 was a

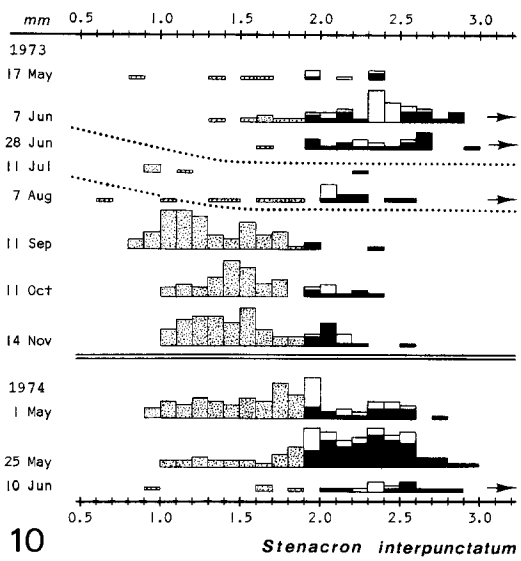


Fig. 10. Life cycle of *Stenacron interpunctatum* from Stn. 12 as represented by width of nymphal head capsules. Solid, open, and stippled bars represent female, male, and unsexed nymphs respectively; arrows indicate presence of emerging adults; dotted lines indicate possible second generation. Scale as in Figs. 2-6.

female about to emerge. Gut analysis of one specimen revealed several chironomid head capsules. The mouthparts of *Spinadis* differ markedly from detritus gathering mouthparts of other Heptageniidae. This species, along with *Anepeorus* and *Pseudiron,* is one of the few predaceous Heptageniidae.

Stenacron interpunctatum (Say)
This species may have separate flight periods in the Little Suamico River (Station 12) (Fig. 10). Adults were present in June and August. The nymphs maturing in August were distinctly smaller than those maturing in June. It is possible that the August nymphs were offspring of the June emerging adults. Samples from the Mullet River (Station 15) contained both mature and tiny nymphs all through the summer. This is probably due to eggs hatching in both fall and spring. There was no evidence of separate flight periods at this river. Although nymphs were very common in Mullet River in 1973, very few were found in the spring of 1974. The reason for this is unknown.

Nymphs were more abundant in slower currents in the Mullet River while in the Pecatonica River (Station 21), they were abundant under rocks in a slough before the slough dried up. Nymphs feed on detritus (Shapas & Hilsenhoff, 1976). *Stenacron interpunctatum* occurs in great numbers in small eutrophic streams in southern Wisconsin where it is sometimes the only heptageniid to be found. Among heptageniids it seems to have an unusually high tolerance for silty environments and slow currents; it also occurs in lakes (Wodsedalek, 1912). Adults are attracted to light.

Stenonema Traver
Nymphs of some species, along with those of *Stenacron,* appear better able to tolerate eutrophic conditions than other heptageniids. The diet of six species was analyzed by Shapas & Hilsenhoff (1976), who found 70-100% of gut contents to be detritus with the remainder diatoms. Variations in amounts of detritus reflect conditions of individual streams rather than species preferences.

Stenonema bipunctatum (McDunnough)
The life cycle in the Pecatonica River (Station 21) (Fig. 11) shows small nymphs appearing in September through November. A few were also found the following spring. Fall hatching nymphs grew rapidly, some achieving most of their growth by the time ice formed. No adults or nymphs with black wingpads were collected, but samples from the St. Croix River (Station 4) showed that emergence apparently began in May and lasted into July.

The species is found in large rivers and localities with abundant rock substrate.

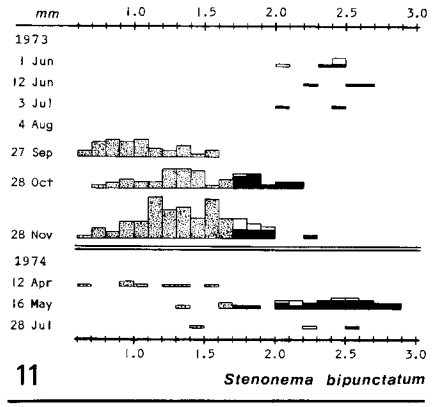
Stenonema exiguum Traver
This species has a growth pattern similar to *S. bipunctatum.* In Big Roche a Cri (Station 13), eggs hatched in September through November and rapid growth occurred until winter. Although mature nymphs were not found until August, it is probable that some emerged earlier. At Otter Creek (Iowa Co.) (Station 18) adults of this species emerged in June. This species is most common in sand-bottomed streams with limited areas of solid substrate, and moderately abundant in cobble bottomed streams and rivers of northwest Wisconsin.

