OBSERVATIONS ON THE BIOLOGY OF TRICORYTHODES ATRATUS MCDUNNOUGH (EPHEMEROPTERA: TRICORYTHIDAE)[1]

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ABSTRACT—As the ecology of the nymphal stages, the behavior of the adults, and the life history of the mayfly genus *Tricorythodes* are poorly known, an intensive study of *T. atratus* was undertaken in northern Minnesota during the summers of 1969 and 1971. Analyses were made of populations of nymphs by dividing them into age groups to determine where each occurs in the streams studied. Stomach contents revealed that nymphs feed primarily on plant materials. Drift-net collections for 24-hour periods were made to provide information about growth, emergence, and oviposition. Frequent observations of emergence and swarming were made. Subimagoes were seen emerging from the nymphal stage underwater, swimming to some emergent object, climbing from the water, and expanding their wings. Emergence of subimagoes appears to be correlated with low light intensity. Swarming of adults occurs soon after daybreak and may continue until mid-morning. Eggs begin hatching in early June, nymphs develop in about five weeks and adults emerge in mid-July. A second peak emergence occurs in late August with occasional individuals appearing as adults into November. The species probably overwinters in the egg stage as mid-winter collections from the streams studied have never produced nymphs.

The mayfly genus *Tricorythodes* has been studied mainly from a taxonomic viewpoint and consequently little is known about the ecology of the nymphal stage, the behavior of the adult, or its life history (Allen, 1967; Berner, 1950). During the summers of the 1969 and 1971 an opportunity to carry out intensive observations made it possible for us to add significant details to our understanding of one species, *T. atratus* McDunnough.

Our study was conducted in Minnesota at the Headwaters of the Mississippi River, Itasca State Park, Clearwater County, and at Birch Creek, near Lake George, Hubbard County, from June through August in each of the two years. We had intended that the entire study be carried out at the "Headwaters" but, after the project was well under way, the nymphal population dropped to a very low level and, concurrently, an accident occurred in which a truck was driven into the stream and gasoline and oil were spilled, damaging the stream environment. After some exploration, we found that Birch Creek had

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[1] Support for this study was provided by the Dayton Natural History Fund and the Department of Entomology, Fisheries, and Wildlife, University of Minnesota. This paper is taken from part of the Ph.D. dissertation of R. J. Hall.

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a high *Tricorythodes* population and was easily accessible for study. As all of the adults reared or captured at both streams were *T. atratus* and as the two streams are separated by only a few miles, we are considering jointly many of the observations made at both areas.

Description of Study Areas

The two sites chosen for this study were conveniently located near the University of Minnesota's Biological Station, which served as our headquarters. The first study area, the Headwaters of the Mississippi River, arises as an overflow of Lake Itasca. At its point of origin and in the areas where the study was done, the river is small, only 12–20 feet wide, and shallow with a depth generally ranging up to a maximum of three feet. Birch Creek, the second site, is likewise small and shallow and in the area studied resembles the Mississippi River Headwaters.

In both streams the beds were composed of sand, silt, gravel, and small stones, although in Birch Creek there were large rocks and small boulders scattered throughout the riffle areas studied. Both streams were well shaded with poplar and willow trees as well as spruce and pine. The aquatic plants that dominated in the Mississippi were *Heteranthera dubia* (Jacq.) MacM., *Ranunculus longirostris* Godr., and *Elodea canadensis* Michx., while a fine film of precipitated organic material covered the rocks. The aquatic plants in Birch Creek consisted chiefly of *Cladophora* sp., fully enveloping the rocks, and the aquatic moss *Fontinalis*. The algae growing along the marginal areas of the stream were predominantly *Spirogyra* sp.

Water in both streams was clear, cool, and generally slightly alkaline to neutral.

Methods

Nymphal specimens for study were collected with a six-inch diameter coffee strainer. At the time that specimens were taken, water temperature was also recorded. In addition, nymphs were removed from water-soaked logs by hand picking and brought back to the laboratory for observation. Owing to their large number of molts, it is difficult to distinguish with certainty any particular instar of a mayfly nymph except the last. A system of categorizing the specimens into size groups was established (Table 1) following the method of Lehmkuhl (1969). Large samples from each of the collecting sites were sorted and classified according to the categories below.

To investigate the phenomenon of drift in *T. atratus*, two stationary drift nets were positioned in midstream near the downstream end of riffles. In both streams the widths were approximately 5 m, depths 0.25 m, and surface velocities 0.38 m/s.

The drift nets measured 15 cm by 30 cm at the mouth and were one meter long. They were constructed of Nitex netting with a mesh size of 471 μ and were supported side by side in the streams by means of iron rods. Detailed descriptions of the nets used are given by Waters (1962) and Holt and Waters (1967).

