THE BIOLOGY OF *CALLIBAETIS FLORIDANUS* BANKS (EPHEMEROPTERA: BAETIDAE)[1]

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Although the mayfly genus *Callibaetis* has been known for many years, little exact information is available concerning its life history, ecology, and behavior. We have, therefore, tried to observe one species intensively over a period of approximately 18 months so that a knowledge of its biology could form the basis for further study.

Callibaetis is noteworthy among North American mayflies because of ovoviviparity[2], which was first described by Needham et al. (1935) and confirmed later by Berner (1941) and Edmunds (1945). *Cloeon dipterum*, of Europe, has also been described as being an ovoviviparous species by numerous workers. Although the phenomenon has not been observed in all species of *Callibaetis*, it is likely that the habit is universal for the genus. The same cannot be said for *Cloeon*.

Callibaetis floridanus Banks was selected as the species for this study primarily because of its availability in all parts of Florida where the observations were to be made. The species has been known since 1900, but the nymph and male were not described until 1941. One of us in an earlier study (Berner, 1950) distinguished two forms of the species, one occurring in the more northern part of Florida, the other limited to the southern end of the peninsula. Our present observations are based mostly on the form from the northern part of the state (form B).

METHODS

Collections of nymphs were made by the usual methods; subimagoes were taken from vegetation in the field; and mated females were collected both at a lighted sheet and light traps, but most were obtained from low spider webs at the banks of a pond near Gainesville. Females, caught in the webs, were often found still living, usually with a reddish mass of eggs, already extruded, adhering to their abdomens. The mass was washed into a jar of water and the young hatched immediately on contact with the liquid.

To compare field-reared nymphs with those reared in the laboratory, the newly hatched insects were kept in cages made from parachute silk fastened to a wire frame; the tops of the cages were covered with clear plastic. At the same time that nymphs were placed in the field cages, others were placed, in lots of 15-25, in pans filled with pond water which had been strained through parachute silk to remove predators and competitive forms. Washed vegetation was also added to each pan. Other nymphs from the same batch were treated in still a third way. These were individually isolated in small jars each with a small clump of filamentous

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[2] The term ovoviviparous is used here in the same sense as in the papers by Berner (1941) and Edmunds (1945).

green algae. It was usually very difficult to isolate the nymphs before they had reached the third instar, but as soon as possible after this stage was reached, they were placed in the jars. Water in the jars was replaced twice weekly with freshly strained pond water and a new piece of alga was substituted for the old. The nymphs usually were measured every second night to determine amount of growth and to observe whether molting had occurred.

Swarming of adults was studied with the aid of 7 x 50 binoculars. Few details of the behavior of the subimago or adult could be obtained in the laboratory; therefore, almost all of the behavioral observations on them were made in the field.

Study Areas

Six different areas were selected for study. The chief observations were made at a temporary, fresh-water pond (Fig. 1) located at Stengel Field, a small airport near Gainesville, Florida. The pond receives a large run-off from the airfield and the water level is subject to extreme fluctuations in short periods of time. The pond is also contaminated by a sewage outlet in one small area. During dry weather the sewage does not run into the pond but when the water level rises the ditch carrying the sewage becomes confluent with the pond. The vegetation of this pond is composed chiefly of temporarily submerged, terrestrial plants. Generally the water is shallow and the usual inhabitations of temporary fresh waters soon invade it.

Four ditches adjacent to roads were also selected for study areas as water remains in them most of the time except for unusually long dry spells. These, also, have the usual components of such temporary situa-

Figure 1. Stengel Field pond during a period of high water.

tions. In the east coastal area of Florida the Sebastian Inlet Mosquito Control Impoundment was selected for investigation. This is a shallow (two to six inches) area of approximately ten acres which has only small and widely separated patches of aquatic plants interspersed with black and white mangrove trees. There are large water temperature fluctuations daily; however, the impoundment is permanent and is fed by a sulfur-water spring.

LIFE HISTORY

DEVELOPMENT: The life cycle of *Callibaetis floridanus* is comparatively short and all stages can be found at all times of the year. Mature nymphs have been collected during every month and collections made at any time of the year will produce nymphs of all instars. We also have records of adults for all months of the year in Florida, even as far north as Gainesville. In this study it was found that the length of time required for nymphal development varies with the time of year during which the nymphs are studied. We believe this variation in time of development is primarily due to temperature. The shortest time recorded from oviposition to emergence of the subimago was 27 days (August 19 to September 14), although other nymphs from the same brood and reared under the same conditions took up to 35 days to complete their life history. These results were duplicated both in the laboratory and in the field. During this period water temperature fluctuated between 28 and 32 C. In late October and early November the complete nymphal cycle took approximately 60 to 75 days. At this time the average water temperature ranged from 18 to 20 C. However, in these latter rearings, the nymphs were kept in the laboratory because there was no convenient standing water in the ponds used for the study and it was extremely difficult to obtain gravid female imagoes. The mortality of the nymphs in this later period also seemed to be much higher than that which occurred during the summer.

