

## THE SWARMING BEHAVIOR OF MAYFLIES (EPHEMEROPTERA)

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In amphibiotic insects, natural selection makes different demands on the immature and adult stages. In the life cycle of mayflies, only one function is incumbent on the adults stage—the production of progeny. Since adult mayflies are not concerned with the problem of obtaining food, their whole organization is adapted for reproductive activity. Flight is virtually the only form of locomotion in alate mayflies. Therefore, the finding of the female, her capture and mating take place in the air. Only in flight is the male able to assume the position needed for mating. Brink (1957) has stressed the striking uniformity of the reproductive system in mayflies, and, obviously, of the position assumed by the partners at the time of mating, which is the same for all Ephemeroptera. Mating is preceded by peculiar swarming behavior, of which the nuptial dances of the males are a characteristic component. This behavior dominates all flight activity in mayflies. It is, therefore, natural that in spite of the primitive wing type in mayflies, their structure is specialized for performing the swarming function (Edmunds & Traver, 1954). This is also true for the whole wing apparatus.

The nuptial dances of mayflies have been described frequently beginning with the 17th century (Swammerdam, 1675). At the present time, a considerable amount of data has been assembled dealing with the swarming behavior of various species, which makes it possible to systematize them. Since the existing information is not distributed very uniformly among the families of the Ephemeroptera, the standardization of swarming behavior presented is not definitive.

It must, moreover, be stressed that swarming behavior, though the dominant form of flight activity in mayflies, does not exhaust all the peculiar features of flight in these insects. The flight activity of mayflies can be described by three flight categories: 1) trivial flight, 2) flight particular to swarming behavior, and 3) migration flight. The purpose of this paper is to analyze the basic characteristics of swarming with special emphasis on the features of flight in mayflies in the course of swarming.

Swarming behavior may be regarded as an example of the general reaction to any element of the landscape, in relation to which a group of insects maintains a stationary position.

The concentration of the males in the swarm and its stationary position are vital conditions for the meeting of the sexes. The maintenance of these conditions is particularly important for mayflies since their sexually mature stage is of very short duration. In addition, because of swarming behavior, the males remain close to the water basin, in which development of the nymphal stage takes place. In the course of the development of swarming behavior, individuals that flew too far from the water were possibly subjected to the action of selection. Subsequently, the stereotype

of behavior was maintained in that individuals that infringed it for one reason or other were eliminated by selection.

Besides the swarming functions referred to above, which can be considered basic, there are secondary ones. Downes (1969) suggests that a situation is created during swarming that facilitates cross-fertilization and the disruption of the swarming mechanism constitutes the beginning of a system that varies from cross-fertilization to facultative parthenogenesis. Normally, the mayfly swarm consists exclusively of males. When atmospheric conditions change, and primarily the humidity conditions, females also may participate in the swarming (Verrier, 1956). Under extreme conditions, the number of males in the swarm falls sharply, as a result of which the females lay unfertilized eggs. Facultative parthenogenesis, therefore, which occurs in some species of Ephemeroptera, may be regarded as a result of the disruption of the swarming mechanism. Degrange (1958-1959 [1960]), however, considers that the deficiency of males cannot entirely explain parthenogenesis. Parthenogenetic development of the eggs, taking place with some delay, may possibly serve to form a life cycle of specific duration.

Mayfly swarms, moreover, always consist of males of the same species. This phenomenon results in the reproductive isolation of the species, though it is no guaranty against random interspecific crosses.

A. The first type of swarming (Ametropodidae, Baetidae, Baetiscidae, Ephemerellidae, Ephemeridae, part of the Heptageniidae, Isonychiidae, Leptophlebiidae, Metretopodidae, Potamanthidae, Siphonuridae). The emergence from the water of the subadults may be more or less prolonged in time. In some species, it lasts the whole season, while in others there is a 2-3 day emergence peak (Macan, 1958). The subimago flies to the bank from the surface of the water where it remains among the plants until the time of moulting to the adult stage. At the time of the nuptial flight, the males are spread out along the shore line of the water basin. With the advent of atmospheric conditions favorable to flight, the males collect together in a swarm.