At hourly intervals the nets were removed and replaced by two identical ones. The debris and organisms caught in the nets were rinsed into an enameled pan, concentrated with a sieve, and stored in individual plastic bags (Nasco Whirl-pac) in a 10% formalin solution. Water temperature, air temperature, and light

Table 1. Characteristics used to separate age groups of *T. atratus* nymphs (after Lehmkuhl, 1969)

Group	Characteristics	Stage
I	Gills poorly developed, thread-like or absent	Newly hatched
II	No wingpads; gills more fully developed than nymphs of Group I	Young nymphs
III	Mesothoracic wingpads present but small	Half-grown nymphs
IV	Mesothoracic wingpads fully developed	Mature nymphs
V	Wingpads swollen or blackened	Nymphs ready to transform

intensity (Weston Illumination Meter—model 156 Quartz Filter) were measured and recorded each hour before the nets were replaced. After the collections were made, the organisms and debris were manually separated in the laboratory. Only eggs, nymphs, subimagoes, and adults of *T. atratus* were retained for study.

Ten bottom samples were collected at random every two weeks above the drift nets using a modified Hess bottom sampler (Waters and Knapp, 1961). The substrate and organisms therein were processed as described above for the drift investigations. In addition, during the winter substrate cores were taken to determine whether nymphs could penetrate to much greater depths beneath the water-substrate interface. Immediately after removing the substrate from the sample, a galvanized circular core sampler (diameter of 34.2 cm) with a serrated edge was placed inside the Hess apparatus (diameter of 34.4 cm) and forced down approximately 15 cm into the substrate. Subsequently, the material was removed and also processed as described above.

Discussion

Habitat selection: It is obvious from repeated observations that protection afforded *T. atratus* nymphs by plants is significant and that plants growing in more slowly flowing water provide more effective protection than those in fast moving water. The aquatic plants *Elodea*, *Ranunculus*, and *Cladophora* appear equally attractive to the nymphs. Generally, older nymphs are found in more slowly flowing water in vegetation or sometimes attached to logs in protected places, while the smaller forms occur in more swiftly moving water. Intermediate-sized nymphs seem to be associated more frequently with faster currents. All age groups were represented in the various habitats examined, although minimally in some, such as submerged, water-soaked logs.

Nymphal food: The nymphs of *T. atratus* are primarily herbivorous, as our examination of stomach contents of freshly killed nymphs pro-

Table 2. Analysis of stomach contents of 50 nymphs collected during June and July

Miscellaneous plant tissues: stem, leaf, and epidermis; pine pollen

Filamentous blue-green algae (Cyanophyta): *Oedogonium* sp., *Oscillatoria* sp.

Desmids (Chlorophyta): *Scenedesmus* sp., *Staurastrum* sp.

Diatoms (Chrysophyta): *Cocconeis* sp.,* *Hantzschia* sp., *Navicula* sp., *Pennularia* sp., *Fragilaria* sp., *Nitzschia* sp., *Cymbella* sp., *Gomphonema* sp.*

* Most abundant food material

duced only fragments of plant tissue, filamentous algae, desmids, and diatoms. The results of the analyses are listed in Table 2.

In addition, we attempted to ascertain whether nymphs would develop more rapidly on *Elodea* or *Ranunculus* covered with epiphytes (predominantly diatoms). The nymphs were kept in water which was not aerated but was changed at frequent intervals. Ten partially grown nymphs were placed in each of two jars with the respective plants and after two weeks we found that the nymphs in both situations were of equal size. The epidermis of the *Elodea* had been entirely eaten and all diatoms had been cleaned from the surface of the *Ranunculus*. Apparently the nymphs do equally well on both foods.

Drift: The phenomenon of drift of stream invertebrates has been known for some time but has been investigated intensively only within recent years. Periodicity, reflected in drift rate, has been studied by Tanaka (1960), Waters (1962, 1965), Müller (1963a, b), Elliott (1967a, b), and others. Additionally, Dendy (1944) and other workers have noted that the drift of stream organisms is a constant factor and has considerable ecological significance.

Variations in drift rate have been attributed to natural events, such as increased rate of water flow (Anderson and Lehmkuhl, 1968; Lehmkuhl and Anderson, 1972), and to manipulation of flow by investigators (Minshall and Winger, 1968), both resulting in an increased drift rate. Furthermore, Elliott (1967a) reported that the tenacity of insects could be correlated with stream velocity. He found that thigmotactic response was greatest in faster flowing water, while in slower moving water, the taxis was reversed, with the organisms swimming about freely. Elliott also observed that these freely-moving organisms may exhibit the phenomenon of jostling, a behavioral competition among a number of organisms for a limited area as well as a limited food supply. Weninger (1968) concluded that along with flow velocity the substrate is of great importance in drift activity.