Needham (1935) stated that the nymphal stage lasts five to six weeks from the laying of the eggs to emergence, however, he gave no data to substantiate his estimate. Dickinson (1948) found mature *Callibaetis floridanus* (form A) nymphs in temporary ponds in the Gainesville area within five to six weeks after the first water appeared in the ponds.

Our observations indicate that *Callibaetis floridanus* nymphs apparently pass through 9 to 11 instars with the most common number being 10 prior to emergence. Taylor and Richards (1963) state "Judging from the number of rings in the Palmen body of an adult mayfly, which Needham et al. state as representing successive molts, the mayfly *Callibaetis* appears to undergo approximately 15 molts." If their estimate is correct, there are 16 instars in the nymphal life of the insect.

Although 235 nymphs were reared and measured, it was difficult to determine the number of molts with certainty. In the early instars the nymphs are of such minute size that it is virtually impossible to find the exuviae to provide conclusive proof of molting. The number of instars was determined by measurement of the living nymphs every other day with an ocular micrometer. Because of the relative size constancy of the head exoskeleton, we selected change in width across the eyes as a criterion of growth. Using this measurement it was usually possible to ascertain size changes in the nymphs. At times, however, very likely due to errors introduced in measuring active, live nymphs, this value seemed to grow smoothly from one size interval to another. Usually there is an easily observable difference in this measurement between instars, but the value does not hold constant. The first two instars are generally rigidly set in size and the nymphs are very similar, but following this stage much variation develops (Table 1).

TABLE 1. VARIATION IN MEASUREMENTS* AS CORRELATED WITH HEAD SIZE OF *Callibaetis floridanus*.**

Instar	Head width	Body Length†	Median filament	Cerci
1	0.13	0.42-0.71	0	0.37-0.67
2	0.17	0.79-1.00	0	1.00-1.08
3	0.21	0.92-1.17	0.29	0.76-1.12
	0.25	1.25-1.50	0.17-0.25	1.17-1.50
	0.29	1.33-1.96	0.13-0.38	0.58-1.66
4	0.33	1.50-1.91	0.25-1.08	1.04-2.00
	0.38	1.83-2.33	0.92-1.50	1.75-2.16
	0.42	1.91-2.41	0.75-1.08	1.75-2.58
5	0.46	1.91-2.66	0.83-1.25	1.91-2.58
	0.50	1.91-2.91	1.08-1.83	2.16-2.75
	0.54	2.33-3.08	1.17-1.83	2.41-2.75
6	0.58	2.50-2.91	1.58-2.16	2.41-2.91
	0.62	2.99-3.24	2.16-2.58	2.83-3.33
	0.67	3.16-3.33	2.50-2.58	3.08-3.41
7	0.71	3.33-3.58	2.41-2.66	3.41-3.54
	0.75	3.49-3.58	2.41-2.58	3.32-3.62
	0.79	3.66-3.74	2.50-2.66	3.66-3.74
8	0.83	2.50-3.00	2.58-1.83	2.50-3.16
9	0.92	3.58-3.83	2.50-2.91	3.62-3.74
	0.93	3.74-4.33	3.04-3.33	4.41-4.58
	1.00	5.16	3.33	4.99
	1.04	6.07-6.36	3.99-4.21	5.91-6.49
	1.08	6.24-7.49	4.08-4.41	6.16-6.66
10	1.21	6.16-7.49	3.99-4.91	5.91-7.24
	1.25	5.41	3.49	5.49
	1.33	8.32	5.41	8.32
	1.37			
	1.41			
	1.45			

* In millimeters.

** 235 specimens measured.

† Excluding antennae and caudal filaments.

On September 14, 1962, a collection of 650 *Callibaetis floridanus* nymphs was made at random from Stengel Field pond. These specimens were immediately preserved for later measurement to attempt to establish a size range for particular instars. That such conclusions as to correlation of size range and instar cannot be drawn is obvious from an examination of Figure 2. The curve is bell-shaped which simply means that the great bulk of the nymphs were in the intermediate-size range. The early instars were too small to be collected in the field and the latter instars were small in number, probably because of the greater natural death rate of older nymphs, predation, and emergence. Further, there are size differences because of sexual dimorphism. The measurement of the head was selected for the study because the changes in abdominal length between instars produces too many inaccuracies to give a reliable indicator of size changes. Additionally, the length of the caudal filaments varies too much to be of any use as a marker for a particular instar.