The number of insects in the swarm may vary. Thus, in the swarming of *Rhithrogena morrisoni* Banks, a few males only were observed (Lehmkuhl, 1970), whereas for *Cinygmula reticulata* McDunn., the swarm was described as comprising hundreds of insects (Lehmkuhl and Anderson, 1970). In this group of mayflies, greater numbers of individuals in the swarm are of relatively rare occurrence.

The flight activity of the swarming insect must be so arranged as to avoid horizontal movement of the individual. Many Diptera remain in the same place because of a complicated trajectory of active flight; hovering is frequent (Downes, 1970). Mayflies with a more simply constructed wing apparatus solve the problem of keeping in place in their own way.

Under completely windless conditions, the nuptial dance of a single male takes place in the following manner. The take-off begins with the body orientated horizontally. Then the angle of elevation (the angle between the longitudinal body axis and the horizon) increases sharply to 90°, after which the take-off proceeds with the body oriented vertically. The take-off trajectory is most often vertical, but it may sometimes be inclined to the horizontal up to an angle of 75-80°. At the apex of the take-off flight, the angle of elevation again changes sharply to 0°, and the male proceeds to the second component of the dance—passive descent, the trajectory of which under the influence of gravity is strictly vertical. In descent, the mayfly body is oriented horizontally and at the bottom of the descent may be in a position in which the head is slightly lower than the apex of the abdomen. Control of body orientation during the take-off flight and descent is evidently achieved by means of the Palmen bodies.

The height of the take-off flight or, in other words, the amplitude of the dance averaged 1 m, but may vary according to conditions. The sequence of active and passive components is repeated several times, after which the male rises somewhat higher, at the same time shifting horizontally (Fig. 1, A). These flights are explained by the return of the male to the swarming site as the upward flight is accompanied by a horizontal movement of the individual.

Many authors (Kolesov, 1927; Spieth, 1940; Berner, 1950; Gordeyeva, 1958, etc.), observing the nuptial dances of different mayfly species, have noted that during the vertical take-off flights, the caudal filaments are folded and aligned with the body. Our observations on swarming in *Ephemera vulgata* L., *Baetis vernus* Curt. and *Cloeon dipterum* L. showed that the caudal filaments assume this position during swarming only under windy conditions (Fig. 2, A). When there is no wind, the caudal filaments of these species are separated, though not very much (Fig. 2, B). They are more markedly separated in trivial flight (Fig. 3) and to the maximum extent during the descent in the nuptial dance.

In describing the "parachute" flight of mayflies, Shvanvich (1949) states that the role of the caudal filaments together with the wings is to slow down descent in the nuptial dance. Because of air resistance, the caudal filaments are pulled apart and draw the apex of the abdomen upwards. The separation of the caudal filaments, however, is a more active movement. In the folded position, they offer less resistance, as can be appreciated from their position during take-off flights in wind.

The wings, during the descent in the nuptial dance, are raised and fixed so that the angle between them amounts approximately to 140°. The legs assume the typical flight position (Fig. 3).

In the absence of wind, the orientation of the males in the swarm may vary. Thus, in a swarm of males of *Ephemera vulgata* L. during 30 seconds (the time needed for counting), about 65% of the males were oriented parallelly to the line of the bank, while the remainder were variously so. Synchronization of movements in the swarm did not occur: some individuals demonstrated ascending flights and others passive descents. In the presence of wind, all males were oriented with the head to the wind, and the dance became less regular because of the greater variation in the amplitude of the dance. In addition to the amplitude of the dance, the velocity of the vertical take-off flights varied: with gusts of wind, the velocity

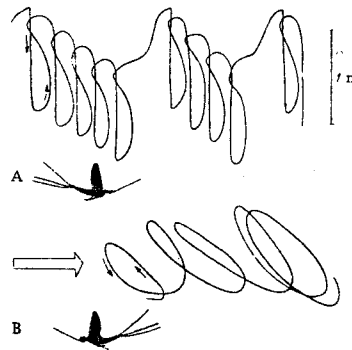


Fig. 1. Flight trajectory of the male of *Ephemera vulgata* L. in the nuptial dance. The mayfly silhouette shows the orientation of the male at the bottom of the descent.