To determine the influence of forces other than stream flow, Holt and Waters (1967) tried artificial lighting during the night hours. Under these conditions, the night-time drift rate decreased indicating that these circadian rhythms appear to be controlled to some extent by exogenous factors. Chaston (1968) has postulated that under normal light illumination the variation in drift-bound organisms is under both exogenous and endogenous controls.

With the exception of Weninger's (1968), Anderson's (1967), Elliott's (1967a, 1968, 1969, and 1971), Lehmkuhl's (1969), and Lehmkuhl and Anderson's (1972) studies, few others have investigated life histories using drift techniques to determine the cycle of a single species from its early stages through the adult. This part of the study of *T. atratus* was undertaken to try to establish a relationship between what is known about the phenomenon of drift and the major phases in the insect's development.

To enable us to recognize eggs of *T. atratus* in drift samples, eggs were taken from females in the act of ovipositing. They were formed in a spherical, greenish cluster under the abdomen and were obtained by touching the females to water in small dishes. The eggs immediately dissociated, settled to the bottom, and adhered. They also attached to any foreign objects in the water.

The eggs are ovate with scales or plates around the outer edge and with numerous small whitish filaments at one end. They measure 0.20 mm. in width and 0.25 mm. in length and range in color from light to dark green. A detailed description and figures of the eggs of this genus are given by Koss (1968).

Eggs were often found in the drift debris (Tables 3 and 4). They never occurred individually but always in clusters ranging in size from 25 to 100 eggs. They adhered to each other by means of the whitish terminal filaments. Bundles of egg masses in the nets were found clinging to filamentous algae or to small pieces of plant epidermis, while many eggs were located inside the remains of the female *T. atratus* thoraxes. Eggs were caught in the nets at various hours of the day and night, a reasonable finding since eggs tend to attach to the aquatic plants and the plants in turn were found in the drift at all hours.

While the eggs were collected at various times throughout the 24-hour period, nymphs of *T. atratus* living in the Mississippi River, however, showed a very distinct periodicity in drift rate, with the peak drift occurring within two hours after sunset (Fig. 1). With the coming of dawn and a consequent increase in light intensity, drift decreased until a minimum rate was reached and remained at that level for the remainder of the daylight hours. A similar pattern of drift was shown by the nymphs of Birch Creek, although fewer organisms were taken.

Table 3. Results of hourly collections of drift-net samples of *Tricorythodes atratus* from the Mississippi River Headwaters. Temperatures given in degrees Centigrade. Collections made on August 16, 1969.

Hour	Temperature		Light intensity foot candles	Total hourly catch						
						Subimagoes		Imagoes		
	Water	Air		Eggs Present	Nymphs	♂	♀	♂	♀	Exuviae
800	22	17	520	—	1	—	—	2	—	—
900	22	19	620	—	—	—	—	2	17	—
1000	22.5	24.5	820	—	1	—	—	—	3	—
1100	23	28	7400	x	1	—	—	—	—	—
1200	24	29	7800	x	2	—	—	—	—	—
1300	24.5	29.5	8400	—	—	—	—	—	—	—
1400	25	29.5	8400	—	1	—	—	—	—	—
1500	26	33	9250	—	1	—	—	—	—	—
1600	26	29	5600	—	—	—	—	—	—	1
1700	26	29	4000	—	1	—	—	—	—	—
1800	24.5	26	3000	x	2	—	—	—	—	—
1900	26	24	1000	x	2	—	—	—	—	—
2000	25	23	280	x	5	—	—	—	—	—
2100	26	20	2	x	10	—	—	—	—	—
2200	26	19	0	x	100	8	8	—	—	1
2300	26	17	0	—	115	5	—	—	—	2
2400	25.5	18	0	x	94	4	—	—	—	—
100	25	20.5	0	x	84	1	—	—	—	3
200	25	20	0	x	71	—	—	—	—	—
300	25	20	0	—	45	—	1	—	—	—
400	25	19.5	0	—	42	—	1	—	—	—
500	24.5	19.5	0	x	31	—	—	1	—	—
600	24.5	20	0.5	—	5	—	24	—	6	5
700	24.5	23	400	—	1	—	—	2	11	1

To determine whether nocturnal activity is associated with stage of development, categories established by Lehmkuhl (1969) were used to separate the nymphs into various size-class/age groups (Table 1). All nymphs collected were categorized according to these criteria. Nymphs fitting the characterizations of Group II were those most frequently taken from the Mississippi River drift, while those from Birch Creek were generally older, falling into Groups III, IV, and V (Fig. 2). Anderson and Lehmkuhl (1968) concluded that mature nymphs could avoid downstream displacement better than smaller ones because of their better swimming abilities. If this is a correct conclusion, one would expect to obtain more of the Group II nymphs in the drift. The Mississippi collection, but not that from Birch Creek corroborated this point.

Table 4. Results of hourly collections of drift-net samples of *Tricorythodes atratus* from Birch Creek. Temperatures given in degrees Centigrade. Collections made on August 22, 1969.

