Ann. Zool. Fennici 19: 81-85. 1982

Swarming behaviour in Ophyra leucostoma Wied. (Diptera, Muscidae)

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Pajunen, V. I. 1982: Swarming behaviour in Ophyra leucostoma Wied. (Diptera, Muscidae). — Ann. Zool. Fennici 19: 81-85.

The swarming behaviour of *Ophyra leucostoma* males consists of stationary hovering below branches of trees and tall bushes. The stationary flight is often interrupted by short chases made towards small flying insects. Rapid circling flights and short chases with no apparent target are performed when other males are present in the close vicinity. Long chases extending several metres from the swarming site are made after flying insects the size of *Ophyra*. In swarms, a regular occurrence is the momentary formation of a pair of males showing a common flight pattern. The inter-male reactions are interpreted as displays advertising the occupancy of a subarea in the swarming site. The swarming behaviour thus closely resembles territorial behaviour.

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1. Introduction

Swarming has been observed in all major groups of Diptera (McAlpine & Munroe 1968, Downes 1969), but only isolated reports have been made on Muscidae. However, swarming in this group differs considerably from the general pattern and its detailed study can contribute significantly towards the understanding of swarming. This paper describes the swarming behaviour of *Ophyra leucostoma* Wied.

2. Swarming sites

The bulk of the observations were made at Tvärminne Zoological Station, on the southern coast of Finland. Swarming was observed on a dry meadow situated some 200 m south of the main laboratory building. The meadow is surrounded by tall bushes and some larger trees. Bushes growing in small groups divide the area into several interconnected clearings. The ground vegetation is interspersed by bare rock.

Swarms occurred only on the northern edge of the meadow. Here a small wooden latrine stands in the bushes, and a faint odour of excrement is perceptible in the surroundings. The main swarming arena was along the path running to the shed, between some tall bushes. Another arena consisted of a 3 m wide opening between the bushes a few metres from the shed. A small swarm often formed along the path near the main arena. In all three places, the branches of surrounding trees partially overhung the arena. The places have been used for swarming during several successive years. In 1980 the area of Tvärminne Zoological Station was searched but no additional swarms were found.

Additional observations were made in 1981 at Lammi Biological Station, central Finland. Here swarming was observed on a small meadow containing solitary birch trees. The area was also being used for a study on carrion flies, and there was a strong odour of decaying meat in the area. Swarms formed below the branches of birches. No swarms were found in the surrounding area.

3. Description of swarming behaviour

In addition to direct observation, ciné-photography was used to study the details of behaviour, using film speeds of 24 and 70 frames per second. Flight paths of individuals in the vertical plane were reconstructed from frame-by-frame comparison. Examples are given in Figs. 1—4.

Swarms occurred only on sunny and calm days. During hot weather, slight overcast did not prevent swarming. No particular data concerning the timing of swarming were collected; swarming could be observed before 10.00 hours Finnish summer time, and during hot weather swarming could continue after 16.00 hours.

The form of the swarm was irregular. In a large swarm near a solitary tree, a denser centre swarm could be distinguished near the lowest branches, about one metre above the ground. This con-