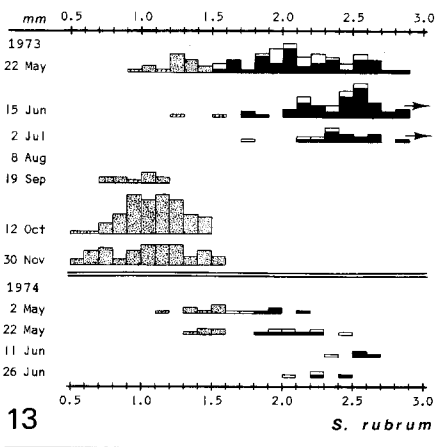
Stenonema fuscum (Clemens)
This is the most common species of *Stenonema* and, after *Stenacron,* the second most common heptageniid in Wisconsin. However, it is less common in the southwestern quarter than elsewhere in the state. In the Mullet River (Station 15) adults flew in June and early July, eggs hatched from July through November and growth proceeded rapidly through fall (Fig. 12). By winter many nymphs had nearly finished growing although some apparently overwinter while small. Small nymphs were more common in a fast riffle while larger nymphs were more numerous in a pool directly upstream. As in the case of *Stenacron* at this station, there was a drastic reduction in numbers of nymphs during the winter of 1973. The life cycle was also studied in the Little Saumico River (Station 12) where the pattern was similar, although adult emergence was over by the end of June.

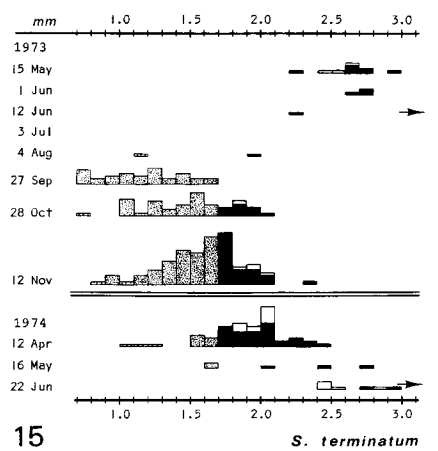
Stenonema integrum (McDunnough)
This species is an inhabitant of large rivers. Apparently, the nymphs spend most of their lives in deep water. In the Wisconsin River, only occasional nymphs were collected until late June when large numbers of mature specimens ready to emerge suddenly appeared at the water's edge.

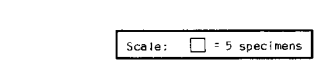
Stenonema mediopunctatum (McDunnough)
Although *S. mediopunctatum* occurs throughout Wisconsin, it appears to be most common in the southern and western counties.

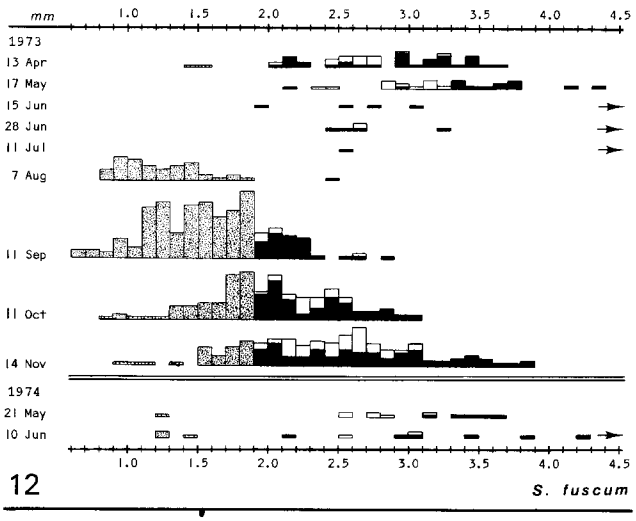
The life cycle in the Pecatonica River (Station 21) (Fig. 14) was somewhat similar to that of *S. fuscum.* Eggs hatched from September to November and growth for

