THE WASMANN JOURNAL OF BIOLOGY

VOL. 14, NO. 1 SPRING, 1956

The Life History of Ephoron album (Say) (Ephemeroptera: Polymitarcidae)

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The spectacular mass flights of the mayflies of the genus *Ephoron* (=*Polymitarcys*) have attracted the attention of numerous naturalists who have commented on the swarming habits of the various species of this genus. From the accounts of swarming of Palearctic species it appears that there is considerable similarity in the nuptial flights of the various species.

Observations on the swarming habits of *Ephoron album* have previously been recorded by Keating (1824:114–115) and Riley (1881). Despite the great interest in this genus no previous detailed study of any species has been made.

In Utah *Ephoron album* swarms in the late evening from late July to early September. During observations on August 28, 1947, at Holladay, Utah, the first male subimago emerged at 7:00 p.m. when the light intensity was ten foot candles. It was not until 7:20 p.m. when the light intensity had dropped to only two foot candles that the subimagos started to emerge in numbers. All the first subimagos were males. They did not fly into the foliage to rest as is typical of most subimaginal mayflies, but kept moving over the water with a strong steady flight. Each subimago established a very routine patrol about two to twelve inches above the water along a twenty-foot stretch of the canal. This flight lasted for less than ten minutes and upon completion the subimago alighted on vegetation or a nearby bridge long enough to molt. During our observations various males required periods of 55 to 80 seconds to shed the skin. The middle and hind legs were attached to the substrate and the wings were laid back along the body at a sharp angle so that by the time the male imago started to emerge, the costal edge of the wing was parallel to the side of the abdomen with the wings extended vertically. The males emerged rapidly and flew away, usually trailing the subimaginal pellicle from the tails. The pellicle was usually dislodged from the tails in flight but the wings were, of course, freed while the insect was at rest. Female subimagos started to emerge at 7:30 p.m. when light intensity was reduced to one foot candle. The emergence of female subimagos from the water coincided with emergence of male imagos from the subimaginal skin. The air temperature at this time was 68°F. The light soon became too dim to register on the meter and direct observation became impossible, but males and females could still be seen swarming in the beams from the headlights of automobiles on the highway which intersected the canal. The egg-laden females were easily recognized by their slower flight and pendulous abdomen. By 7:45 p.m. a number of ovipositing females were floating on the surface of the water. At 8:00 there was noted a sudden decrease in the activity of the swarm coincident with a noticeable lowering of temperature. By 8:05 p.m. the temperature had dropped to 62°F. and only an occasional female came to the lights. At 8:07 the last living specimen was seen depositing her eggs on the bridge railing in front of the car lights.

After the flight was completed, there was an average of eight dead adult mayflies per square foot on the surface of the water and many others had perished at nearby lights. Two days before, on August 26, the flight was many times greater than on the night the above observations were made. The weather was cooler on August 26 and the swarming stopped about 15 minutes earlier.

Additional observations have been recorded near Kearns, Salt Lake County, and the Green River at Hideout Canyon. Near Kearns on August 31, 1950, the subimaginal males started to emerge from the canal in appreciable numbers at 6:45 p.m., soon after sundown. At this time light intensity was about 100 foot candles. Imago males started to appear in the swarm within five minutes after the first major emergence of male subimagos.

At 7:05 when the light had dropped to one foot candle the swarm was very extensive, and some specimens could be seen copulating. Each male was patrolling a stretch of the stream. The rapid flight of the males and the great number of individuals gave the flight a somewhat "frantic" aspect. Females often dropped down from above and touched a male briefly in flight. At this time the female mayflies were not positively phototropic and the males were only moderately so. The swarm was so great that it appeared like a dense white cloud hanging over the canal, more concentrated about three feet above the water but extending upward as high as twelve feet.

Within a few minutes many pairs were seen mating above the stream. The male approached the female from beneath as do most ephemerids, but the couples remained in copula for only a few seconds at a time. Swarming reached its greatest intensity at this time. The copulating females were all subimagos and it is apparent that only the male sheds the subimaginal pellicle.