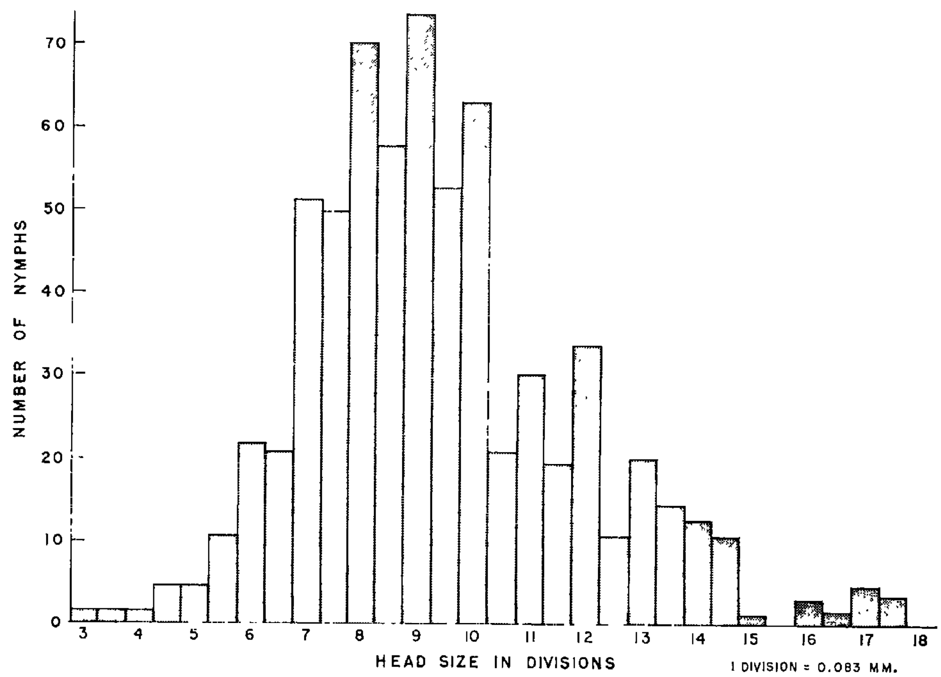

Figure 2. Measurements of head widths of 650 *Callibaetis floridanus* nymphs.

When a series of nymphs of a selected instar is measured there is a considerable amount of variation within that one instar (Table 2). For our evaluation only female nymphs in the last instar were selected. The considerable size variation in body length may have been due, in part, to the fact that the nymphs were collected during different times of the year. From our observations, it seems that the general size of the population varies as a unit. From April to August, specimens taken from the Stengel Field pond were predominantly in the smaller size range. During late August and early September there was a trend toward increase in size, until in late September and October the large size predominated. At that time the pond dried and the study, of necessity, ceased.

TABLE 2. Measurements of Eight Last-Instar, Female Nymphs (all figures in millimeters)

Head Width	Thorax Width	Total Length*
1.00	1.41	5.17
1.04	1.41	6.07
1.04	1.41	6.41
1.08	1.25	6.24
1.08	1.66	6.82
1.25	1.41	5.41
1.33	2.08	8.15
1.33	2.08	8.32

* Excluding antennae and caudal filaments.

Nymphal Stages: The first instar nymph hatches at the moment of contact of the egg with water by breaking the chorion. As the species is ovoviviparous, the eggs are retained in the body of the female for about a week with each female carrying four to five hundred of them.

The newly hatched nymph is quite active. Measurements made of these first instar forms showed a head width of 0.13 mm. and a body length, not including caudal filaments or antennae, varying between 0.52 and 0.71 mm. Cerci measure between 0.37 and 0.67 mm.; the median caudal filament is not present at this stage (Table 1). The head and the thorax are approximately equal in width. Five ocelli are present on the dorsal surface of the head, the two posterior ones will become the compound eyes and the three anterior will remain as the true ocelli. However, in the first instar this division is not obvious. There are no gills.

Transformation of the first to the second instar takes approximately three to four days under summer conditions, where the water temperature ranges between 28 and 32 degrees centigrade. The second instar nymph is quite different from the first instar and more closely resembles the later instars. Now there are six pairs of gills, all single and minute; the eyes have differentiated enough to distinguish the simple from the compound. The width of the head measures 0.17 mm. and the body length varies from 0.79 to 1.00 mm. The median tail has still not developed, but the cerci are between 1.00 and 1.08 mm. in length.