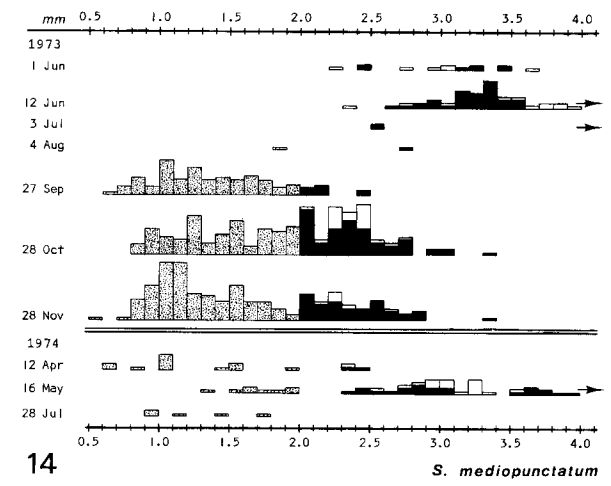


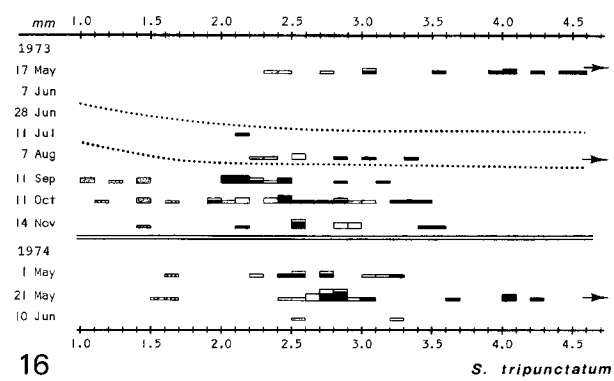












Figs. 11-16. Life cycles of *Stenonema* as represented by width of nymphal head capsules: 11, *S. bipunctatum* from Stn. 21; 12, *S. fuscum* from Stn. 15; 13, *S. rubrum* from Stn. 14; 14, *S. mediopunctatum* from Stn. 21; 15, *S. terminatum* from Stn. 18; 16, *S. tripunctatum* from Stn. 12 (dotted lines indicate second generation). Solid, open, and stippled bars represent female, male, and unsexed nymphs respectively; arrows indicate presence of emerging adults.

many proceeded almost to completion before winter freezing. The presence of small nymphs in April 1974 indicates the late hatching nymphs may have overwintered as eggs. Emergence began in June and lasted until early August. The life cycle was also studied at the Mullet River (Station 15) where the pattern was similar with adults emerging in June and July. Small nymphs were more common in fast water, larger nymphs in slower current.

Stenonema pulchellum (Walsh)
Although a series of nymphs adequate for life cycle study was not obtained, collection records indicate that this species has a life cycle similar to *S. rubrum*. Emergence took place in June in both northern and southern Wisconsin.

Stenonema rubrum (McDunnough)
As with other univoltine species, small nymphs appeared in late summer, growth took place throughout fall and winter, and adults emerged in June and July in the Mecan River (Station 14) (Fig. 13) and the Mullet River (Station 15). Nymphs were very common on submerged logs.

S. rubrum is found in the northern two-thirds of Wisconsin in streams that have large areas of rock substrate.

Stenonema terminatum (Walsh)
This species is also univoltine (Fig. 15). Newly hatched nymphs appeared in September, growth took place through the fall and winter, and adults emerged the following June. An emergence was observed at Otter Creek (Station 18) in late June at dusk. Subimagos emerged from nymphs floating at the surface and, when free of the exuviae, flew straight up until lost to view. Like *Heptagenia diabasia* and *Stenonema exiguum, S. terminatum* is primarily a large river and sand-bottom stream dweller. This accounts for its almost complete confinement to southwestern Wisconsin.

Stenonema tripunctatum (Banks)
This species is bivoltine under favorable conditions (Fig. 16). The first emergence at the Little Suamico River was in May. Small nymphs appeared in July and a second emergence took place in early August. The mature nymphs of the summer generation were much smaller than those of the spring generation. In September, nymphs ranging from very tiny to large were present. Growth occurred up to winter, resuming the following May. The bivoltine cycle hypothesized here differs from the univoltine cycle reported by Clemens (1913) for Georgian Bay *S. tripunctatum* and by Lyman (1955) for Michigan. Ide (1935) reported it to be bivoltine in some Canadian streams. Unfortunately, no other populations could be regularly sampled to see if the situation in the little Suamico River was typical for Wisconsin populations.