A—nuptial dance in still air; B—nuptial dance in wind. The arrow shows the wind direction.

of the take-off flight increased. The take-off flight begins with the body oriented horizontally, but proceeds with an angle of elevation of about 45°. The trajectory of the active and passive components becomes slanting as the male seeks to compensate for drift caused by the wind in the passive component stage (Fig. 1, B).

With a wind velocity markedly exceeding flight velocity, the mayflies naturally cease swarming and alight on the grass. However, we noted swarming of mayflies of the genus *Caenis* Steph. with a wind velocity that reached 5.6 m/sec. The active components of the dance with the body oriented horizontally lasted throughout the whole duration of the take-off flight. The caudal filaments were folded the whole time except at the bottom of the descent, where for a moment they became separated. The amplitude of the dance varied from 10 cm to 1 m. In spite of this, the swarm drifted with the wind the whole time.

In addition to the adaptations mentioned above for swarming under windy conditions, some small species of mayflies belonging to the genera *Caenis* Steph. (Eaton, 1888) and *Baetis* Leach (Needham et al., 1935), and also according to our observations on the genus *Centroptilum* Eth., accelerate the descent by working their wings. According to Flower (1964), small insects with relatively large legs and cerci have a high body resistance. For small species, this circumstance counteracts drift even in gentle wind at the time of the passive component of the dance. A slight movement of the wind is almost always present, particularly at open sites. Acceleration of the passive component of the dance, therefore, may be regarded as adaptive for small mayfly species.

The maintenance by the male of the swarming position depends on its flight abilities and its capability for orienting itself in relation to the elements of the landscape. Special studies have revealed that the faceted eyes and the antennae are of primary importance in the control of the flight trajectory by the insect. The exceedingly simple structure of Johnston's organ in mayflies—a ring of bipolar nerve cells in the second antennal segment (Needham et al., 1935)—provide grounds for thinking that the antennae in mayflies are not a



Fig. 2. Male of *Ephemera vulgata* L. in the nuptial dance.

A—nuptial dance in still air; B—nuptial dance in wind.

specialized organ. Consequently, is based on the flagellum of the pedicellus under the control of the lateral eye, which enables the insect to maintain its position in the air no more than this requires the insect in relation to the presence of wind. Wind velocity gives rise to drift in relation to the lateral eye, which maintains its position in the air. The lateral eye has shown that it can maintain its position for any positions for example, the lateral eye of *vulgata* L. is not more than 1 m/sec.

Control of the lateral eye in addition involves the lateral eye. An attempt by the insect to maintain its position in the air by the lateral eye. The well-developed lateral eye is indicative of the importance of the lateral eye in control. The compound eye is larger than those of the lateral eye (divided morphologically) and a lateral eye may be very small. The lateral eye may be very small, while a head of the lateral eye is present. The division of the lateral eye into elements of the lateral eye. The lateral eye, in principle, is composed of elements of the lateral eye.

It is accepted that the lateral eye in mayflies is superpositioned on the compound eye. The appositioned visual system is adapted for the lateral eye and are characteristic of the lateral eye. Swarming mayflies may be observed for 24 hours. Some mayflies may be observed while others are observed during swarming occur.