Within a few minutes after copulating the females exhibited a strong phototropism. In an attempt to get eggs for experi-

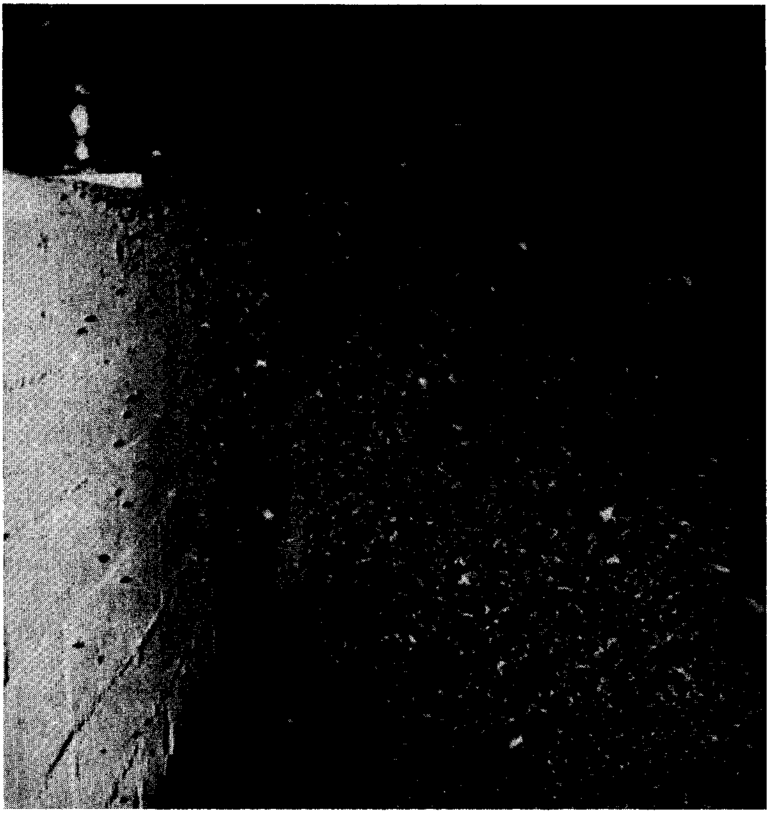

Figure 1. Adults of *Ephoron album* swarming over a canal at Kearns, Utah. Note the lantern on the bridge railing at upper left and males clinging to sidewall of bridge while shedding the subimaginal pellicle.

mental purposes a gasoline lantern was placed in a pan of water on the bridge railing (fig. 2). The females completely filled the pan in a matter of seconds; to make room for more females it was necessary to remove handfuls of specimens from the pan (fig. 1). When the pan was filled a miniature "waterfall" of females cascaded over the railing of the bridge to form a great fluttering, humming mass of insects on the road below.

The swarming was finally completed by 8:05 p.m. after which not a single living insect could be seen. No sudden drop of temperature coincided with the ending of the flight so it appears that while lower temperature might stop mayfly swarming it certainly is not the normal causative factor in its termination in the case of *Ephoron album.*

Ephoron album illustrates a great shortening and specialization of the nuptial flight. The male emerges from the subimaginal pellicle just in time to be ready for mating with the emerging female subimagos. The entire life of the winged stages is crowded into less than an hour and a half of crepuscular-nocturnal existence at a time when there are few enemies to prey on them. Fish must take a toll of the emerging nymphs, but the greatest toll of adults is taken by spiders of the genus *Tetragnatha* and by the attraction of lights leading many of the gravid females away from the water.

The eggs were exuded from the oviducts in two elongate-oval, compressed packets. The females rarely fly with the egg packets extruded as indicated in the figure given by Needham (1920, *et al.*), but usually extrude the eggs immediately upon contact with water. The females each plummeted to the surface and drowned during oviposition. The substance that cements the eggs together will coagulate in alcohol, but it dissolves immediately in water and the eggs sink singly at the rate of about six inches per minute. The tiny threads of the polar caps uncoil and the eggs stick to the surface of any object they strike. Later numerous eggs were recovered attached to sand grains, vegetation, etc., from the canal bottom.

Within a month after the eggs were collected, the developing nymph was visible within the chorion, the most obvious features being the five black dots on the head, the two compound eyes and the three ocelli. At this time the nymphs occupied about half so great that it appeared like a dense white cloud hanging over the canal, more concentrated about three feet above the water but extending upward as high as twelve feet.

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the egg. No change in the appearance of the embryo was observed during the next six weeks.