The median caudal filament first appears as a stump at the beginning of the third instar and has a length of 0.17 to 0.29 mm. The cerci measure approximately 0.76 to 1.49 mm. All seven pairs of gills are developed but they are still single and minute. Head width has begun to show a considerable amount of variation and ranges between 0.21 and 0.25 mm. and body length varies between 0.92 and 1.5 mm. The time interval between the second and third and between the third and fourth instars, lasts from two to five days with the most common period being three under summer conditions when the temperature ranges between 28 and 32 degrees C. The time interval is consistent with the suggestion of Taylor and Richards (1963) of an average of two to three days for each instar.

The fourth instar, also lasting from two to five days, cannot be differentiated from the third except in size. The head width lies between 0.29 and 0.38 mm.; body length between 1.33 and 2.33 mm.; cerci are 0.58-2.16 mm.; and the median filament ranges from 1.3 to 1.5 mm.

Beginning with the fifth instar, the gills are all present and are compound as in mature nymphs. From this stage onward the variability becomes so great that development or size change in each instar cannot be characterized. Table 1 is a summary of the comparative measurements of the nymphs as correlated with head width. In it an attempt has been made to indicate instar by head sizes, but it can be seen from this table that there is an overlap in this characteristic so that there are no clear-cut size groups distinguishing the various instars.

The transformation to the subimagal stage occurs in late afternoon or early evening. In an earlier study (Berner, 1950), it was reported that emergence in the field in February took place between 3:45 and 4:00 p. m. Our observations made chiefly between June and September show a peak of emergence between 6:00 and 9:00 p. m. in the field. In the laboratory emergences on August 18 and 19 peaked between 8:15 and 9:15 p.m. (Fig. 3). On those two dates sunset occurred at 7:10 p. m. and the light intensity during the hours of emergence of the insects ranged between 50 and 0 foot candles. Similar observations made on September 9 and 10 showed that the mayflies were emerging between 6:00 and 7:30 p. m. On these latter dates the sun set at approximately 6:45 and light intensity ranged from 100 to 0 foot candles. Further observations both in the field and laboratory confirm these emergence times.

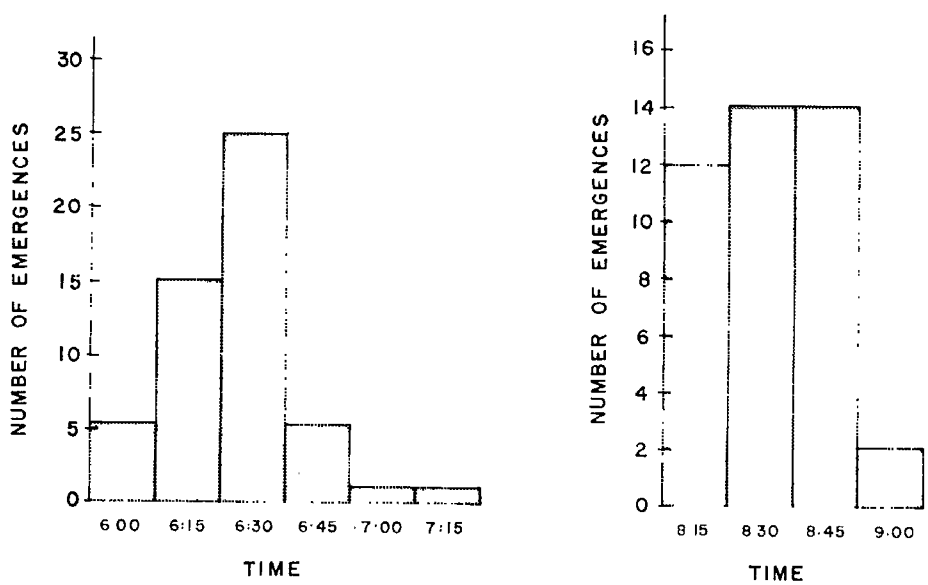

Figure 3. Emergence of subimagoes of *Callibaetis floridanus* at 15-minute intervals. Left graph shows numbers emerging, beginning at 6:00 p.m., during the evening of September 9 and 10; the graph on the right begins at 8:15 p.m. and shows emergence during the evenings of August 18 and 19.

The transformations described above were those of nymphs which had been caught during the morning of the day on which the observations were made. Nymphs kept in the laboratory for more than one day seemed to lose their normal synchronization and, although they still emerged in the evening, the hour ranged from 6:00 p. m. to 2:00 a. m.