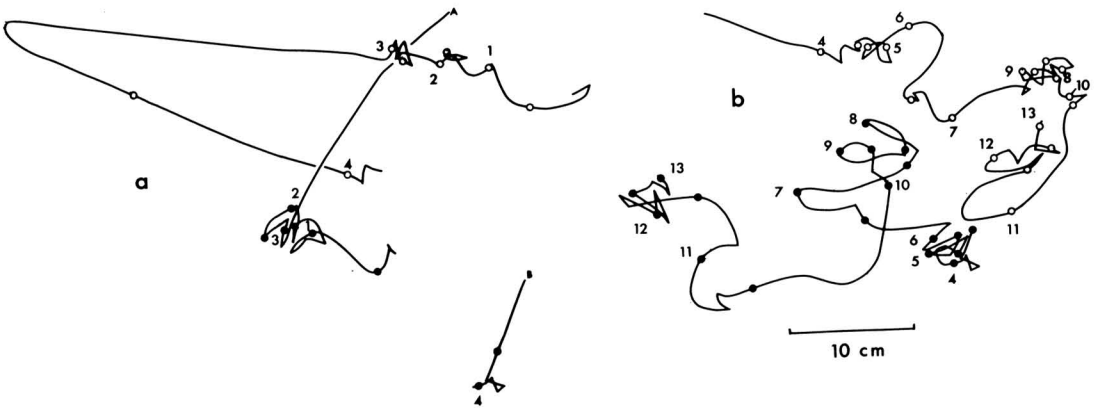

Fig. 1. Flight tracks of a pair of males, filmed from the side. The positions at half-second intervals are indicated by dots, the numbers refer to seconds from the start of the sequence. a) The males shift slowly to the left maintaining their relative positions: note the typical vertical movements during hovering. Then one male makes a sudden short chase to the left and another follows some 30 ms later, flying rapidly to the right. Its flight path is obscured by vegetation between points A and B. The interval from the start of forward flight to the tight turn at the end of the chase by the first male was about 130 ms. The slow return flight restores the original distance between the males. b) The males continue hovering, gradually regaining their original relative positions. These are maintained during a shift to the left.

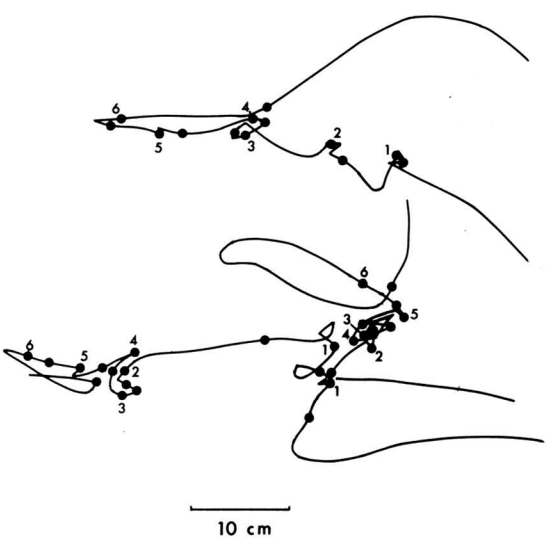

Fig. 2. Flight paths of males in a loose swarm. The positions are given at half-second intervals, the numbers refer to seconds from the start of the sequence. At the beginning of the sequence two males return from a long chase and change position gradually while hovering. The third male returns slightly later, hovers in position, then makes a short chase to the left. One of the early arrivals responds by flying to the right, then makes a chase to the right.

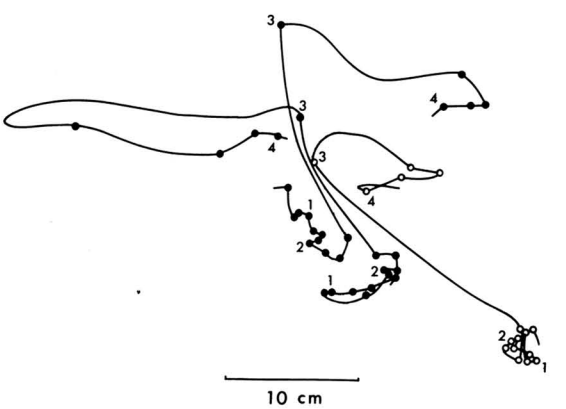

Fig. 3. Simultaneous short chase by three males, followed by circling. The positions of the males are given at 250 ms intervals.

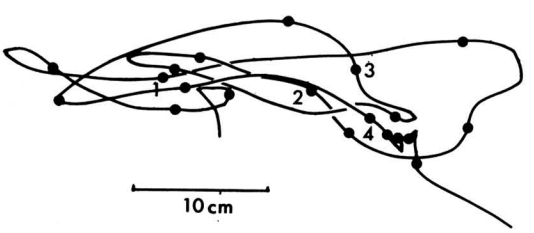

Fig. 4. Patrolling by a solitary male. The positions are given at 250 ms intervals.

sisted of 5—7 individuals occupying a volume of about one cubic metre. Around this centre, additional males were in a looser formation, the uppermost being a maximum of 2.5 metres above the ground. In swarming arenas bounded by surrounding bushes the swarm was denser and the vertical separation between the males flying at low and high altitude was only 75—100 cm. No females were observed in the swarms.

Several repeatable patterns can be recognized in the swarming behaviour. They can be described as follows.

