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STUDIES ON THE BIOLOGY OF THE EPHEMER-
OPTERA. II. THE NUPTIAL FLIGHT¹

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The spectacular nuptial flight of the ephemerids early attracted the attention of scientists. Swammerdam (1675) recorded the emergence, nuptial flight, and oviposition of *Palinogenia longicauda* on the rivers of Holland. He misunderstood the character of the nuptial flight and thought fertilization took place after the eggs had been deposited in the water. Reaumur (1742) observed the nuptial flight of *Ephoron virgo* at Paris. Both Swammerdam and Reaumur studied species whose flights take place at dusk or after darkness has fallen, and thus they had great difficulty in seeing the actual behavior of the insects. When Collinson (1746) observed the flight of *Ephemera vulgata* at Winchester, England, he noted that copulation took place in the air and saw the typical up-and-down movements of the individuals. In 1750, he reported the observations of John Bartram on an ephemerid species from the Schuylkill River, Philadelphia. Bartram had seen a typical flight and also concluded that copulation was achieved in the air. Charles de Geer (1755 and 1771) observed *Ephemera vulgata* in Sweden, and saw that the male copulated with the female by placing himself beneath her and then bending his abdomen upwards. Because of the short time that the copulatory act lasted, he was not able to ascertain where the male grasped the female with his fore legs. Eaton (1883) has given a brief account of the behavior of the ephemerids during the nuptial flight, and since then many workers have noted certain characteristic and interesting aspects of the flights of these insects. Morgan (1913), Needham (1927), and Needham, Traver, Hsu, etc. (1935) have dealt with the subject at some length. There are, however, phases of the problem that have not been elucidated; to present these data properly, it is necessary to review the problem in its entirety.

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THE NUPTIAL DANCE

On the basis of present information, all species of ephemerids, except for possibly a few parthenogenic ones, engage in a nuptial flight during their brief life as winged individuals. This flight results in copulation and the insemination of the female. Although there are variations and modifications to the flight, as will be noted later, it typically follows a rather standard pattern. Such a standard flight pattern can be observed in genera as diverse and distantly related as *Baetisca*, *Hexagenia*, *Siphonurus*, *Ephemerella*, and *Baëtis*.

Briefly, the general pattern of this phenomenon, in which the males play the dominant role, is as follows: After preliminary patrolling, a number of males gather near or over a body of water, into which the females will ultimately oviposit, and commence an attractive and characteristic up-and-down dance. Sometimes the aggregation consists of countless individuals; at other times it is made up of only a few males. Now and then a solitary male can be seen in flight. The upward motion of the dance is accomplished by the individual flying upward and forward with strong, steady wing strokes. Meanwhile the fore legs are stretched forward, the straightened body is elevated anteriorly and slopes downward posteriorly; the caudal cerci are parallel with each other and extend posteriorly along the longitudinal axis of the body. Having propelled himself upward and forward for a brief time, he then ceases flying and, due to the force of gravity, floats earthward with the wings extended upward and somewhat outward. At the same time much of the body, especially the thorax, comes to be almost parallel with the earth while the posterior end of the abdomen is bent slightly upwards. The long cerci extend divergently backwards and upwards. These cerci are always divergent and never parallel during the downward movement. The fore legs are kept extended forward and are bent slightly upwards. Except possibly for the diverging of the cerci, the position assumed in the downward flight is entirely passive and due to air resistance and gravity rather than to any activity on the part of the individual. The long cerci and fore legs seem to serve as balancers and stabilizers in this passive downward movement. It is to be noted that the

fluted, fan-like character of the wings is helpful in maintaining the individual on an even keel. As Needham, Traver, Hsu, etc. (1935, p. 103) have pointed out, the specimens often sway from side to side as they passively descend. This is due to the effect of the wind currents upon the inactive, lightly balanced individuals as they float earthward.

In such a nuptial dance there is no sign of timing among the insects. Thus some are ascending while others are descending, and so a constant passing and re-passing takes place.

