To Dr. Michael D. Hubbard
With Compliments
Eino Savolainen

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Swarming in Ephemeroptera: the mechanism of swarming and the effects of illumination and weather

EINO SAVOLAINEN

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Swarming was studied in *Ephemera vulgata* L., *Siphlonurus linnaeanus* (Etn.), *Heptagenia fuscogrisea* (Retz.), *Leptophlebia marginata* (L.), *L. vespertina* (L.), *Caenis horaria* (L.), and *Centroptilum luteolum* (Müll.) at three localities in southern Finland.

Each species swarmed close to a shoreline above a swarm marker. In *L. vespertina* populations differed in swarming behaviour. In *L. marginata* differences in the shape, size and density of the swarms, in swarming height and in orientation of individuals in the swarms indicate the presence of two sibling species.

S. linnaeanus swarms in the morning and evening twilight, and *L. marginata* and *L. vespertina* in sunshine, whereas *C. horaria* starts swarming in the afternoon and continues until the late evening. *E. vulgata*, *H. fuscogrisea* and *C. luteolum* swarm mainly in the evening, but *E. vulgata* also in the morning; these species may also swarm during the day, depending on temperature and amount of cloud.

The time of swarming of each species is affected by light intensity and air temperature. The higher the temperature, the later the time and the darker the twilight at which evening swarming takes place. However, swarming is apparently also controlled by internal factors. Swarming is prevented by wind at velocities of 1.5 to 2 m/s, depending on the species. It may also be arrested or prevented by high or low air temperature. In *S. linnaeanus* it was not directly affected by humidity. In its major features, swarming in mayflies resembled swarming in Nematocera.

E. Savolainen, Department of Natural History, Kuopio Museum, Kauppakatu 23, SF-70100 Kuopio 10.

I. Introduction

True aerial swarming is a widespread rhythmic aspect of insect behaviour (e.g. NIELSEN & HAEGER 1960, MCALPINE & MUNROE 1968, DOWNES 1969). Ample data have been published on the swarming of Diptera, particularly for Chironomidae and Culicidae (e.g. MCALPINE & MUNROE 1968, DOWNES 1969), but the swarming habits of other insects are poorly known. Data on mayflies mainly concern flying habits and copulation behaviour, and little is known about the swarms or the factors governing swarming.

Swammerdam (1675) appears to have been the first to study swarming in mayflies. Spieth (1940), Brodskii (1973) and Grandi (1973) made important contributions to our knowledge of their swarming, whilst Brinck (1957) and Degrange (1960) studied their reproduction and mating, and Müller-Liebenau (1960) made observations on the swarming periods of central European species.

This paper aims at elucidating the whole range of swarming behaviour seen in Finnish mayflies on the basis of observations on six representative species, *Ephemera vulgata* L., *Siphlonurus linnaeanus* (Etn.), *Heptagenia fuscogrisea* (Retz.), *Leptophlebia marginata* (L.), *L. vespertina* (L.), *Caenis horaria* (L.) and *Centroptilum luteolum* (Müll.). Studies were made on swarms and swarming sites, and on the effects of illumination and weather factors; the possible role of endogenous mechanisms was taken into account. In connection with this study Holopainen (1970, 1973) studied the behaviour of individuals and various aspects of reproduction.

II. Material and methods

1. Study areas

Field observations were made mainly at Maarianvaara, Kaavi, E. Finland (62° 51′ N, 28° 52′ E), on two islands, Matkonsaari and Tulisaari, in the lake Rikkavesi, along the river Syrjäjoki and on an esker between two lakes, Munajärvi and Kaitajärvi. Observations were also made on the shore of lake Keitele at Vesanto, central Finland (62° 56′ N, 26° 07′ E) and on the shore of lake Pääjärvi in Lammi, southern Finland (61° 03' N, 25° 03′ E) (Fig. 1).

