

THE SWARMING BEHAVIOUR OF STREAM INHABITING MAYFLIES
(EPHEMEROPTERA)

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Summary. The swarming behaviour of 25 species of Ephemeroptera, belonging to the families Siphonuridae, Baetidae, Heptageniidae, Leptophlebiidae, Ephemerellidae, Caenidae and Ephemeridae, was studied at Middle European localities.

In imagines, five types of sexual flight activities were distinguishable: dancing flight of males, offering flight of females, flight of the copulation-wheel, upstream migration and oviposition flight.

Dancing flight and offering flight occur at species-specific swarming sites. Most species swarm above the stream or above its bank. Only a minority of species prefer sites widely alongside the stream. The flying height during swarming is species-specific, too. Some species fly as low as 0.2 m, others tend to swarm up to 10 m, in some situations up to 20 and 30 m or more above water level. There is no connection between larger taxonomic units and swarming site or flying height. Closely related species rather show remarkable differences.

Dancing flight of males is characterized by dancing movements and chasing responses. The former follow very simple trajectories. Concerning their directions, four behavioural types were distinguishable: /1/ vertical fliers, /2/ horizontal fliers, /3/ diagonal fliers and /4/ vertical fliers with often repeated diagonal upward movements. The manner of dancing behaviour is characteristic of larger taxonomic units /families, genera, species-groups/.

As in the dancing movements, there also exist different types of chasing response in the males and offering flight in the females. As a result, more than five types of combinations of behavioural elements must be distinguished within the whole order Ephemeroptera:

Type A: Males dance horizontally. Females move in a similar manner when ready to mate. Chasing responses are directed dorsally.

Type B: Males dance diagonally. Other behavioural elements are similar to type A.

Type C: Males dance vertically. Behaviour of females varies intraspecifically, tending to a flight manner similar to that of conspecific males. Chasing responses as in types A and B.

Type D: Dancing movements strongly resemble Type C whereas other behavioural elements are characteristic: offering flight follows a relatively complicated trajectory and chasing responses point more or less ventrally.

Type E: Males dance nearly vertically and females hover within the swarm or move very slowly. In contrast to all the other types, the chasing response seems to be reduced.

The types A, B, and C, may be grouped together because of similarity in their chasing response which points to any dorsal direction. On the other hand C, D and E have in common the vertical dancing movement displayed by the males. In the whole order there shurely occur more than those five behavioural combinations, nevertheless the system is throught to be a framework of a classification of swarming behaviour of mayflies.

All behavioural elements during these swarming activities are fixed remarkably. This and their distribution within the taxa agrees well with differences in morphology between members of the different types, especially in the compound eyes of males.

Other sexual activities of mayfly imagines are more uniform. The copulation wheel is formed at the swarming site, mostly within the swarm. The couple often remains flying during this activity, moving away from the site. Thus, mating ends outside the swarm. Its duration varies between 3 sec. and 2 1/5 min., being more or less species-specific.

In some species an upstream migration follows. Choosing of egg-laying sites is remarkably poor. The oviposition flight is characterized by dancing movements, sometimes resembling the dancing flight of conspecific males. In other cases more complicated dancing patterns are exhibited by the females. These serve as a defence mechanism against mayfly males that often disturb the females engaged in egg-laying.

In contrast to that the dancing movements of the males during swarming seem have more than one biological role. Apart from the possibility of incapability to hovering flight, the following should be taken into consideration: /1/ Apparently the dancing movement is necessary for sex-recognition, /2/ it increases the likelihood of perceiving females, and /3/ it serves as a defence mechanism, in this case against predators. Some of these biological roles seem to be primary ones occurring in almost all species, whereas others - as secondary ones - are restricted to single species.