The insects always face into the wind if there is any air movement. If the air currents are strong and gusty, then the individuals are often blown away or down into the surrounding vegetation. In a moderate or gentle breeze, however, the forward component of the upward flight just about equals the backward component of the downward drop and the individual rises and falls repeatedly in about the same area. If there is a slight breeze or if air movements are completely lacking, then the downward drop is vertical or almost so and the individual moves forward with each upward flight. After a number of upward and forward flights and downward drops, the insect makes a quick reversal and faces in the opposite direction. There then occurs a repetition of the ups and downs. Thus, invariably the nuptial swarm is maintained over a relatively small area and all the individuals fly in parallel directions.

Ephemerids can reverse their direction of flight with almost lightning-like rapidity, can fly upward, downward, forward, and, as is recorded below, they can hover; but they are apparently incapable of lateral flight movements.

After the dance of the males has continued for a time, individual females come flying into the swarm. Unlike the males, they fly on an even keel, parallel to the ground, but usually in the same direction as the males. The combined methods of flight of the two sexes result in the female flying above a male that is dancing up and down. The male recognizes the female and on his up-flight approaches her from below, seizes her and the pair immediately joins in copulation. De Geer (1755) was the first to report that the male seizes the female from below, but he did not see how it is accomplished. The feat is accomplished

because of the male's ability to supinate his entire fore tarsi and bend them backwards and thus grasp the pronotum of the female with his tarsal claws. Considerable speculation has arisen as to the exact spot on the female that the male grasps. Needham (1927) and Needham, Traver, Hsu, etc. (1935, fig. 13) indicate that the mesonotum at the wing roots is the chosen spot. All other workers have indicated the pronotum. My own observations suggest that the posteromedial edge of the pronotum is the point of attachment.

Almost simultaneously the male bends the end of his abdomen upward and forward and grasps the eighth abdominal segment of the female with his genital forceps. At the same time the penes are inserted into the genital ducts of the female which open on the conjunctival membrane between the seventh and eighth sternites. In such a position the head of the male lies under the mesothorax of the female. Thus the thorax of the male extends posterior to that of the female and the male's abdomen is bent acutely upward and forward.

The united pair continues to fly but, with few exceptions, its combined flight powers are not sufficient to support them for long and they gradually descend toward the ground. Generally the two separate before they reach the substratum over which they have been flying. Thus the copulatory act is restricted to a few seconds. In *Siphloplecton basale*, however, not only does the united pair continue its combined flight but it is able to avoid other males that attempt to displace the copulating male. Repeated timings on this species have shown that even here copulation lasts only from one to one and one-half minutes.

Sometimes pairs will remain in copula even after they have descended to the substratum. De Geer (1771) observed pairs of *Ephemera vulgata* upon the vegetation. Needham, Traver, Hsu, etc. (1935) relate that many pairs of *Siphonurus* sp.? were observed to light on a parked car. Eaton (1883) observed a pair of the genus *Ecdyonurus* remaining in copula for at least "six or seven minutes after they had come to rest." Pairs of *Siphloplecton basale* will remain in copula when captured in an insect net. Needham (1927) found a pair of *Cinygmula mimus* in copula even after the insects had been killed in a cyanide jar.

A figure of this pair has been published but is not typical in that the male is too far forward with respect to the female, his abdomen is not sufficiently bent, and the fore tarsal claws reach to the middle of the mesothorax instead of to the posterior edge of the prothorax. A much more accurate picture of copulation is given in "The Biology of Mayflies" (1935, fig. 13) except that the fore legs of the male are not delineated correctly.