	Temperature				Total hourly catch					
			Light intensity foot candles	Eggs Present		Subimagoes		Imagoes		
Hour	Water	Air			Nymphs	♂	♀	♂	♀	Exuviae
800	20	15.5	720	—	—	—	—	1	3	—
900	20.5	20	2600	x	1	—	—	3	43	3
1000	21.5	26	4200	x	1	—	—	21	11	—
1100	22	24	6800	—	1	—	—	2	3	—
1200	23.5	25	7300	x	1	—	—	4	1	—
1300	24.5	26.5	8000	—	1	—	—	—	—	—
1400	25	29	8400	—	—	—	—	2	—	1
1500	26	26	7400	x	1	—	—	—	—	—
1600	25	31.5	6000	—	—	—	—	—	—	—
1700	26	27	4400	—	—	—	—	—	—	—
1800	26	26.5	2700	—	—	—	—	—	—	—
1900	25	25.5	700	—	1	—	—	—	—	—
2000	24	19.5	0	—	—	—	—	—	—	—
2100	23	15.5	0	—	1	1	—	—	—	—
2200	22	15	0	—	8	1	—	—	—	—
2300	22	14.5	0	—	11	1	—	—	—	—
2400	21.5	13	0	—	3	1	—	—	—	1
100	20.5	11.5	0	—	8	2	—	—	—	—
200	20.5	11.5	0	—	7	—	—	—	—	1
300	20	10	0	—	4	—	—	—	—	—
400	20	10	0	—	2	—	—	—	—	—
500	20	9	0	—	3	1	—	—	—	—
600	19	9	0.2	—	—	—	2	—	—	1
700	19	9	220	—	—	—	—	—	—	—

Waters (1965) suggested that organisms leave the benthic regions and appear in the drift for only a short time before returning to the bottom. The differential positioning of the nets in the streams, then, could account for some of the differences in the total numbers of nymphs and their size classes represented in the samples from each stream. Müller's (1954) "Colonization Cycle" (i.e., migration of adults upstream, oviposition at the limits of their habitat range, and subsequent downstream drift of larvae) might also help explain the discrepancies in collections from the two streams, for it again involves the positioning of the nets. If the nets were placed close to the area of oviposition, eggs and young nymphs might be expected to be predominant in the drift, as well as a large number of female imagoes, for generally they do not return to flight after egg deposition. If the

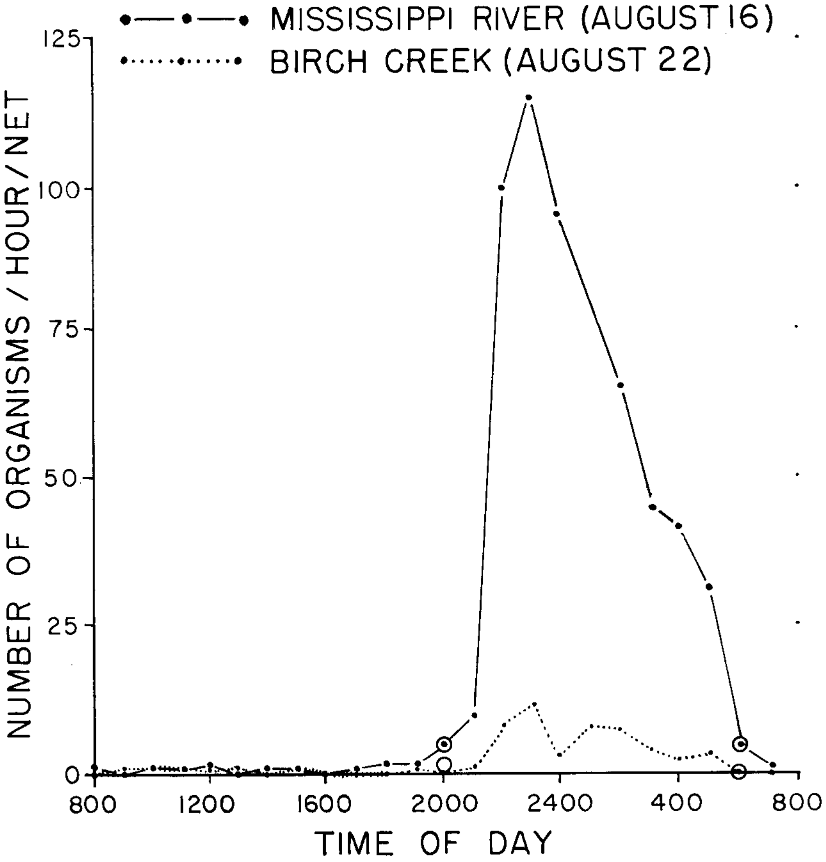

Fig. 1. Drift rate of *T. atratus* nymphs based on number of organisms collected per hour per net over a 24-hour period. Closed circles indicate sunrise and sunset.

nets were relatively distant from the oviposition area, the older age groups of nymphs could be more prevalent in the drift collections.