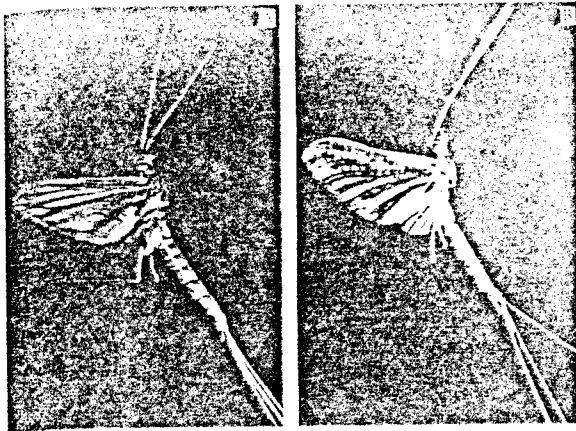


Fig. 2. Male of *Ephemera vulgata* L. at the beginning of the take-off flight in the nuptial dance.

A-nuptial dance in wind; B-nuptial dance in still air.

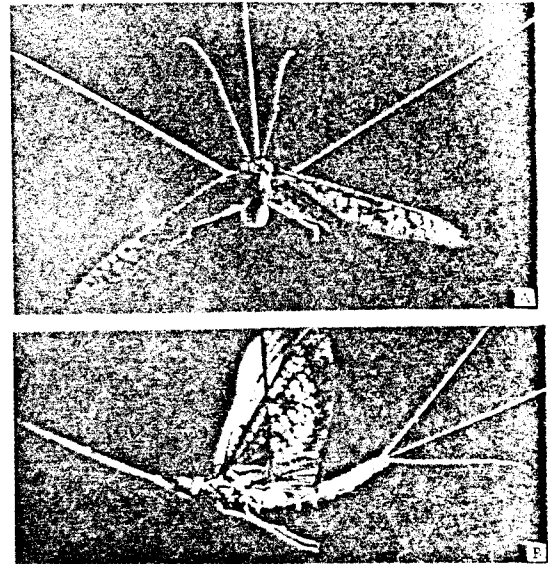


Fig. 3. Male of *Ephemera vulgata* L. in the trivial flight regime.

A-front view; B-side view.

specialized organ. The principle of their action, consequently, is based on the perception of the movement of the flagellum of the antennae in relation to the pedicellus under the influence of the external load, which enables the insect to assess its velocity in relation to the air and to stabilize its flight course, but no more than this (Heran, 1969). Flight in the swarm requires the insect to control its velocity strictly both in relation to the elements of the landscape and, in the presence of wind, in relation to the air. An increase in wind velocity gives rise to a reflex increase in velocity in relation to the air, as a result of which the insect maintains its chosen position in relation to a given element of the landscape or marker. Observations have shown that mayflies are able to maintain stationary positions for a wide range of wind velocities. Thus, for example, the swarming of males of *Ephemera vulgata* L. is not disrupted in wind with gusts of 4.3 m/sec.

Control of its position in relation to the marker, in addition involves an optomotor reaction, i. e., the attempt by the insect to maintain a specific gliding velocity for a background picture through the eyes. The well-developed faceted eyes of mayflies are indicative of the important role they play in flight control. The compound eyes of the males are considerably larger than those of the females and are frequently divided morphologically into an upper division (frontal eyes) and a lateral division (lateral eyes). The frontal eyes may be very large, fungoid or ampullaceous in form, while a hemispherical form is characteristic of the lateral eyes. In cases where no morphological division of the eyes occurs, the structure of the optic elements of the upper divisions may differ, nevertheless, in principle from the structure of the optic elements of the lower divisions (Zimmer, 1897).