The subimaginal molt of *Callibaetis floridanus* has been reported as occurring about seven to nine hours following emergence of the winged stage (Berner, 1950). Taylor and Richards (1963) observed the subimagal stage to last approximately 12 hours under laboratory conditions. Certainly, transformation to the imagal stage takes place on the morning after emergence and it may occur any time between 6:30 and 10:00 a. m. from June through October. The hour of transformation seems to be correlated with weather conditions but on any given day most of the insects molt about the same time. We noted that the molt occurred in the field approximately 15 minutes after the subimagoes were exposed to bright sunlight.

MOLTING

NYMPHS: Molting of the nymphal exuviae occurs at time intervals which are dependent upon speed of maturation and growth of the individual. Ecdysis was observed taking place at all times of the day and night, but the great majority of these molts occurred between 3:30 and 10:00 P. M., with the greatest number concentrated between 6:30 and 8:00 P. M. It is an extremely rapid process and difficult to observe in detail. The nymph does not show any unusual activity prior to molting and this compounds the difficulty of close observation. Generally, after several seconds of violent swimming activity the nymph pushes upward and forward from a mid-dorsal split in the skin. We observed very few cases of death resulting from trouble during molting, and these were generally because the nymphs were somehow unable to become completely free of their exuviae.

Immediately after shedding, the nymph is light green, and during the stadium becomes dark brown. The period during which the nymph is ready to transform to the subimago is one of the most dangerous in the life of a mayfly. At this time the nymph is not only forced to leave the protective background of aquatic vegetation so that it is exposed to aquatic predators, but also any difficulty in the actual emergence process often results in death. We have observed mortality rates as high as 14 per cent in *Callibaetis floridanus* at the time of emergence due to factors other than predation.

The emergence of the last instar nymph to the subimaginal stage is much more easily observed than the nymphal molts. Not only is the actual emergence slightly slower but the event is noted by a changed pattern of activity. The first indication of approaching emergence is the disappearance of normal feeding activities and increasing unrest. The nymph then stops feeding and clings to submergent vegetation, often flexing tail and abdomen over the head. The immediate signs of emergence are characterized by marked agitation. The nymph darts wildly and in a random fashion, resting only for seconds in rather unnatural positions, sometimes upside down, sometimes on its side or at the surface. At the beginning of this stage the nymph is relatively pale but soon there is a rapid darkening of the integument until it becomes dark brown. The gills beat constantly and rapidly, the beat at times becoming an almost steady trembling. When the nymph rests, the whole body expands and contracts rhythmically with the head moving smoothly forward and back from the body and with legs following the same slow, pulsating rhythm. The nymph begins spending more and more time at the water surface. After from two to ten minutes of this activity, with an average of about five minutes, a split occurs in the median dorsal area of the mesonotum. The subimago then pushes forward breaking through the cuticle covering the head. The wings are pulled from the nymphal sheaths, immediately opened, and are ready for use. The subimago then leaves the exuviae and flies from the surface of the water to nearby vegetation.

The act of emergence is very rapid. We have studied it most intensively in those subimagoes which emerged with folded wings and were, therefore, not able to fly from the water surface. In general, these insects are marked by having a longer period of underwater agitation prior to emergence. Perhaps an imperceptible split may have appeared in the exuviae permitting water to leak in, resulting in either wet wings or the death of the nymph. We have not observed any nymphs to survive which attempted to emerge without success for more than 15 minutes. After this length of time the movements become feeble and death soon results.

SUBIMAGO: The subimago, which emerges in late afternoon or early evening, flies immediately to nearby vegetation to rest quietly until the following morning when the subimaginal molt takes place. Even though molting occurs during the transformation to the imaginal stage, there appears to be no size change and the subimago and the imago are both similar in that respect to the mature nymphs (Table 3).

TABLE 3. MEASUREMENTS OF FIVE FEMALE IMAGOES (in millimeters).

Head Width	Total Length*	Wing Length
1.04	5.07	5.16
1.08	4.99	5.14
1.33	9.61	7.32
1.41	8.73	7.65
1.46	9.82	7.82

* Excluding antennae and caudal filaments.

Sometime during the night the subimagoes move away from the nymphal habitat. This observation has been repeatedly confirmed by the fact that large concentrations have been found 200 or more feet away from water. In the migration large numbers are trapped in low hanging spider webs spun on vegetation over the water or at its edge.

When ready to transform the subimagoes begin greater activity. They fly readily if the vegetation on which they are resting is disturbed. If not disturbed, they swing the abdomen slowly from side to side. The wings, held upright, soon begin to jerk and flutter slightly. They are then slowly extended laterally until completely separated, with the jerking and fluttering motions continuing. The body is finally pushed forward and upward in the exuviae and the imago appears with legs folded close to the body. Wings are pulled from the subimaginal wingsheath and rapidly unfold to be held vertically, clear and glistening in the sunlight.