Another factor that should be considered in explaining differences in numbers of nymphs collected at the two sites is the amount of brush hanging over the water, often with many branches extending below the water surface. When such submerged branches were lifted from the water, we observed that many nymphs of *T. atratus* were present on the branches and leaves. Preferential placement of drift nets near such over-hanging vegetation could be a factor that would affect the results when comparing drift samples from different areas.

Data in Tables 3 and 4 support our observations that the female

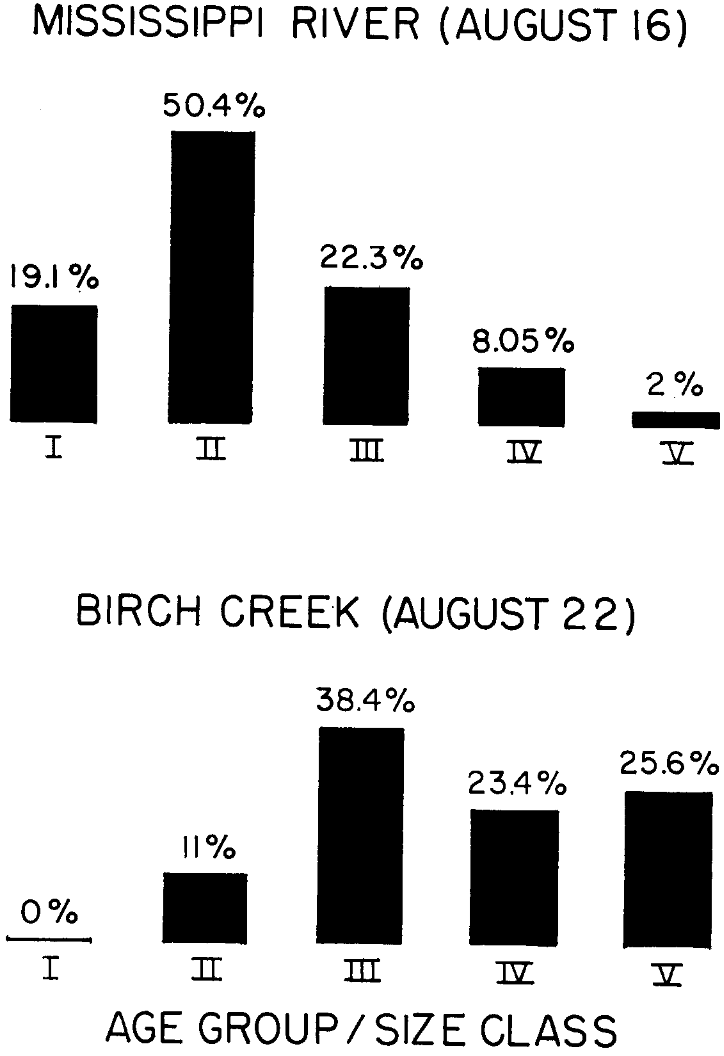

Fig. 2. Size class of *T. atratus* nymphs based on 24-hour drift collections. Bars indicate the percentage of total collection in each size class.

subimagoes emerge in the evening when there is a significant drop in light intensity and begin emerging again in the early hours of the morning when the light intensity just begins to increase (Fig. 3). There is apparently a positive correlation between a low level of light and emergence time of the female subimago. The conclusion that low light intensity and emergence of the female are correlated was con-