VARIATIONS OF THE NUPTIAL FLIGHT

There are variations to the typical flight described above that should be noted. Eaton (1883, p. 9) writes that Heptagenia and its allies maintain a hovering position so that they are "locally designated in the valley of the Axe (Devon) as Yellow Uprights." Cook (1940) observed such a behavior in *Stenonema vicarium*. I have seen it repeatedly in various members of the genus *Stenonema*. In such cases the flight varies from the typical in that the male, instead of moving up and down, *hovers on an even level*, a dance accomplished by the insect assuming the following position: the body is held rigid and straight with the longitudinal axis almost perpendicular to the ground. The fore legs are extended along the axis of the body. The caudal cerci are held widely divergent and almost parallel to the ground, *i.e.*, almost at right angles to the longitudinal axis of the body, while the wings are rotated forward. An individual when flying in this manner is reminiscent of a feeding humming bird. In such a position the male can hover in one place or move forward and parallel to the substratum at a slow rate. It can not fly sideways or reverse its flight. In order to achieve a reversal of direction, the individual tips forward abruptly and flies in normal manner for a short distance, *i.e.*, a foot or so, reverses and then reassumes the hovering flight. What factor or factors are responsible for the individual assuming the hovering type of flight are obscure. Apparently only some members of the family Heptageniidae are capable of this variation. It is to be noted that such a flight pattern is assumed only when there is no wind.

DOWNWARD FLIGHT MOVEMENTS

Not always is the downward drop of the male in the nuptial dance passive. Sometimes he actually flies downward. Need-

ham, Traver, Hsu, etc. (1935, p. 103) report that *Baëtis flavistrigia* makes the upward part of the flight with great rapidity while the downward passive drop gives the impression of a dogbane seed floating earthward. If, however, the nuptial flight of this species is conducted in a brisk breeze, then the downward drop is accomplished by vigorous movements of the wings and it is just as rapid as the upward movement, and the individual keeps rising and falling in an almost vertical line. So far as my observations go, such downward wing-movements are restricted to small, light, fragile species. It has not been observed in large, heavy-bodied species.

SUBSTRATUM COPULATION

Practically all species of ephemerids mate in the air, although Eaton (1883, p. 10) reports that *Plethogenesia papuana* mates on the surface of the water. In this species the fore legs of the males, because of the abbreviated tarsi, are short. A similar condition is found in the species of the genera *Mortogenesia* and *Anagenesia*. It is possible that the species of all three of these specialized genera may mate on the surface of the water.

Occasionally species that normally mate in the air will attempt to copulate while on a firm substratum. Reaumur (1742) observed that the male individuals of *Ephoron album*, when attracted to land near his lantern, would attempt to copulate with females with whom they came in contact.

While watching a pair of *Ephemera guttulata* on the underside of a *Platanus occidentalis* leaf, I observed that the male brought himself parallel and close beside the female, grasped her abdomen with his genital forceps and proceeded to copulate in the usual manner. In this instance, the fore legs of the male were not used and both individuals remained attached to the leaf.

SEMI-NOCTURNAL AND NOCTURNAL SPECIES

Species of genera such as *Ephoron*, *Campsurus*, and *Palinogenia* emerge just at darkness or even during the night. Since the meso- and metathoracic legs of the females and the males of *Campsurus* are either absent (*Campsurus*), or so weak (*Ephoron* and *Palinogenia*) that they can not support the individuals,

they mate immediately; the females oviposit, and then the individuals of both sexes die. The total life span of the winged stages in such species is from one to four hours. The nymphs of these are negatively phototactic and positively thigmotactic burrowing forms that normally never come in contact with the light. Thus a complete generation may exist without the individuals seeing daylight. Such species do not indulge in a typical nuptial dance. The males fly rapidly back and forth over the body of water from which they have emerged. The flight is parallel or almost so with the water and without the up-and-down motion. Tientsuu (1935) reports that *Ephoron ladogensis* males have an undulating flight. Every so often the individuals quickly reverse their direction of flight. This, plus the rapid beating of the wings, gives these forms the appearance of being in a great hurry. Just how the males find the females in the total or almost total darkness, I have never been able to observe exactly. All these males have undivided compound eyes that are relatively small. Perhaps their vision is extremely acute, but fragmentary observations indicate that they may establish contact by tactile rather than visual means. In this connection it should be noted that these species usually emerge in great numbers. This plus the fact that the nuptial flight is held close to the surface of the water insure a relatively large chance for actual contact between individuals. The method of copulation seems to be the same as in all other species.