These eggs were then subjected to a series of experiments. In each case several hundred eggs were used; each sample consisted of eggs from several different areas in two stock pans, and all eggs were collected on the same night, August 31, 1950. All of the experiments except number 7 started on November 20, 1950, and were as follows:

1. A Petri dish of eggs in water was refrigerated at 52°F. for three days. After removal from the refrigerator the eggs were kept under observation at room temperature. The first eggs hatched January 22, 1951, and hatching continued for the next ten days; the elapsed time from the start of refrigeration until hatching was 62 days, three days in the refrigerator and 59 days

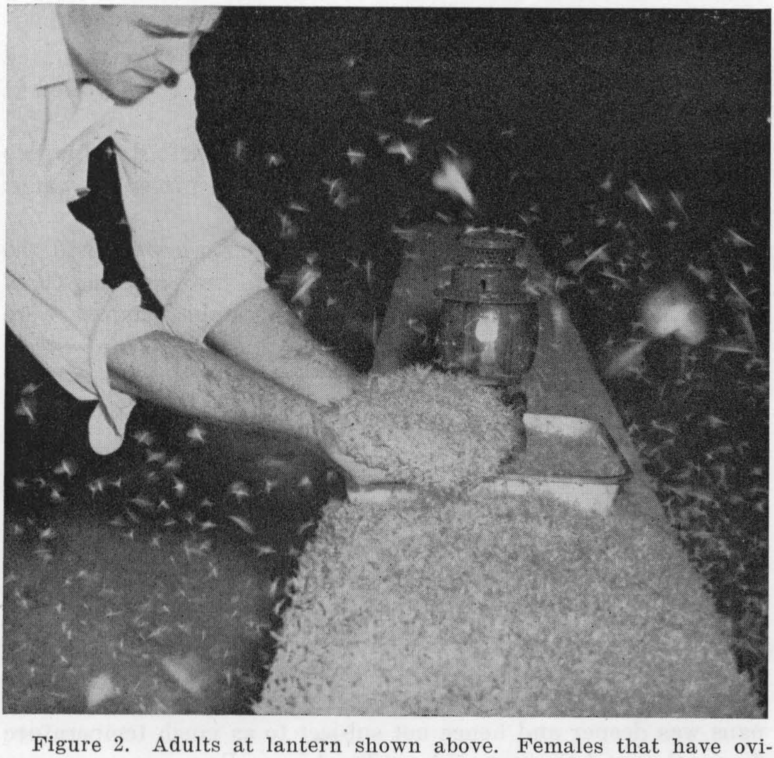

Figure 2. Adults at lantern shown above. Females that have oviposited are being removed by hand to make room for additional females coming to the light.

at room temperature. Controls which were left at room temperature still had not hatched six months later.

2. Conditions were as in experiment 1 but the eggs were allowed to remain in the refrigerator for 14 days. The first eggs hatched on January 22, 1951, and continued to hatch for the next six days. Thus in this experiment the eggs hatched within 62 days after being subjected to cold, but only 48 days were spent at room temperatures. The eggs completed hatching within a shorter time than in experiment 1.

3. Conditions in this experiment were like those in experiment 1 except that the eggs were refrigerated for one day only. None of them had hatched six months later.

4. The eggs in this Petri dish were placed in the freezing compartment of a refrigerator. The water in which the eggs were immersed was frozen solid. None of the eggs hatched within a six-month period.

5. A number of eggs were dried out first, then refrigerated for two weeks. None of these eggs hatched after being placed in water for six months.

6. Eggs were allowed to dry out and were left dry for two weeks at room temperatures. They were then placed in water. None hatched within six months.

7. Eggs which were left in the original stock pans had the same appearance on May 3, 1951, as they had the preceding October, i.e., the eyes, ocelli, and body of the contained nymph were still visible in the same position. On May 3, a series of these eggs was placed in the refrigerator at 52°F. for three days. These eggs began to hatch 48 days later, as contrasted to 62 days for the November experiment.

Controls were kept for all of the above experiments and neither these eggs nor those in the original stock pans hatched within the six-month observation period.

In one case a number of eggs were left in a pan similar to the main stock pans but with only a shallow film of water over them. Apparently this shallow layer of water was cooled enough during the night to serve as a hatching stimulus, for many of these eggs hatched at a later date. The water in the main stock pans was deeper and hence not subject to as much temperature fluctuation and the eggs did not hatch.

As a result of the removal of the water in the irrigation canals during the winter months it was obviously impossible for the nymphs of *Ephoron album* to overwinter as active individuals in the canals at Holladay or Kearns, therefore it was of considerable interest to find the conditions under which the eggs remained until the following spring before hatching.

