

## The Mating System of Chironomid Midges (Diptera: Chironomidae): A Review

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(Received September 9, 1987)

**Abstract** In chironomid midges, copulation occurs either in the air by swarming and/or on the ground (or water) by searching. In the swarming tactics, males form an aerial swarm at a landmark which includes no resource and copulate with females actively entering the swarm. In the searching tactics, however, males search for females, who participate passively in mating, and copulation occurs at the emergence site or resting place. In species having both these mating tactics, males have the possibility of copulating with virgin females by searching prior to swarming. However, due to the spatial and temporal convergence in the distribution of both sexes for mating, the swarming tactics may secure high mating rates of females even under situations of low adult density where high mating rates could not be secured by the searching tactics. In such conditions, the swarming tactics may be advantageous for both sexes. Interestingly, in the marine chironomids and the Himalayan wingless glacier midge, copulation only occurs on the ground (or water) by searching. In these species, extremely severe environmental factors (e.g. strong sea breezes or low temperatures) may have forced the midges to abandon the swarming habit.

In many species of chironomid midges and other dipterans it has been observed that males form an aerial swarm at a landmark which includes no resource for females, and copulate with females entering the swarm in the air (Downes, 1969; Sullivan, 1981, etc.). In other chironomid species, however, males search for females at the emergence site and copulate on the ground or water (Hashimoto, 1976, etc.). However, some chironomid species combine these tactics and copulation occurs both in the air by swarming and on the ground by searching (Syrjämäki, 1964; Oliver, 1968; Sasa, 1978; Kon et al., 1986).

“Landmark mating”, like swarming, is one of the most puzzling tactics in insect mating systems. Why do males make mating aggregation in spite of the severe competition for mates? Why do females actively go to the swarm regardless of its including no resource? Furthermore, if the swarming behaviour is adaptive, why do some chironomid species not show swarming behaviour? Answers to these questions may be obtained from comparative studies on the mating system of several species in which copulation occur by swarming and/or searching.

In the present paper, the mating system of chironomid midges is reviewed and a general discussion is made on the differences between the swarming and searching tactics. Finally, the evolutionary origin of swarming behaviour is also considered.

### *Classification of the Mating System of Chironomid Midges*

Two distinct mating tactics, swarming and searching, have been observed in chir-

onomid midges. Based on these mating tactics, the mating systems can be grouped into three types. In the first mating takes place only in the air by swarming, in the second in the aerial swarm and on the ground by searching and in the third only on the ground (or water) by searching.

In many chironomid species, mating is known to occur in the aerial swarm (*Spaniotoma minima*, *Metriocnemus longitarsus*, *Chironomus dorsalis*: Gibson, 1945; *C. strenzkei*: Syrjämäki, 1965; *C. pseudothummi*: Syrjämäki, 1966; *C. salinarius*: Koskinen, 1969; *C. plumosus*: Hilsenhoff, 1966; Römer & Rosin, 1969; *C. riparius*: Caspary & Downe, 1971; *C. thummi* and *C. piger*: Mielbradt & Neumann, 1976, *C. yoshimatsui*: Kon, 1984). However, in such species, without controlled studies under field and laboratory conditions it is difficult to exclude the possibility of mating also occurring on the ground. In a few species, it has been shown that mating may occur only in the air (*C. riparius*: Caspary & Downe, 1971; *C. yoshimatsui*: Kon, 1986). The mating system of these species can be regarded as the first type.

The second type, in which mating occurs both in the aerial swarm and on the ground, has been reported in several species (*Glyptotendipes paripes*: Nielsen, 1962; *Stictochironomus crassiforceps*: Syrjämäki, 1964; *Pseudodiamesa arctica*, *Diamesa geminata* and 2 *Chaetocladius* spp.: Oliver, 1968; *Tokunagayusurika akamusi*: Sasa, 1978; Kon et al., 1986). It has been suggested that, in *Chironomus pallidivittatus*, mating occurs on the ground and possibly also in the aerial swarm (Hein & Schmulbach, 1971). It has not been discussed which of the first and second types is more ancestral in the mating systems of chironomid midges, nor is it known which ecological factors are related to the difference between the first and second types of mating system.