In these species, the female remains during her entire winged existence a subimago.

COMPOUND EYES OF DIURNAL SPECIES

Except for the semi-nocturnal or nocturnal species, the ephemerid males have large eyes that are greatly expanded on the dorsal surface. In many the eyes are actually divided into a large dorsal and a smaller ventro-lateral portion. This condition reaches its extreme development in *Baëtis* and its relatives where the dorsal part is carried upward on a stalk and the visual elements face dorsally while the small ventral portion is more rounded and the visual elements face outward somewhat as in the normal insect eye. Even in those species in which the eye is not completely divided morphologically (such as *Hexagenia*,

Stenonema, *Siphonurus*, etc.), it is easily seen that there is a functional division.

Repeated observations indicate that the dorsal part of the eye is used by the male to recognize the female as she flies over him while he is engaged in the nuptial dance. In the morphologically divided eye types where the dorsal part faces upward (*i.e.*, *Baëtis*, *Pseudocloëon*, etc.), the upward component of the nuptial dance is almost vertical. Conversely those species which do not have the eyes separated morphologically and in which the upper part is only slightly larger than the lower part (*i.e.*, *Siphonurus*, *Hexagenia*, *Stenonema*, etc.), the upward movement of the nuptial dance is not vertical but forms about a forty-five degree angle with the substratum.

The focal distance of the upper part of the eye apparently is rather short. The male seizes only those females that come within a short distance of him. The males normally are able to identify the females of their own species, but often they make mistakes, if other insects are flying in the same immediate area. I have seen *Stenonema fuscum* males repeatedly attempt to copulate with caddis and stone flies. A *Cinygmula mimus* male was captured while trying to mate with a large chironomid. This may explain Venour's observation (1906), upon *E. dancia* males mating with female subimagoes that had just emerged and were forced to fly through the nuptial dance in order to reach the surrounding vegetation. Ide (1930), has also observed male imagoes of *Callibaëtis americanus* mate with female subimagoes of the same species.

The lateroventral part of the eye is employed by all species to prevent the individual from coming into close proximity with large objects or protuberances of the substratum. The ephemeropterids, especially the males during the nuptial flight, are extremely alert and have a rather keen vision. Anyone who has collected ephemeropterids can testify that while flying they avoid with great consistency any object that projects from the background. Thus if a bridge crosses a stream over which they are engaged in nuptial flight, they will invariably avoid it, rising when they approach it so that they maintain the same distance from it that they do from the surface of the water. When a collector places

himself upon the bridge, they fly still higher over the spot where he is standing. This holds true whether he moves or remains perfectly still.

TIME OF FLIGHT

As indicated above, most species are diurnal. These species mate during the day or at twilight, the exact time depending upon environmental and seasonal differences as well as upon specific peculiarities.

In general those small species having hyaline wings and males in which the abdominal segments 2-7 are hyaline or semi-hyaline mate during the middle of the day and only rarely at twilight. Thus species of *Baëtis*, *Callibaëtis*, *Pseudocloëon*, *Cloëon*, *Centropetium*, *Paraleptophlebia*, *Habrophlebia* and *Habrophleboides* are often seen swarming at various times in broad daylight. I have a record of *B. moffati* mating at seven o'clock in the morning.

Large, dark, heavy-bodied, conspicuous species such as *Hexagenia*, *Ephemera*, *Potamanthus*, *Isonychia* and most members of the family *Heptageniidae* usually swarm from just at sundown to darkness.

No hard and fast rules can be drawn for any species because environmental effects play a large part in the timing of the nuptial dance as can be seen by the following typical observation.

While collecting on Spring Creek in Yellowstone Park, Wyoming, July 7, 1936, a thunder shower of small dimensions developed about five o'clock in the afternoon. The spot where I was collecting was on the edge of the storm area and only a few raindrops fell at this point. Individuals of both sexes of *Ephemera simulans* appeared and engaged in a nuptial flight. In a few minutes the storm disappeared and the individuals immediately dispersed and were not to be seen until they reappeared just at sundown about two hours later. Repeatedly I have observed, in many diverse genera, that the appearance of a storm with its attendant drop in temperature and light intensity will stimulate adult ephemerids to activity. Perhaps the relative humidity is also important since the ephemerids are rather sensitive to desiccation.