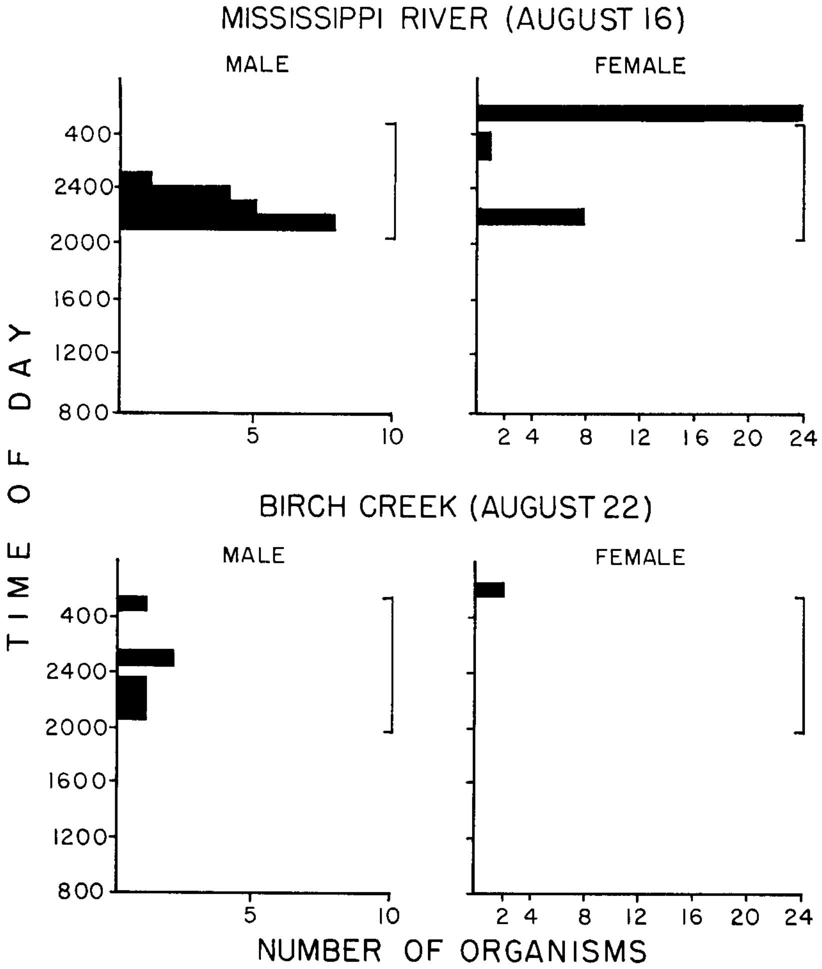

Fig. 3. Number of *T. atratus* subimagoes collected at the time of emergence over a 24-hour period. Bracket to the right of each graph indicates hours when light-meter readings were too low to record.

firmed by our laboratory observations and by field experiments with a light trap. We noted that the females never emerged at times other than when the light intensity was at a low level, and we never observed emergence of this sex after dark.

Our observations that most females oviposited about 9:00 a.m. are confirmed by the data given in Tables 3 and 4; however, it is apparent that the process must have begun as early as 8:00 a.m. and continued to 10:00 a.m. on the dates that 24-hour drift samples were

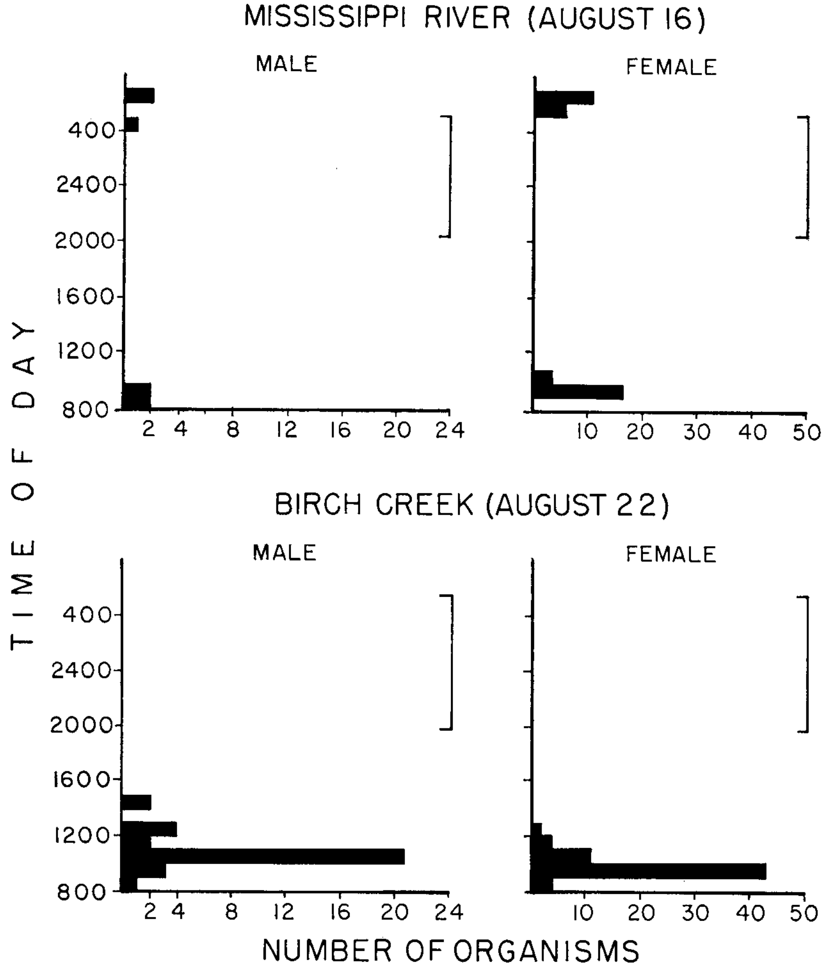

Fig. 4. Number of *T. atratus* imagoes collected in the drift after they returned to the water. Collections were made over a 24-hour period. Bracket to the right of each graph indicates hours when light-meter readings were too low to record.

taken (Fig. 4). We believe, further, that these data are substantiated by the fact that females do not usually return to flight after egg deposition but simply drop onto the water surface, an observation which we have made repeatedly in the field.