Within about 15 seconds after the beginning of molting, the adult has emerged and moved forward from the shed skin. The tails may not yet be completely freed, but the adult continually flexes the abdomen until at last they are pulled entirely clear. The new adults remain motionless for at least 20 to 30 minutes, are extremely hesitant about flying, and when disturbed will only move to a nearby holdfast and again become motionless. If the wings are touched against anything during this quiescent period, they may adhere to it. This quiet period may therefore be correlated, with the period required for drying and hardening of the exoskeleton.

Mating Flights

Mating flights of *Callibaetis floridanus* have been observed twice in an open field near the Stengel Field pond in Gainesville. The flights took place in the morning beginning at 9:15 and 10:30 A. M., 20 or 30 minutes after the subimaginal molt. On another occasion in August, at 6:50 a. m., a single male was seen rising and falling as though participating in a mating flight, and between June and October, numerous imagoes were observed flying up from the vegetation between 6:50 and 10:30 a. m.

The adults clung motionless to the vegetation until approximately one to three minutes before the beginning of the mating flight. At this time they began to move the front legs up and down, then soon took to the wing. Once initiated, the flight occurred over an open field, rather than over water. The flight is sudden and follows a zigzag path upwards to a height of from 4 to 25 feet. There is then a rapid and abrupt rise and fall ranging from several inches to as much as two feet. Females fly into the swarm of males and fall into the rhythm.

Males seem to approach the females from below as in other species of mayflies. After copulation in the air, the females were noted resting on vegetation and the males returned to join the swarm. The two swarms observed were small, the number of adults in flight at any one time being only three to five over a ten square foot area of the field, even at a time when the nymphal population in the pond was very high.

In a personal communication, Dr. R. L. Blickle reported that on April 11, 1957, at Sebastian, Florida, he observed a flight of *Callibaetis floridanus*. He first noted the imagoes at 6:20 a. m. when the temperature was 21.5 C., and they were still in flight when he left the area at 7:30 a. m. The mayflies were dancing over an area of at least ten acres. In his observations Dr. Blickle noted the adults hovering at a height of from four to twenty feet above the ground. At the time, the wind was from the east, ranging from two to seven, but mostly below five miles per hour, and the humidity was 80 per cent. The temperature ranged from 19.5 C. at 5:40 a. m. to 22 c. at 7:30 a. m., when his observation ceased.

Dr. Maurice Provost (personal communication) reported a similar flight which he observed near Fort Pierce, Florida. He noted that the hovering adults were so thick that the vegetation over several acres was shimmering with them. We saw no large swarms during our observations, probably because of drought conditions.

Shortly after the swarming flight, the males die. Even in captivity they generally do not live longer than 21 hours after emergence from the nymphal stage, although some have been kept alive for nearly two days (Berner, 1950). Females, however, become quiescent when they settle on vegetation and may live for five to seven days or longer until oviposition. As has been pointed out previously (Berner, 1941), longevity is apparently correlated with ovoviviparity.

OVIPOSITION

The females oviposit early in the morning approximately five to seven days after the mating flight. On arrival at the pond at Stengel Field with the first dim light of dawn, around 5:45 a. m. in July and August, the surface of the water was already littered with females which had very recently died. Ovipositing females fly immediately to the water surface where a milky mass of eggs is extruded within one to five seconds after landing. When the female oviposits, she lays the abdomen flat on the water surface, releases the eggs, and then floats, wings held upright. One or two minutes later, as she attempts to leave the water's surface, the female generally fails and floats motionless with the wings still held upright. After a while, as she struggles to rise, her wings become caught in the surface film and she is trapped. About 20 minutes from the beginning of oviposition the female is dead from exhaustion.

If mated females are kept without water or do not have their abdomen dipped into the water between five and seven days after mating, they will die soon after a period of activity without extruding the eggs. Females captured after mating and held until the eggs mature, will readily release them when the tip of the abdomen is touched to water. Captive, mated females remain quiescent until time for oviposition and then they become extremely active, fluttering about in the container in which they are held. If they are not touched to water after this point is reached, they will die within about six hours. However, under natural conditions when caught in spider webs, the female will expel the eggs even though she is not in contact with water.

Live females taken from spider webs located six to eight inches above the water surface, often had a viscous reddish-brown mass of eggs protruding from the ventral surface of the abdomen which was released upon dipping in water. The mass would hatch into young five to ten seconds later.

NYMPHAL ECOLOGY

HABITAT: *Callibaetis floridanus* nymphs can be found in a wide variety of aquatic habitats. We have collected them in many ditches and temporary ponds. They have been taken from sinkhole ponds, cypress swamps and the quiet zone of slow streams. One of us in an earlier discussion (Berner, 1950) reported their occurrence in the Florida Everglades.