The presence of male plumose antennae to detect female flight sound may not always indicate that, in that species, mating actually occurs in the aerial swarm under natural conditions. Conversely, at least in the chironomid midges, the absence of male antennal fibrillae suggests that the species may have the third type of mating system in which mating occurs only on the ground (or water). In marine chironomids males have simple female-type antennae and mating occurs only on the ground or water. Hashimoto (1962, 1970) has shown that marine chironomids are comprized of three main phyletic groups: the Clunionini, Telmatogetonini (Clunioninae) and *Pontomyia* (Chironominae), and that these may be further grouped into two morphologically and ethologically convergent types. One is the walking type in which both sexes are isomorphic and males walk to search for females. This has been observed in the Telmatogetonini and Clunionini except the genus *Clunio* (Hashimoto, 1962, 1964, 1970, 1976). The other is the gliding type in which females undergo a marked degeneration and lose their mobility and males glide fluttering on the water surface in search of newly emerged females or female pupae. This has been observed in *Clunio* (Clunioninae) and *Pontomyia* (Chironominae) (Hashimoto, 1957, 1959, 1962, 1970, 1976). These species having the third type of mating system, are supposedly derived from the species having a swarming habit and male plumose antennae. As suggested by Hashimoto (1962), the open rocky shore habitat of the marine chironomids is always exposed to strong sea breezes and such conditions may have forced the midges to abandon flight.

These types of searching behaviour, walking and gliding, are also known in the genus of *Diamesa*. In the Himalayan wingless glacier midge (*Diamesa* sp.) mating occurs

in the snow around the glacial melt-water drainage channel which is the larval habitat (Kohshima 1984, 1985). In this species it is likely that males walk in search of mates around the emergence site (Kohshima, personal communication). In *Diamesa japonica* males glide on the water surface of a rapid stream and copulate with newly emerged females (Kon, unpublished). These two species do not have a swarming habit nor male plumose antennae. However, as noted earlier, mating is known to occur both in the aerial swarm and on the ground in *Diamesa geminata* (Oliver, 1968). It is very interesting to study this genus, *Diamesa*, from the viewpoint of the relationship between ecological factors and evolution of mating systems.

#### *Differences Between Searching and Swarming*

As discussed by Thornhill and Alcock (1983), it is usual that males invest their effort to encounter potential mates because the gain from multiple copulations is larger in males than in females. Males search for mates in areas where they have the greatest likelihood of encountering available females, whereas females participate passively in mating. Therefore, the female distribution, which may be determined in accordance solely with their own needs, becomes the preceding condition for the distribution of searching males. In insect mating systems the major searching sites are the emergence site, the foraging site and the oviposition site (Thornhill & Alcock, 1983). In chironomid midges males usually search for mates at the emergence site and it is unlikely that copulation occurs at the foraging site because the adults of most chironomids take no food.

In *Clunio* spp., mating occurs at the emergence site by searching, but in fact, the emergence site and the oviposition site cannot be discriminated due to the extremely short adult life span. In these species, females copulate and oviposit at the emergence site during a short period after emergence (Hashimoto 1962). In *Clunio tsushimensis* and *C. aquilonius* males search for female pupae on the water surface. After locating a female pupa the male assists the female to emerge and then copulates with her (Hashimoto, 1957, 1962, 1969). In *Clunio takahashii* and *C. purpureus*, males search for a female pupa in the nest tube on the sea algae, and copulate with the female whose anterior end, covered with the pupal skin, is still lying within the nest tube (Hashimoto 1965, 1976). In *Clunio* spp., since the habitat is restricted to the intertidal zone of the rocky shore (except the *Clunio balticus* which has a pelagic life; Olander & Palmén, 1968; Heimbach, 1978) and the emergence time is also restricted depending on the semilunar and/or tidal rhythms (Hashimoto, 1965; Neumann, 1966; Neumann & Honegger, 1969), it seems very efficient for males to search for mates at the emergence site. However, in *Tokunagayusurika akamusi*, males search for newly emerged females at the resting place, the lakeside vegetation, at the peak emergence time. As suggested by Kon et al. (1986), in this species it seems probable that searching at the resting place is more efficient than that at the emergence site because the former, the lakeside, is narrower than the latter, the lake surface, and because females may be available for longer at the resting place than at the emergence site.