A combination of factors—latitude, elevation, season, temperature, humidity, light intensity, and atmospheric pressure—rather than any single one is probably responsible for stimulating the imagoes to leave their resting place on the surrounding vegetation and indulge in the nuptial dance. Thus the species that normally mate at twilight will sometimes be found mating in the middle of the day.

PLACE OF NUPTIAL FLIGHT

Although no perfect rule can be drawn, members of each genus are fairly consistent in the locality selected for the nuptial dance. Ephoron and Campsurus mate over the water; Ephemera over the water or close by; Hexagenia along the edge of the shore; Siphloplecton, Cænis, Choroterpes, Stenonema, Iron, Heptagenia, Cinygmula, and Rhithrogena usually but not always engage in their nuptials over the surface of the water. I have, however, observed exceptions in all of these genera.

In comparison, I have never seen Blasturus, Tricorythus or Ephemerella, with the sole exception of the early spring *E. subvaria*, swarming over the water. These three genera all choose open areas a distance from the stream for their dance.

Small, clear-winged species of Thraululus, Habrophlebia, Habrophleboides, Baëtis, Cloëon, Pseudocloëon, and many species of Paraleptophlebia choose small openings in the trees or bushes along the edge of a body of water. Only seldom are they seen over the water.

Species of Isonychia and Siphonurus choose almost any spot: sometimes over the water, sometimes over a grassy meadow, sometimes in the tree-tops. Individuals of a single species may be found in different localities on the same day at the same time.

Ephemerids, both males and females, often mistake wet roads for bodies of water, and forms which normally mate over water will often be found dancing and ovipositing over a road.

The height at which the dance takes place is also extremely variable. Generally when a strong wind is blowing, the individuals are close to the ground. Under normal conditions most species dance from five to thirty feet above the substratum. A

few, such as *Ephemerella*, usually conduct their dance high in the air, about thirty to one hundred feet above the ground.

FATE OF THE MATED INDIVIDUALS

Copulation achieved, the female flies off to deposit her eggs. The male, being polygamous, returns to the dance. This dance may continue for several hours. For species that mate at twilight, darkness is the limiting factor to the dance of the males. In species of *Campsurus* and *Ephoron* the nuptial dance lasts until the individuals are exhausted. Apparently the same thing happens to numerous individuals of other species.

The males of most species, if they have not mated or are not exhausted, return at the end of the dance to the vegetation and await the dance of the following day. Careful watching of a dance will always show that a large percentage of the males fly back into the surrounding vegetation. Since they are unable to feed in the winged state, they must live upon stored energy. A still greater danger is that of desiccation. I have often seen males fly rapidly from the vegetation and drop down upon the surface of the water with wings outspread. After remaining in this position for a few seconds, they would then fly back into the vegetation. As is well known the adult ephemerid's body surface is hydrofugic. Experiment has shown, however, that the area of the degenerate mouthparts is not hydrofugic in the imagoes and that individuals are capable of imbibing water. Apparently the males referred to above return to the water for a drink.

In any case, the winged life span of an ephemerid is relatively short and has only one function: the fertilization and oviposition of the ova.

CONCLUSIONS

1. All ephemerids, with the exception of a few parthenogenic forms, as adults engage in a nuptial dance which insures the males copulating with the females.

2. This dance and the copulatory movements follow a rather standard pattern for all species of the order. This is another evidence that the order is monophyletic.

3. There are a few modifications to the standard dance pattern. These (hovering, horizontal and vertical) are modifications to meet specialized conditions.

4. The dance may take place at any time of day or night depending upon the species and environmental conditions. Within limits, however, each species has a preferred time for mating.

5. Various genera usually choose specific types of localities to engage in the dance.

6. The males of many species live several days and engage in several nuptial dances. They apparently counteract desiccation by their ability to imbibe water.

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