The nymphs have a wide range of tolerance to water conditions. Dissolved oxygen was found to range from 0.7 at 5:00 a. m. to 5.25 p. p. m. at 3:00 p. m. on a sunny day. The majority of specimens collected during this study have come from water with a pH varying between 6.0 and 7.0, but they have been recorded from very acid and very basic conditions, where the pH ranged lower than 4.0 and above 10.0 (Berner, 1950).

Callibaetis floridanus nymphs are also tolerant of some salinity, and it is the only North American mayfly for which this is known to be true. All of the nymphs used in this study have come from fresh-water, but experimentally they were found to be able to live in, and emerge normally from water with salinities up to 12 p. p. t., approximately one-third that of sea water. These observations are in agreement with those of Berner and Sloan (1954), who reported nymphs in an area subject to tidal fluctuations.

Nymphs have been found associated with a wide variety of vegetation. In the Stengel Field temporary pond the vegetation was composed predominantly of submerged terrestrial plants until late August, when mats of green algae became common. The terrestrial vegetation included the following: *Corydalis micranthum* (Engel M.), *Descurainia pinnata* Walt., *Geranium carolinianum* Walt., *Rumex* sp., *Vicia sativa* L., and *Trifolium carolinianum* Walt. These plants also comprise the main vegetation of the area in which the subimagoes molted and the mating flights took place.

The plants associated with other study areas were more predominantly aquatic and included *Hydrocotyle* sp., *Galium* sp., *Pontedaria* sp., *Ceratophyllum* sp., and *Chara* sp. In addition, *Callibaetis floridanus* nymphs have been recorded in association with *Micranthemum micranthemoides*, *Lugwigia* sp., *Myriophyllum* sp., *Polygonum* sp., *Saururus cernuus*, and *Eleocharis* sp.

The nymphs tend to occur in the tangle of vascular plants rather than among the mats of algae. They were never collected in areas covered with water hyacinths or duckweed. Reasons which might account for their absence were suggested in "The Mayflies of Florida" (Berner, 1950).

FEEDING: Analysis of the stomach contents of nymphs showed them to be non-specific plant feeders. The bulk of the food material was composed of plant epidermis, but also included the algae *Spirogyra*, *Ulothrix*, *Protococcus*, *Mougetia*, *Hydrodictyon*, *Oedogonium* and diatoms. The predominance of epidermis was probably the result of the fact that the nymphs examined were taken from the Stengel Field temporary pond in which the vegetation was almost entirely terrestrial and which was in the process of dying with concurrent decay of tissues. This would make the stripping of the epidermis from the dead plants much easier than stripping it from living aquatic plants.

Food material passes through the digestive tract of the nymph very rapidly. During active feeding we have observed the nymphs extruding a mass of fecal matter in volume equal to about one-third to one-fourth the volume of the digestive tract every twenty to forty seconds. This observation seems to be in agreement with the statement of Dethier (1954), regarding feeding and digestion of phytophagous insects, that one-half to two-thirds of the food taken is eliminated as feces. He further states that during digestion of plant materials, most of the proteins, fat and simple carbohydrates are utilized, oil is secreted but not used and cellulose and starch are excreted unchanged.

WEATHER: Rainfall is, of course, of great influence on aquatic populations. During years of heavy rainfall when the roadside ditches and temporary ponds are filled to overflowing, the population of *Callibaetis floridanus* rises to a peak. It seems that the nymphs may be found in every puddle and the adult population is drawn in large numbers to the lights in windows nearby. Conversely, during years of drought, the population size decreases greatly. The nymphs can be found only by wide and intensive collecting and are scarce when found. Weeks of careful nightly checking of lighted store windows in towns may often yield not a single adult or subimago. The temporary pools are dried and in most cases even the permanent waters areas are shrunken in the face of continual drought. All of the members of the ecosystem are forced closer together with very unfavorable effects upon the numbers of *Callibaetis floridanus*. Rainfall influences the population in other ways also. Emergence and swarming may be greatly hampered by heavy downpours. The winged stages are very dependent upon a high moisture content in the air. Subimagoes are unable to complete the final molt successfully under dry conditions, and adults will usually die within 24 hours if not kept in a fairly moist atmosphere.

Temperature also influences rates of development. Degree of tolerance to low and high temperatures is rather striking. Nymphs have been collected from water less than a degree above freezing and have been found in shallow water in the summer at a temperature of 34.5 degrees centigrade, a temperature close to the upper lethal temperature of the species (experimentally determined to be between 35 and 38 degrees C.). When the water temperature ranges as low as 0 to 5 degrees C., the nymphs become so lethargic that they may become easy targets for predators.