In Wisconsin, this species is most commonly found in lakes, including the Great Lakes. When it occurs in streams, it shows a definite preference for slower currents. Apparently very tolerant of pollution and eutrophic stream conditions, it seems to avoid clean streams. In Otter Creek (Sauk Co.) it was not found at Station 16 but occurred downstream where there is agricultural run-off. It also occurred in the East Branch of Honey Creek, a highly eutrophic stream two miles west of Otter Creek, flowing parallel to it and similar in size and geology.

This species is apparently extinct in its type locality, the city of Milwaukee.

Discussion

Known distributions of Heptageniidae in Wisconsin have been previously published elsewhere (Flowers & Hilsenhoff, 1975). Species distribution appears highly correlated with distributions of certain stream habitats. *Epeorus vitreus, Heptagenia hebe* and *Stenonema rubrum* occur in clean streams with abundant rock substrates. Since such streams are widespread in northern Wisconsin but rare in southern counties where there is extensive eutrophication from agricultural run-off, these three species have a predominantly northern distribution. *Heptagenia diabasia* and *Stenonema terminatum* are abundant only in sand-bottomed streams with limited solid substrate, typical of the 'driftless' area in southwestern Wisconsin (see Fig. 1). *Stenonema exiguum,* although more widespread, is also most common in this habitat.

Heptagenia flavescens, Pseudiron sp., *Spinadis* sp., and *Stenonema integrum* are apparently restricted to deeper streams, *Rhithrogena* spp. are restricted to shallow pebble riffles, *Stenonema tripunctatum* is primarily a lake species, and *Arthroplea bipunctata* is found in temporary ponds. The distribution of these species is dependant on the occurrence of their restricted habitats. In some cases, a systematic search for these species will probably extend their known ranges.

The widespread distribution of *Stenacron interpunctatum, Stenonema fuscum,* and *S. mediopunctatum* reflects their tolerance of a wide range of environmental conditions.

A variety of life cycles occur within the Heptageniidae of Wisconsin. The fauna includes univoltine and bivoltine species and species with emergence and growth patterns that make it difficult to identify separate generations. Univoltine species can be divided into 'winter' species (eggs hatching within one month and nymphal growth occurring in fall and often winter), 'summer' species (eggs or early instar larvae diapausing through winter with nymphal growth occurring the following spring), and those species with two broods or with extended emergence periods due to eggs hatching both in the fall and in the following spring. The bivoltine species have spring and summer generations. Table 3 (highly modified from Landa, 1968) lists the species exhibiting each of these life cycles.

Most Heptageniidae in Wisconsin are 'winter' species. Their period of maximum growth occurs in fall and winter when fallen leaves are abundant and in spring when algae and diatom growth is at a maximum. Under these conditions, interspecific competition for food is reduced. The three 'summer' species *(Arthroplea bipunctata, Heptagenia lucidipennis, Rhithrogena pellucida)* could undergo diapause as either eggs or very tiny nymphs; laboratory rearing will be necessary to determine which. *Rhithrogena pellucida* and *Heptagenia lucidipennis* gain the advantage of temporal separation from other heptageniids (and many other insects) occupying the same stream habitat, while *Arthroplea* can exploit vernal ponds, an environment unoccupied by other heptageniids.

Table 3. Developmental cycles of Wisconsin Heptageniidae.

Univoltine species	
"Winter species"; eggs hatch about one month after oviposition, nymphs grow in fall, winter and the following spring.	
Epeorus vitreus	*Stenonema exiguum*
Heptagenia flavescens	*S. fuscum*
Rhithrogena impersonata	*S. integrum*
R. jejuna	*S. mediopunctatum*
R. undulata	*S. pulchellum*
Spinadis sp.	*S. rubrum*
Stenonema bipunctatum	*S. terminatum*
"Summer species"; eggs or early instar nymphs diapause through winter until following spring.	
Arthroplea bipunctata	*Rhithrogena pellucida*
Heptagenia lucidipennis	
Species with eggs hatching both in fall and spring, resulting in extended adult flight periods.	
Heptagenia diabasia	*Stenacron interpunctatum*
H. hebe	
Bivoltine species	
Species with a winter generation as in the "winter species," followed by a short summer generation.	
Heptagenia pulla (?)	*Stenonema tripunctatum*
Stenacron interpunctatum	