Hovering. The male hovers in one position, maintaining its orientation for some time and changing it by abrupt turns. There seemed to be some tendency to face the nearby vegetation or against the direction of the wind. Sometimes the flight consists of slight sideways wobbling or up and down movements. The males appeared to maintain their station with aid of the surrounding vegetation and other males in the swarm. Station keeping appeared to be stronger in denser swarms at Tvärminne. Nevertheless, a male can slowly change its station up to 50 cm during a single bout of hovering.

Patrolling. Between bouts of hovering the male can engage in slow flight forward, followed, after a 10—30 cm advance, by a tight banking turn. The male can continue this type of flight for 10—15 s, remaining in an area of some 20—30 cm diameter.

Chasing. The male suddenly accelerates to rapid flight. The initial flight path is often straight, but in later stages, especially when the male attempts to follow a flying insect, it is conspicuously curved. Long intense chases, in which several males can participate, often extended several metres from the swarming site. This behaviour was evidently triggered by flies the size of *Ophyra,* but not all apparently suitable targets were effective. The great flight speed made accurate observation difficult and the outcome of these chases is not known. The return flight was usually made at lower speed, with sudden terminal deceleration when approximately the original station was reached. Often some of the males failed to return to the swarm after a long chase.

Shorter chases, 20—200 cm in length, were frequent. Some of them were made in order to investigate small Diptera, particularly small Muscidae and Syrphidae flying in the swarming area. The males often attempted to track the objects and the terminal parts of the flight paths were, accordingly, curved. Actual contacts with the targets were rare. However, short chases also occurred when no apparent targets could be recognized. These chases had straight flight paths and were made in a rigid fashion. The frequency of chases was correlated to the number of males present. Often two or several males reacted almost simultaneously, but the direction of flight was not necessarily the same.

Circling. In the typical form of this reaction, the male suddenly flies along a nearly circular path at high speed. The diameter of the path is about 20 cm. In most cases the plane of flight was almost horizontal. The flight is not directed to any target, although sometimes a male may fly towards or around another male. Another difference from the short stereotyped chases is the rapid return flight to the original station.

During swarming at least 80 % of the time was spent in hovering. Solitary males could also engage in bouts of patrolling. Occasional changes of station were made by slow normal flight. When several males were hovering near each other, they tended to restrict their movements. A swarm usually appeared to consist of pairs or triplets of males, maintaining a minimum inter-individual distance of some 10 cm and following a common flight pattern. Denser swarms maintained their structure often for several minutes and the original pattern was restored after chases. The males appeared to use their neighbours as principal reference points in station keeping. Sometimes, when a male made a short chase, others attempted to track it for 10—20 cm.

A solitary hovering male made short chases mainly towards recognizable targets or to avoid the attentions of individuals of other species. In dense swarms, on the other hand, males performed circling and short chases at a frequency of 5—8 cases per minute, even when foreign targets were lacking. Circling appeared to be induced by the presence of other males in close proximity. The arrival of a new male near an established male often induced this reaction. Repeated circling was often performed by males about to leave the area for a rest.

Stereotyped short dashes made towards and past other males often induced dashes or clear avoidance reactions, and disturbances involving several males could ensue. The almost simultaneous chases had the superficial appearance of one male attacking another, but the shortness of the flight and the absence of actual contact do not support this interpretation. Only rarely did two males engage in prolonged circling and longer chases, in which one clearly attempted to follow the other's flight path. Sometimes one of the participants left the arena after such interference.

The males were not marked and could not be

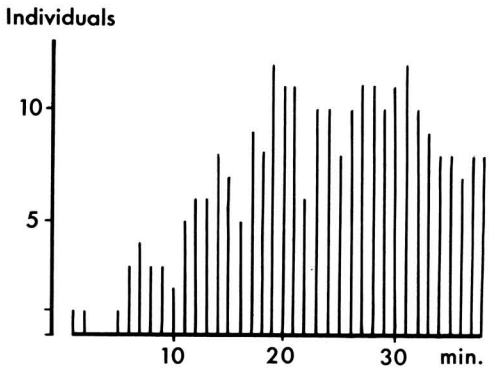

Fig. 5. Variation in the number of males in a single swarm. The values give the maximum numbers present at successive one-minute intervals.

identified with certainty. Observations on solitary males and small swarms suggest, however, that a single bout of swarming activity could continue for at least half an hour. The variation in the number of swarming males (Fig. 5) suggests considerably shorter average values. Resting males used the vegetation surrounding the arena as perches.