PREDATION: All stages of *Callibaetis floridanus* are sought by predators. Small fish formed the most highly predacious group of the aquatic fauna. When the fish population in an area increased the nymphal population usually decreased, and when the fish became very abundant, nymphs were usually completely exterminated. Second, and almost equal in importance as predators, were the dytiscid larvae and the belastomatids. The Naucoridae are also extremely predacious, but are not as common as the above mentioned groups. Other groups observed to prey upon *Callibaetis floridanus* nymphs include Odonata and Hemiptera (Notonectidae, Corixidae, and Nepidae).

As the temporary ponds dried, birds became serious predators on the fauna. It was not possible to tell that they were feeding on mayfly nymphs specifically, but our observations indicated that they ate anything that could be caught. Boat-tailed grackles (*Cassidix mexicanus*), red-winged blackbirds (*Agelaius phoeniceus*), killdeer (*Charadrius vociferus*), and one snowy egret (*Florida thula*) were seen feeding from dawn to dusk at the Stengel Field pond.

The population of *Callibaetis floridanus* seems to fluctuate seasonally between temporary and permanent bodies of water and the fluctuation is related to the abundance of predators (Table 4). During the winter when the predator population is at a low point and the temporary ponds are usually empty, the permanent bodies of water support a substantial population of mayfly nymphs. As warm weather arrives and the associated

TABLE 4. COMPARATIVE EFFECTS OF PREDATION ON NYMPHAL POPULATIONS OF *Callibaetis floridanus* IN TEMPORARY AND PERMANENT PONDS.

	STENGEL FIELD*	Predators		ROUTE 26**	Predators		GIFFORD PLOTS†	Predators	
	Nymphs	Fish	Others	Nymphs	Fish	Others	Nymphs	Fish	Others
Jan	0	0	0	+3	0	0	+3	0	0
Feb	0	0	0	+1	+4	+4	+3	+1	+1
Mar	—Water—First week—			+3	+1	+2	+3	+1	+1
Apr	+4	0	+3	+1	+3	+4	+2	+1	+2
	——Dried——								
May	—Water—Second week—			0	+4	+4	0	+3	+4
	+3	0	+2						
June	0	0	+2	0	+4	+4	0	+4	+4
July	+2	0	+2	+1	+2	+2	0	+4	+4
Aug	+3	0	+4	0	+4	+4	0	+4	+4
Sept	+4	0	+1	0	+4	+4	0	+4	+4
Oct	+5	0	+1	+1	+2	+4	+1	+3	+2
Nov	——Dried——			+3	+1	+1	+1	+3	+1
Dec	——Dried——			+3	+1	0	+2	+1	0

Callibaetis floridanus

0 = None
+1 = Less than 1/scoop—very low
+2 = 1/scoop—low
+3 = 1-2/scoop—medium
+4 = 11-30/scoop—high
+5 = 30 or more/scoop—very high

Predators

0 = None
+1 = Less than 0.2/scoop—very low
+2 = 0.2-1/scoop—low
+3 = 1-2/scoop—medium
+4 = 3 or more/scoop—high

* Temporary pond.
** Permanent pond beside road.
† Permanent impoundment.

fauna begins to increase in numbers, the *Callibaetis* population starts to decrease. Ususally by the time the predator population is approaching its maximum, the temporary ponds contain water with the fauna consisting only of such fleeting forms as fairy shrimps. The *Callibaetis* population now seems to move to these ponds and increases along with the increasing predator population. One large advantage of life for the mayfly in temporary ponds is the frequent absence of fish, one of the most effective predators. By late fall as the ponds dry, the permanent bodies of water decrease in number of predators and *Callibaetis* nymphs flourish there again.

Dragonflies are the most successful predators on the subimaginal and adult stages. They patrol the ponds in large number in the morning, and one of the first evidences of a mayfly mating flight is the heavy concentrations of erratically darting dragonflies. In addition to taking adults in flight, we have observed both dragonflies and damselflies take subimagoes or adults which were resting on vegetation.

Spiders are effective mayfly predators, snaring both emerging subimagoes and ovipositing imagoes in their webs or catching the insects at the water surface.

Birds likely eat the winged stages but we have been unable to verify predation. Decimation of adult populations appears to be attributable chiefly to dragonflies and damselflies.

In spite of high mortality rates from predation, molting accidents, and disease, the insects are still highly successful as a result of the large number of young produced, adaptive concealing coloration, and the speed of movement of the nymphs.

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