It is accepted that the upper divisions of the compound eyes in mayflies can be considered as possessing superpositioned vision and the lateral divisions appositioned vision. Eyes with superpositioned vision are adapted for work under conditions of poor light and are characteristic of nocturnal insects. Mayfly swarming may take place at different times during the 24 hours. Some species have diurnal peaks of activity, while others are nocturnal in flight. Most frequently, swarming occurs at dusk or at sunrise. In this case,

the light changes rapidly, which causes difficulties in determining the degree of light to which the flight activity of the different species of Ephemeroptera is adapted. Harris (1952) assessed the light intensity at which average flight activity occurs in mayflies as exceeding 10 000 lux. It was established that species such as *Ephemera danica* Mull., *Paraleptophlebia cincta* Retz., *Baetis scambus* Etn., *Centroptilum luteolum* Mull., *Cloeon simile* Etn. and various others, also with divided compound eyes, have a flight adapted to a high level of light intensity. Consequently, the frontal eyes of males function during the day in counterbalance to the view that they are organs of nocturnal vision. Evidently, the division of the compound eyes in males into two functional parts has a different significance.

Acuity of vision in the compound eye of insects is known to be more marked the more ommatidia there are in the same angle or, in other words, the smaller the angle between adjacent ommatidia. This conclusion applies to vision in the resting insect. Autrum (1949) has shown that vision in the insect in movement is markedly different. For the eye of the moving insect, a single object is perceived as a succession of flickers. For its perception, the ommatidia must possess well contrasted sensitivity and low inertia, while high angular density of the optic units is not essential (Mazokhin-Porshnyakov, 1965). Eyes with large inter-ommatidial angles are found advantageous since in such a position light perception of the neighboring ommatidia will not change too quickly. In the mayfly *Ephemera vulgata* L., the interommatidial angle is  $2^{\circ}14'$ , i. e., greater than in insects belonging to other orders (Odonata, Orthoptera, Lepidoptera, Hymenoptera and Diptera). On this basis, the particular adaptation of the eyes in mayflies to vision in flight can be appraised. For vision in movement, moreover, the large size of the facets is a contributory factor. For distinguishing small objects (such as the females) moving with a high angular velocity, it is best for the image of the object to remain as long as possible within the confines of a

a single ommatidium. The upper divisions of the compound eyes of the males have larger facets, as compared with those of the lateral divisions. The function, therefore, of distinguishing the female in flight is incumbent upon the upper divisions of the compound eyes, while with the lateral divisions, the male orients itself in relation to the elements of the landscape.

The male mayfly, therefore, guiding itself visually, flies to the marker and then, at the time of the nuptial dance, controls the flight trajectory and velocity in such a way that the image of the marker glides past the eye in an anterior-posterior direction during the active component of the dance. As only the active component of the nuptial dance is controlled by the insect, the glide past the eye in a specific given interval of time takes place in the same direction. The angular displacement of a small marker will take place too quickly and in this case, the male will seek to impart a specific velocity to the occurrence of the image of the marker on the lateral divisions of the eyes.

The passive component of the nuptial dance is evidently more adequate for identifying the female since at this time the frontal eyes of the male are turned upwards. This applies primarily to species with an ampullaceous form of frontal eyes or one closely resembling it. The movement of the male in a vertical plane at the time of the nuptial dance results in its area of constant vision being only above. The female, the flight trajectory of which is below or to the side in relation to the male, will not be detected by the latter. The position of the frontal eyes of the male, therefore, is correlated with the character of the nuptial dance.

As swarming markers, the males of this group used large objects of relatively rare occurrence: the shores of lakes, roads, rows of plants on the littoral etc. It is essential for the marker to be in the immediate vicinity of water. The same marker may be used for swarming by different species at different times within the 24 hours.

Over a marker with extensive boundaries, several separate swarms of a single species may occur simultaneously. The joining of the swarm by new males is determined evidently by a reaction to the insects already swarming. But in addition, it is possible that some details invisible to the eye of the observer, as for example, the irregular distribution of high grasses, may be used as small markers suitable for the formation of local swarms.