In the swarming tactics, females actively participate in mating. This is one of the essential differences between the swarming and searching tactics. Males form a swarm at a particular swarming site which includes no resource for females, and females come

there in order to copulate. Both sex seems to independently come to the swarming site by being visually attracted by the species-specific swarm marker. In order to ensure the encounter between both sexes at the swarming site, it is necessary for the timing of flight activity of both sexes to synchronize. In *Chironomus yoshimatsui*, it has been shown that the circadian rhythm of flight activity plays an important role to coincide both sexes (Kon, 1985). Furthermore, in several species, a seasonal change in the timing of swarming and mating has been observed (Syrjämäki, 1966; Römer & Rosin, 1971; Mielbradt & Neumann, 1976; Kon, 1984). A mechanism whereby the timing of flight activity is shifted seasonally is advantageous in multivoltine species because there may be seasonal change in the optimal time zone for swarming and mating.

As a result of the spatial and temporal convergence in the distributions of both sexes for mating, swarming tactics may secure high mating rates of females even under low population densities, a situation where high mating rates cannot be attained by the searching tactics. In such conditions, since females must copulate once before oviposition it is hardly surprising that they actively enter a swarm. Furthermore, it also seems likely that, under conditions of low densities, the swarming system may also be advantageous for males, in spite of the seemingly severe competition for mates.

If the female cost of travelling to a swarm is negligible, individual females need only have swarming tactics in order to secure a consistently high mating rate. However, for individual males, it should be more adaptive to also have searching tactics. The advantages of males having both these tactics is exemplified by *Tokunagayusurika akamusi* (Kon et al., 1986), where males have the possibility of copulating with virgin females by searching prior to swarming. From this viewpoint, it seems rather puzzling that there are species, like *Chironomus yoshimatsui*, which have only the swarming tactics.

On the other hand, as mentioned earlier, in marine chironomids (Clunionini, Telmatogetonini and *Pontomyia*) and the Himalayan wingless glacier midge (*Diamesa* sp.), extremely severe environmental factors (e.g. strong winds or low temperatures) may have forced the midges to abandon the swarming tactics.

#### *Evolution of Swarming Behaviour*

As pointed out by Thornhill and Alcock (1983), the landmark mating areas, like a swarming site, are the most puzzling mate-location sites in insect mating systems. They have noted that Parker's (1978) suggestion, that males waiting at the edge of a resource area perhaps gain a reproductive advantage because of a female preference for rapid mating, may apply to swarming species. Pajunen (1980) gave an alternative suggestion that male swarming behaviour originated from territorial behaviour, but he did not explain how the swarming site was evolutionarily determined. These suggestions apparently assume that the distribution of available females, which may be determined depending on the females' needs, precedes the distribution of males. However, at present, and probably also in the past, there seems to be no resource for females in the neighbourhood of the swarming site of chironomid midges. If the presence of a resource for females is not assumed to precede the swarming system, it is difficult to explain how a swarming site was determined through the evolutionary process. Thus, the origin of swarming behaviour remains unknown.

### Acknowledgments

I thank Prof. E. Kuno, Drs. T. Abe, M. Imafuku and S. Kohshima, Kyoto University, for helpful advice and critical reading of the earlier draft of the manuscript. I am much indebted to Prof. T. Hidaka, Kyoto University, for his invaluable advice and encouragement in the course of the present study.

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