Only *Stenonema tripunctatum* in the Little Suamico River showed a clear bivoltine life cycle. Lyman (1955) found this same species in Michigan to be univoltine with three staggered broods. Evidently, local conditions play an important role in determining the type of life cycle of *S. tripunctatum.*

The life cycles of *Stenacron interpunctatum* and *Heptagenia hebe* are difficult to classify. Both vary from stream to stream and probably depend on water temperatures and other environmental conditions. This variability is consistent with findings of Ide (1935) who showed that a species could have different life cycles in different areas of the same stream. In the Little Saumico River, the warmest stream studied, *Stenacron interpunctatum* is probably bivoltine while in colder streams the same species is univoltine but with overlapping broods (hence its appearance in two categories in Table 3) *Heptagenia hebe* and *H. diabasia* apparently have overlapping broods. In the case of *H. hebe,* the population in the warmest stream (Mullet River) had a higher proportion of nymphs hatching in spring than did other populations. In addition, many of these spring-hatching nymphs apparently never grew to maturity. This suggests that there is a temperature threshold above which development does not occur. The generally northern distribution of *H. hebe* is further evidence for this.

Stenonema bipunctatum, S. fuscum and *S. mediopunctatum* also show evidence of nymphs overwintering as eggs or as early instars. However, such nymphs make up only a small fraction of the total populations and we have therefore included these species in the 'winter' category.

Hynes (1961) and Landa (1968) have proposed classifications of life cycles of European mayflies. Landa's classification has been used by Clifford, Robertson & Zelt (1973) to classify life cycles of some Canadian mayflies. However, a difficulty with any life cycle classification scheme is that certain mayfly species will fall into more than one category depending on environmental conditions. We have found that *Stenacron interpunctatum* has a variable life cycle within Wisconsin and *Stenonema tripunctatum* is bivoltine in Wisconsin and apparently univoltine in Michigan. Clifford *et al.* (1973) found similar variability in the life cycle of *Baetis tricaudatus.* This illustrates the importance of studying a species at more than

one locality. As our knowledge of mayflies increases, it is probable that more species will be found to have life cycles that can change according to local conditions. Life cycle classifications are likely to have most value when used to compare local populations. On the other hand, it is risky to classify species on the basis of life cycles known from one or a few areas.

Nymphs of most Heptageniidae in Wisconsin are detritivores feeding on a mixture of algae, diatoms and dead vegetable matter which they scrape off rocks or submerged pieces of wood. (Shapas & Hilsenhoff, 1976). Stomach contents of 30 Plecoptera and Trichoptera found by Shapas & Hilsenoff to be predaceous were examined. No identifiable fragments of Heptageniidae were found, although many fragments of caddisflies and other mayflies were present. This suggests that in Wisconsin, Heptageniidae are not a major food source for carnivorous insects.

Heptageniid nymphs are often important and sometimes dominant components of aquatic insect faunas in streams. Percentage of heptageniids and other groups of insects in 13 of the stations sampled during fall or spring months, are given in Table 4. If these samples had been taken in mid-summer, Heptageniidae would appear less numerous, as most are in the adult or egg stages at this time. Within a stream the largest rocks seem to shelter the most nymphs, supporting Hughes' conclusion that mayfly nymphs actively seek out the largest hiding place in their field of vision (Hughes, 1966). Pieces of wood seem to be especially attractive to may *Stenonema* and *Heptagenia.*

Heptageniids of sand-bottomed streams *(Heptagenia diabasia, Stenonema exiguum, S. terminatum)* cling to submerged logs, brush and man-made substrates. These species are also found in streams with extensive rock substrate, but never in the great numbers typical of their populations in the sand streams. This suggests that they can exploit the sand stream habitat, but are at a competitive disadvantage in other streams. *Stenonema exiguum* and *S. rubrum* in particular appear to have mutually exclusive ranges. At Big Roche a Cri Creek in Adams Co., a sand stream, *S. exiguum* predominates and *S. rubrum* is rare while a few miles away at the Mecan River, a rocky stream, the reverse occurs. These two species occur together in numbers only in large rivers where possible habitats are numerous and diverse.