4. Interpretation of behaviour

No connection could be established between swarming and mating, but it is possible that long intense chases were initiated by *Ophyra* females. The energy used in swarming is considerable and the males can therefore be expected to gain some advantage from this activity. Swarming seems to occur in a habitat with certain olfactory signs which possibly indicate a suitable larval habitat. The swarming males might thus attempt to occupy a place where it is highly probable that they will find a mate. It is also possible that the hovering males can maintain higher flight speeds and can give chase more readily than resting males. They can also detect approaching females more effectively.

The swarming of *Ophyra* has clear social features. The males recognize each others as conspecific males. The coherence of the swarm and the concentration of males at a few selected places suggest that there is some form of attraction between the males. Although several apparently suitable swarming sites exist in the area, there is a clear hierarchy of preference between particular sites.

The minimum distance observed between the males means that there is a limit to the number of males a given arena can contain. A hovering male thus occupies a portion of contested resource and maintains its occupancy by its presence. The hovering can be interpreted as display behaviour advertising this. As circling seems to be connected with dense swarms, it may be an additional, perhaps stronger, form of display. Short chases, often performed almost simultaneously by neighbouring males may also have this function. The tendency to form pairs of males also supports this interpretation. Aggressive behaviour is usually directed towards a specific opponent.

5. Discussion

Insect swarming has been regarded as behaviour facilitating the meeting of the two sexes by concentrating the individuals at a suitable place at the correct time and also otherwise securing conspecific pair formation. At the causal level, swarming is generally interpreted as the reaction released in mature individuals by specific environmental factors and certain topographic releasers, swarm markers. Consequently, much effort has been expended in determining these factors, and surprisingly little detailed information exists about the swarming behaviour. Some accounts, however, suggest that the features observed in swarming *Ophyra* may be widespread. Communal hovering is known in Tabanidae (Bailey 1948, Blickle 1959), and the males seem to observe a certain inter-individual distance and react to intruding males. The swarming in Rhagionids of genus *Symphoromyia* includes chasing and rapid circling between males (Hoy & Anderson 1978). Okubo & Chiang (1974) detected momentary pairwise flight and chasing in *Anaretes pritchardi* Kim.

Pajunen (1980) suggested that the swarming behaviour of male insects could be interpreted as a type of territorial behaviour. This interpretation places more significance on the existence of inter-male reactions in swarming. The swarm is not regarded as group of males attracted independently by the swarm marker, but as an organized group competing for the space delimited by the swarm marker. The analysis of swarming in *Ophyra* supports this interpretation. The stationary hovering by males facilitates detection of the organization of the swarm, but this interpretation can obviously be extended to other Diptera that rely on visual recognition of mates. The behaviour of males can be inter-

preted as territorial display. On the other hand, the hovering males also act as releasers attracting further males to the swarming site. Wenk (1965) drew attention to the fact that only some suitable swarming sites were occupied by Simuliidae, and also demonstrated experimentally that swarms attracted solitary males.

If a swarm is interpreted as a collection of temporary territories, there should be an upper limit to number of males that can be accommodated by a swarm marker. Koyama (1962) found that the swarm size in *Fannia scalaris* Fabr. was limited by inter-male reactions. Wenk (1965) suggested that males of Simuliidae compete for optimum position near the swarm marker. In *Anaretes pritchardi* the males swarm along one edge of the swarm marker, and there appears to be a linear relation between the length of the marker and the number of males (Okubo & Chiang 1974).

The territoriality hypothesis of swarming gains support from the existence of territorial behaviour, at least in Syrphidae (Parmenter 1944, Collet & Land 1975a, Maier & Waldbauer 1979). Territorial defence consists of the tracking of approaching insects, chasing and spiralling flights, and even physical contact. The resemblance to the display in *Ophyra* is obvious. Aerial patrolling by solitary males, as well as station keeping by males of many species of Muscidae, Calliphoridae and Tachinidae (Downes 1969, Collet & Land 1975b) also show a clear tendency towards site attachment and differ from true territoriality only in the lack of defensive behaviour. The swarming in *Ophyra* can be evolutionarily derived from these types by assuming that the mating stations become topographically concentrated, and the territorial defence weakens to the level of stereotypic display.

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Received 30. X. 1981
Printed 18. VI. 1982