Swarming in some species may take place under conditions in which visual contact with water is absent. Sometimes the marker over which the swarm is located may be at a distance of more than 1 km from water (Bogoescu and Tăbăcaru, 1969). Under these conditions, the function of preventing the dispersal of the population is fulfilled entirely by a small marker contrasting with the form of the earth or sky. The formation of swarms at some distance from water is characteristic of mayflies of the genus *Ephemerella* Walsh (Spieth, 1940). In addition, according to our observations, mayflies of the genus *Cloeon* Leach frequently swarm far from water. It is interesting that in one of the species of this genus, relatively high toleration of a dry atmosphere was noted, as compared with that of other mayflies (Inagaki, 1970).

The height of the swarm above the marker is determined primarily by the possibility of visual contact with it. The flight trajectory is controlled by the

insects only within the boundary layer, whereas beyond its confines wind determines the flight direction of the insects (Johnson, 1966). The thickness of this boundary layer depends on the flight velocity of the insects in still air and is sharply diminished in wind. Wind, therefore, limits the height of swarming above the ground.

The height of swarming in mayflies, i.e., the distance from the lower boundary of the swarm to the ground, was estimated by Spieth (1940) as being 1.5-9 m, though a number of authors (Spieth, 1940; Cooke, 1942; Bogoescu and Tăbăcaru, 1969) have mentioned very much greater heights for swarming in some species. The increase in the height of swarming may be due both to change in atmospheric pressure (Cooke, 1942) and to increase in the number of insects in the swarm (Lyman, 1944; Berner, 1950). For species swarming at dusk, a gradual increase in swarming altitude is noted due to the avoidance of cold air near the ground. Usually when an object at ground level is chosen as a marker, the mayfly swarming altitude rarely exceeds 5 m.

Thus, the swarm is formed. The female mayfly flies from the water over the row of plants on the littoral intersecting it at a right angle and, when no swarm is encountered, flies back again with a change in altitude. This continues until the female flies through a swarm. According to Kolesov (1927), the male reacts to the female only when the altitude of the flight trajectory of the female above the swarm does not exceed 50-80 cm. Since the eyes of the female mayfly are considerably smaller than those of the male and are not divided into two sections, the female probably detects the marker and not the swarm. Mating usually takes place in flight, after which the male again returns to the swarm. A single female can be repeatedly fertilized, while the male may fertilize several females at swarming time (Eaton, 1888). The possibility of polygamy and polyandry increasing the chances of the production of progeny is ensured, therefore, by the swarming mechanism described.

As can be seen from the enumeration above of the families of species with the first type of swarming, this type of behavior in the swarm is characteristic of most of the present-day mayflies. It is evident that a number of different phylogenetic branches have given rise to these families (Edmunds, 1962). Since the probability of an independent origin for this type of swarming is slight, the first type of swarming is considered the most generalized one in the swarm behavior of the insects of this order.

B. The second type of swarming (Heptageniidae: *Heptagenia* Walsh, *Stenonema* Trav.). The behavior of the males of this group in the swarm differs markedly from that considered above (Eaton, 1888; Cooke, 1940; Spieth, 1940). The male soars above the stream at a single site or slowly moves forwards parallel to the surface of the water and the line of the bank. At this time, its extended body is oriented perpendicularly to the surface of the water, while the caudal filaments are separated so that the angle between the longitudinal axis of the body and the caudal filament amounts to 90°. To retain its position relative to the marker, the male changes to trivial flight from time to time and flies backwards, after which it again moves forward in a hovering condition.

In the presence of wind, the character of the flight of the male in the swarm changes. Most frequently, the flight trajectory assumes the form of a loop reminiscent

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The eyes into two functional groups considered apically. Since the extent of the males extends on both eyes adapted to this area was. Thus, in the case of the female to the female to it.

C. The Palingeniidae males of this surface of the assume the form (1951) writes Edm. flew with Odonata". His swarming by *Oligoneuria* of the genus *Oligoneuria* *Ephoron albipennis* compensates essential for expression that

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of that which occurs in the first type of swarming under windy conditions (Thew, 1958).