Male adults began falling to the water surface at 8:00 a.m. and continued to do so as late in the afternoon as 2:00 p.m., as reflected in the 24-hour drift samples (Fig. 4). The male longevity has also been confirmed by field observations.

Emergence of the subimago and transformation to the adult: Several factors appear to affect the emergence patterns of the females. When the current velocity was high, the subimagoes emerged directly from the stream; however, in the more slowly flowing water, or in the absence of current, the females were seen to climb from the stream and fly to the overhanging branches. When the humidity was high, the subimagoes remained on the trees until rays of sunlight struck them, at which time molting occurred, and the adults would then fly to a height of about 35–50 feet. When the humidity was low, however, they would molt faster, usually within two or three minutes.

The pattern of male emergence observed was similar to that of the female except that the event did not occur until light intensity was so low that our meter gave a zero reading. Males began to appear on the wing at 9:00 p.m. and continued to emerge until 1:00 a.m. A few additional subimagoes emerged between 4:00 and 5:00 a.m. (Fig. 3). With the first signs of dawn, emergence ceased.

Because the molt from nymph to subimago occurs so late in the evening, or in the early hours of the morning, it was difficult to make detailed observations of this event in the field. Consequently, large numbers of Group IV (mature) nymphs were brought to rearing cages in the laboratory. They were kept in white-enameled pans to which small sprigs of *Ranunculus* and blades of grass were added as resting places. The rearing cages were placed in an area where they were exposed to fluctuating outside temperatures.

In mid-July at 9:55 p.m., just at dark, one *Tricorythodes* nymph was observed molting to the subimaginal stage underwater. Rather than being expanded vertically or horizontally, the wings remained folded against the thorax and the subimaginal insect then swam underwater to an emergent blade of grass, crawled up on it until it was free of the water, and remained quiescent. Soon thereafter it opened its wings into the normal position of the subimago. At 10:05 p.m. of the same evening three other nymphs behaved in an identical manner. The four subimagoes were transferred to pint jars and placed on blades of grass. At 4:20 a.m. one subimago transformed, the process taking approximately two minutes. Within 15 minutes the three other mayflies had molted but the time required of exuviation varied slightly. Three of the four imagoes retained the subimaginal exuviae on the caudal filaments for an additional two or three minutes. Subsequent observations, including those conducted in an artificial stream with a sand and gravel substrate, have confirmed the underwater emergence pattern of *Tricorythodes*. Final corroboration of our observations will require intense field study of this phenomenon.

Many additional observations of subimagoes show that exuviation generally requires about one minute. Mississippi River males collected between 10:30 p.m. and 2:00 a.m. molted to the imaginal stage between 4:30 and 5:30 a.m.; those from Birch Creek taken between 9:00 and 10:00 p.m. reached the adult stage between 2:00 and 3:00 a.m. Females, regardless of time of emergence, apparently molt to the imago stage shortly before mating, with some females molting immediately after emerging and others waiting as long as two hours. Molting was observed to occur between 7:45 and 8:30 a.m. in early to mid-August. Although we have no data to support the hypothesis, we believe that molting is controlled in part by humidity, temperature, and time of emergence under natural conditions. That molting does occur at an earlier hour is obvious for we have seen ovipositing females as early as 5:00 a.m., just at dawn, in mid-July.

Mating flights: Male and female *Tricorythodes* show differential flight patterns. Individual females flying over a stream displayed the usual mayfly behavior, progressing in an up-and-down movement as diagramed in Fig. 5. We observed single males flying with a rather different movement—producing more of a gliding up-and-down effect (Fig. 6). As the males assembled into swarms, the flight pattern changed to resemble that of the individual female, perhaps the change serving in part as an attractant to the female.

As the sun rose on July 8 and July 13, we saw large swarms of male *Tricorythodes* 25–30 feet above the Mississippi River. Later, in early to mid-August, we observed males patrolling over the stream at a height of 30–50 feet. At times, we noted thousands of males flying at this height in the jerky, up-and-down pattern described above. The insects seemed to favor tree-top level for their flight, where light was somewhat greater than at lower elevations. The swarms of males moved in unison as though there were a cloud of black spots suspended in the air. Occasionally the swarm would descend sufficiently so that we were able to collect a large number of the males by sweeping a net through it. We took very few females in these sweeps.

We observed females in small groups of three of four flying upstream and directly into the large swarm of males, and while there appeared to be a constant flow of females into the male assemblage, we never observed the actual mating of *T. atratus* with certainty. After the entry of a large number of females into the swarm, the flight continued for another 20–30 minutes after which the individuals began to disperse so that there was no longer a single large swarm. Still the males continued their up-and-down flight at a height of 25–30 feet. After leaving the swarm, the females dropped to stream level to begin oviposition.