The eggs do not hatch in the fall in nature but develop up to a certain point, and then go into a diapause and remain in this condition until such time as they receive a stimulus to start renewed development. From the experiments outlined above it would appear that cooling of the eggs for several days will provide such a stimulus, but one day (see experiment 3) is apparently insufficient. From a comparison of experiments 1 and 2 it is suggested that the required post-diapause development starts when cooling is started rather than after the eggs are returned to higher temperature. The temperature of the room where the experiments were conducted was warmer during experiment 7 than during experiment 2, and the eggs developed and hatched more rapidly at these higher temperatures. Eggs that were frozen, or dried, or both, did not hatch during the experiments.

In the canals the water is cut off at the source as soon as the crops are harvested or when there is no demand for irrigation water, and the canal gradually dries up. When the canal at Kearns was visited in early March of 1951 it was completely dry. Some of the bottom material was gathered and taken to the laboratory where it was flooded with tap water which was then circulated by a pump. Examination of this bottom material revealed a number of eggs. None of these were observed to hatch in the laboratory.

The usual date for flooding the canal is early April but on April 1, we visited the canal at Kearns and found it full of water. One week later we returned to the canal and secured a small amount of bottom material which contained a number of early instar nymphs. Although we are not sure of the date of flooding, it is certain that the time was less than 30 days and probably only a week or so. It is apparent that the eggs hatch within a short time after being flooded; this tends to support the indication from the comparison of experiments 1 and 2 that the time from the date at which cooling of the eggs begins is an important factor. Yet it is apparent from a comparison of the results of experiments 1, 2, 7, and field data that the eggs are not simply stimulated to begin a series of events that will lead to hatching of the eggs within a set time. Water temperatures must have a great deal to do with the rate of development. Field and laboratory data together indicate that the eggs proceed to a state of diapause within the first month after they are laid; the water then cools off with the approach of winter but shortly after this process starts the water is withdrawn and the eggs remain in the mud in the canal bottom where they are subjected to prolonged periods of freezing and drying. Shortly after being flooded with water in late March or early April the eggs hatch. In the larger rivers and probably under most natural conditions the eggs are never subjected to drying but are dependent upon winter temperatures of the water for the hatching stimulus.

In light of the data gathered from field studies, the results of experiment number 4 where no eggs hatched after being frozen appears contrary to what would be expected, but it may be that the eggs must gradually be conditioned to such cold, as they probably are in nature, rather than being transferred from warm to freezing temperatures in less than an hour. A similar explanation would apply to results of experiment 5 where no eggs hatched after freezing and drying. There is also the possibility that those eggs of *Ephoron album* on the surfaces that are exposed to the rigors of freezing and drying do not hatch in nature and that the nymphs that are found in the canal result from eggs that are washed below the surface where they are more protected. The sample of dry bottom material secured in the spring from which the eggs would not hatch (see above) included the top four inches of the bottom of the canal and we are without an explanation for the failure of the eggs to hatch.

The canal at Holladay where we studied this species in 1947 remained dry until April 27 when the water was turned into it from the Jordan River narrows about 20 miles away. On August 26 and August 28, tremendous swarms of adults issued from the canal and lesser flights are known to us at this point as early as August 3. Even if the eggs had hatched within three days after the canal was flooded, the great bulk of the nymphs would have spent only 18 weeks in developing. It appears then that the actual period of development for most specimens is from 14 to 17 weeks although a number continue to emerge for a week or two beyond this period. On October 1, we were unable to locate a single nymph in the canal. Ulmer (1924:26) reports that nymphs of this genus (as represented by *E. virgo* Oliv.?) require two years of nymphal development.

In the Jordan River, the adults start to emerge in late July. As the river has water in it at all times the eggs apparently hatch after a prolonged period of cold during the winter. Perhaps the eggs hatch earlier in the year here than in the canal; at least, the adults emerge earlier.

Ephoron album nymphs are found in the rivers and canals of northern Utah where there is a moderate current. They have been found only in a lightly compacted clay-sand mixture which is soft enough to burrow into, yet firm enough to keep the walls of the burrow from caving in. So characteristic is the consistency of this bottom material that it soon becomes possible to predict the probability and even the approximate number of specimens that can be expected from a sample just by examining the bottom material.

The nymphs live in burrows with the head upward. They remain about two inches down in the burrow in the daytime but come to the surface at night. This is an important factor in collecting these nymphs with an Ekman dredge for daytime collectings result in many nymphs being chopped in half by the jaws of the dredge while in evening or night collections the jaws of the trap snap shut below the level where the nymphs are concentrated.

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