The eyes of the males in this group are divided into two functional divisions, but unlike those of the group considered above, they are not approximated apically. Since in the nuptial dance no vertical movement of the male occurs, the area of its constant vision extends on both sides of it. With the divisions of the eyes adapted for detecting the female situated apically, this area was delimited by a narrower spatial sector. Thus, in the second type of swarming, the male reacts to the female whose flight trajectory is located laterally to it.

C. The third type of swarming (Oligoneuriidae, Palingeniidae, Polymitarciidae). The swarming of the males of this group usually takes place close to the surface of the water (2.5-5.0 cm). The nuptial dances assume the form of rapid horizontal flights. Edmunds (1951) writes that the males of Lachlania powelli Edm. flew with the velocity of the "swiftest of the Odonata". High flight velocity was also noted during swarming by Eaton (1888) for the males of the genus Oligoneuria Pict., by Verrier (1956) for mayflies of the genus Oligoneuriella Ulm. and by Thew (1958) for Ephoron album Say. High velocity flight evidently compensates for the lack of a constant zone of vision essential for locating the female. One has the impression that the swarming male "seeks" the female.

Females fly at the same altitude as the males or a trifle lower. From time to time, one of the females flies steeply upward, and this movement engenders a response reaction in the males, which begin to follow the female. In other words, the female, as is normal, flies through the swarm oriented in this case horizontally. The eyes of the male, therefore, must be adapted for distinguishing the female, the beginning of the flight trajectory of which is below it and laterally to it.

In fact, the lower divisions of the compound eyes of the males of Oligoneuriella rhenana Imh. are more markedly developed than in the females. The same thing, though to a lesser extent, has been observed in Palingenia longicaudata Oliv. and Palingenia sublongicaudata Tshern.

According to Verrier (1956), all the ommatidia of the eyes of the males of this mayfly group are functionally uniform and possess appositioned vision. It is, therefore, unclear how the male detects the female in conditions of low light intensity. Flight in some species is adapted to a high level of light intensity; others are able to fly with various light intensities, while a third group swarm mainly at night. In cases where flight takes place in the early morning, during the day or early in the evening, the picture of swarming described above occurs. In particular, normal swarming has been observed in these conditions in Oligoneuriella rhenana Imh. (Pinet, 1967) and Palingenia sublongicaudata Tshern. (Kosova, 1967).

In the genera Campsurus Etn. and Polymitarcys Etn. (Spieth, 1940) and in Povilla Nav. (Hartland-Rowe, 1958), as a rule flight takes place in conditions of low light intensity. It is characteristic that the highest numbers of known cases of massive flight have been described for the genera Palingenia Burm. and Polymitarcys Etn. (Ulmer, 1918; Neizvestnova-Zhadina, 1930; Pavlovskiy and Lepneva, 1948; Fishkis, 1955; Chernova, 1962, etc.). In massive flight, the insects emerge from the water so rapidly and in such

numbers that those newly emerging force those in flight into higher layers of the air. As a result, a column of mayflies rises over the emergence site, in which both males and females occur. Undoubtedly, under these conditions the chances of the meeting of the sexes are enhanced. It is, therefore, possible that the mechanism involved in detecting the female at night is not based on vision but on a different type of recognition. In any case, sexual dimorphism of the compound eyes is generally absent in mayflies of the genus Polymitarcys Etn.

Within the limits of the group discussed, therefore, one can follow all stages of transition from swarming of the third type to the behavior in which synchronized massive flight has an adaptive significance.