On July 8 at 5:00 a.m., just at dawn, and on July 13 at 5:30 a.m., we saw females flying approximately 6–8 feet above the water's surface, patrolling up and down over a limited section of the stream. The flight up- and downstream occurred from one to four times,

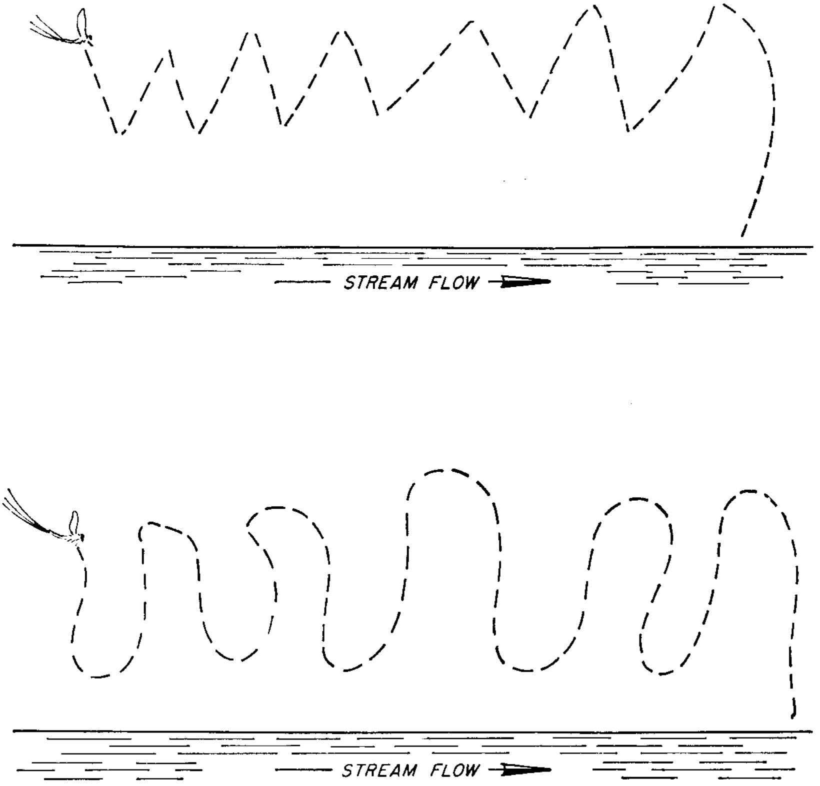

Fig. 5–6. Diagrammatic representation of flight of individual female *T. atratus* imagoes, terminated by dropping onto the water surface. 6, Diagrammatic representation of flight of lone males of *T. atratus* prior to swarming. Following swarming, males drop to the water surface.

suggesting that the females may have been searching for a suitable oviposition site. Once committed, the female descended swiftly to the water, broke through the water surface over clumps of submerged vegetation, apparently oviposited, and then either remained on the water or rarely returned to the air. We observed flights of females only over water, with oviposition generally taking place at the upstream end of a riffle area.

The flights in early to mid-August seemed to begin as early as 6:15–6:30 a.m., with the females leaving the swarming males around 9:30 a.m. After 10:00 a.m. few additional females were seen (Figures 2 and 3; Tables 3 and 4). Our observations of times of swarming are consistent with those of Leonard and Leonard (1962) who reported seeing *T. stygiatus* flying from 4:30–10:00 a.m.

The adult life of *T. atratus* clearly shows that it is but a brief part of the species' entire life history, lasting only nine to ten hours, beginning at dusk and terminating soon after the sun is well above the horizon.

Life cycle: From our study of numerous bottom samples we have observed that the eggs hatch early in June, the nymphs develop for approximately five weeks, and the adults start to emerge in mid-July. There appears to be a second peak emergence in late August with some adults emerging continuously from mid-July to November.

Our study of winter samples leads us to believe that this species overwinters in the egg stage because no nymphs have ever been taken during that time period in drift, bottom, or core samples. Continued emergence from mid-July until November, plus the fact that small nymphs were collected in late summer and fall bottom samples, indicates that this species is multivoltine. Subsequent detailed analysis of extensive benthic and drift sampling should clarify the above observations and will be reported at a later date.

ACKNOWLEDGMENTS

We wish to express our sincere appreciation to Dr. Calvin Fremling, Winona State College, Winona, Minnesota, who gave advice on, and assisted with, some of the initial field observations. We also acknowledge with thanks the help of Dr. Charles Holt, Bemidji State College, Bemidji, Minnesota, who provided most of the drift equipment and Dr. T. F. Waters, Department of Entomology, Fisheries, and Wildlife, University of Minnesota, who also provided some of the equipment and who critically reviewed the manuscript. We are particularly indebted to Marjorie Collings Hall, for assisting in the field work and for reading the manuscript.

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