Stenonema and *Stenacron* are both found in slower currents not tolerated by other genera (except pond-dwelling *Arthroplea*). We observed that both these genera used their gills to generate water currents along the body, while *Heptagenia* can only flick all their gills in unison and *Rhithrogena* and *Epeorus* cannot use their gills at all for water circulation.

Adult Heptageniidae were difficult to collect. Apparently, the subimago flies into the highest available trees immediately after emerging. Adults were collected at only a few stations, those in cleared areas with only a few trees near the water. Most adults were beaten from vegetation 4-6 m high. None were found in low vegetation.

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Table 4. Percentage composition of insect fauna at selected stations. D = deep riffle; S = shallow riffle; P = pool. Collections at Stations 5 and 18 were made in May 1974; all other collections were made in November 1973.

Order \ Station	1	2	3	5 S	5 D	10 S	10 P	11	13	14	15 S	15 P	16	18	19	21
Ephemeroptera - all	46.6	54.4	54.0	23.8	33.6	48.8	81.3	59.0	40.9	69.4	58.8	90.6	50.3	36.9	4.1	70.1
Heptageniidae	44.0	14.8	13.0	7.2	3.1	13.5	29.1	51.0	20.6	7.8	58.8	90.0	12.9	31.8	1.5	67.0
Coleoptera		.2	7.0	13.6	21.2	3.8	1.7		1.6	2.5	5.3	4.7	2.6	2.3	1.2	2.6
Diptera	3.4	27.7	7.0	16.5	24.9	7.2	6.7	11.0	4.4	3.4	4.6	1.8	1.9	7.9	25.3	22.7
Neuroptera				.1			.5									
Odonata				1.4	1.0		.2		.8							.2
Plecoptera	31.0	13.0		12.5	10.9	37.4	7.7	24.0	9.1	3.6	4.3		31.0	23.3		2.2
Trichoptera	19.0	4.6	32.0	31.9	10.4	2.8	1.9	3.0	43.2	21.1	27.0	2.9	14.2	29.5	69.4	2.2
Hemiptera								3.0								

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Summary

1. Nineteen species of Wisconsin Heptageniidae were found to have univoltine life cycles while two and possibly one other species have bivoltine cycles.

2. Of the univoltine species, three *(Arthroplea bipunctata, Heptagenia lucidipennis, Rhithrogena pellucida)* pass the winter as eggs or very small nymphs and develop during spring or early summer. Other univoltine species develop in fall, winter and early spring.

3. *Heptagenia diabasia, Heptagenia hebe* and *Stenacron interpunctatum* have more than one univoltine brood since part of the eggs hatch in fall and the rest hatch the following spring.

4. *Stenacron interpunctatum, Stenonema tripunctatum* and possibly *Heptagenia pulla* are bivoltine, at least in some Wisconsin streams. These species can also be univoltine, depending on local conditions.

5. Except for *Arthroplea bipunctata,* which inhabits temporary ponds, *Heptagenia pulla* and *Stenacron interpunctatum,* which are occasionally found in large lakes, and *Stenonema tripunctatum,* which is usually found in lakes and ponds, heptageniid nymphs require running water habitats. Current is an important factor in the distribution of a species in Wisconsin streams. In general, fast riffle areas are required by *Epeorus* and *Rhithrogena,* moderate to fast riffles are inhabited by *Heptagenia* and some *Stenonema* and slow currents are inhabited by other *Stenonema* and *Stenacron. Heptagenia flavescens, Spinadis, Pseudiron,* and *Stenonema integrum* occur in deep water.

6. Availability of solid substrate also affects heptageniid distribution. While most species are found only in areas with abundant rocks, *Heptagenia diabasia, Stenonema exiguum* and *Stenonema terminatum* occur in greatest numbers in sand-bottomed streams with limited amounts of wood or debris for substrate.

7. Although Heptageniidae are frequently abundant in streams, they do not seem to be an important source of food for carnivorous insects.

8. Based on scattered observations, subimagos emerge at dusk from the water's surface and immediately seek the treetops. Adults live two to four days.

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