The aggregate nature of the group considered is clear. Divergence from the first type of swarming apparently occurred independently of the different phylogenetic branches. At the same time, the extent of the divergence was not uniform in the family Oligoneuriidae on the one hand and the families Palingeniidae and Polymitarciidae on the other. The representatives of the last two have still preserved in trivial flight the passive component of the nuptial dance of the first type—gliding (Buldovskiy, 1935a; Tientsuu, 1935), whereas the Oligoneuriidae have lost it in connection with the tendency to rapid flight. The tendency to massive flight is more clearly perceptible in the Palingeniidae and the Polymitarciidae. In this connection, they are close to the representatives of the genus Hexagenia Walsh, the nuptial dances of which also undergo changes in connection with the synchronized flight of a large number of individuals (Cooke, 1952). In addition, for some species of the family Palingeniidae, abatement of the flight function is characteristic. In the highest degree, this applies to Chankagenesia natans Buld.: the males and females of this species, employing their wings, are only just able to skim over the water (Buldovskiy, 1935b).

D. The fourth type of swarming (Caenidae and possibly Tricorythidae). Swarming in this group of mayflies may take place both over the water and over the littoral. The insects in the swarm have a nuptial dance reminiscent of that in the first type of swarming (Needham, 1908). The flight trajectory of the male in the swarm, however, may be more complex, with a more frequent alternation of the active and passive component. In some males of the genus Caenis Steph., we noted in the swarm a spiral trajectory for insects flying upwards.

The males of this group have widely separated appositioned eyes that are not divided into two functional parts.

The ratio of males to females in swarms recorded by Miron (1960), amounting to 620:2 in Ephemerella ignita Poda, 150:9 in Rhithrogena grisocola Bog. and 68:18 in Caenis macrura Steph., shows that the swarm of the last species includes both sexes. We noted a similar sex ratio in swarms of Caenis horaria L. (130:34) and Caenis undosa Tiens. (50:8). The presence of females in the swarm is evidently characteristic of this group of mayflies. In the case of close contact of individuals of different sexes in swarms with high insect densities, receptors other than the eyes may become important. In this connection, the sexual dimorphism of the antennae of mayflies of the genus Caenis Steph. appearing in the form and size of the pedicellus strikes attention. Since the females have larger wings, the sound intensity and possibly its tone differ as between the sexes. On this basis, the suggestion can be put

forward that during swarming in conditions of low light intensity, the antennae also assist in detecting the female.

#### SUMMARY

In the flight activity of the male mayflies behavior is predominantly associated with swarming. As regards the swarming site, mayflies form three groups; 1) species swarming over water; 2) species swarming over the littoral but maintaining visual contact with the water; 3) species swarming in conditions where there is no visual contact with water. Swarming altitude rarely exceeds 5 m. Four types of swarming are distinguished.

The first type of swarming is characteristic of species belonging to the families Ametropodidae, Baetidae, Baetiscidae, Ephemerellidae, Ephemeridae, Heptageniidae (part of the genera), Isonychiidae, Leptophlebiidae, Metretropodidae, Potamanthidae, Siphonuridae. The following are the characteristics of this type of swarming: 1) the swarm consists of males; 2) the swarm is located above a marker; 3) the males in the swarm demonstrate nuptial dances consisting of a sequence of active and passive components; 4) the female flies through the swarm and is captured by the male; 5) the male detects the female visually.

The second type of swarming occurs in some species belonging to the genera *Heptagenia* Walsh and *Stenonema* Trav. (Heptageniidae). Unlike the first type of swarming, the nuptial dance of the male of this group assumes the form of hovering.

The third type of swarming is characteristic of species belonging to the fam. Oligoneuriidae, Palingeniidae and Polymitarciidae. This type of swarming differs sharply from the first and second types. The nuptial dance of the male is represented by rapid horizontal flights parallel to the surface of the water. The massive flight of mayflies of this group evidently compensates for the impossibility of the male detecting the female visually in conditions of low levels of light intensity.

The fourth type of swarming occurs in the species of the fam. Caenidae and possibly Tricorythidae. The nuptial dance of the male is analogous to that of swarming in the first type. Both males and females may participate in swarming.

In swarming of the first, second and third types, the position of the divisions of the compound eyes of the male adapted for detecting the female is correlated with the character of the nuptial dance.

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