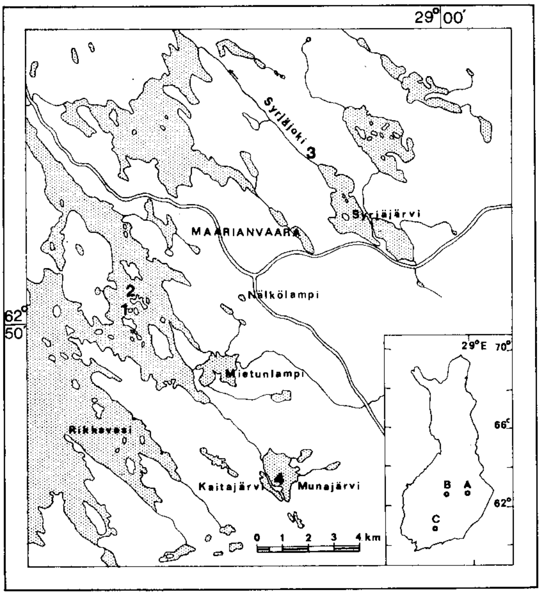

Fig. 1. The localities. In the smaller map A = Kaavi, B = Vesanto and C = Lammi. The larger map shows the Kaavi area; 1 = Matkonsaari, 2 = Tulisaari, 3 = Syrjäjoki and 4 = Munaharju.

Matkonsaari. An island about 150 × 100 m, with rocky shores fringed by a sparse belt of short trees and bushes. In the dense forest at the centre the trees range from 5 to 13 m in height. Most observations were made at the SE corner of the island, where there are only a few trees but a continuous underbrush of dwarf shrubs (Fig. 2).

Tulisaari. A wooded island, about 600 m long, except for its bays with rocky shores. Observations were made at two bays, Kalliolahti and Päivälahti. Kalliolahti is about 40 × 100 m and sheltered from winds (Fig. 3). Some underwater boulders breach the surface, which is covered with floating leaves of water plants; horsetails (*Equisetum*) grow sparsely along the shores, which are rocky except at the innermost part of the bay itself. There and along the N shore a belt of sedges (*Carex*) up to 8 m wide is separated from the dense woodland by a treeless belt of dwarf shrubs 5 m wide. On the S shore the trees extend right to the shoreline.

Päivälahti is about 60 m long and measures 70 m across its mouth. It is exposed to southerley winds (Fig. 4). At the mouth of the bay the shores are rocky, with many boulders, but at the innermost part the shore is no longer rocky. The vegetation resembles that at

Fig. 2 SE end of Matkonsaari.

Fig. 3. Kalliolahti.

Fig. 4. The innermost part of Päivälahti bay and the east shore.

Fig. 5. The Syrjäjoki locality.

Fig. 6. SE end of the Munaharju esker.

Kalliolahti. At its widest point along the E shore, the sedge belt is about 10 m wide. Dense woodland begins immediately behind this sedge belt.

Syrjäjoki. This river about 5.5 km long, 1.5 to 10 m wide and 0.2 to 1.5 m deep, flows mostly through a flat stretch of forested bog; in some places the water flows slowly. Observations were mostly made below the rapids about 150 m downstream from lake Syrjäjärvi. On the NE bank dense forest reaches the water-line, while on the SW bank a belt of sedges about 30 m long and 10 m wide lies between the shore and the forest (Fig. 5). Observations on *E. vulgata* were also made at a site about 500 m from the rapids (p. 20).

Munaharju. An esker between the lakes Munajärvi and Kaitajärvi, about 1.5 km long, 40 to 200 m wide, and 10 to 15 m high at its highest point, covered by dense pine forest with dwarf shrubs, patches of moss and lichen, and numerous boulders (Fig. 6).

Lammi. Observations were made at Pappilanlahti, a bay in lake Pääjärvi. The shore is fringed by belts of horsetail and sedge of varying widths.

Vesanto. The observations were made at Ritolahti, lake Keitele. The bay has a rocky shore, with a rather narrow sedge belt.

2. Methods

Field observations were made from 1967 to 1974, when possible for several weeks in succession. Additional observations were made to check the results.

Time of sunrise and sunset. Mean values for the times of sunrise and sunset (for the 4 years 1971—1974) were calculated by Professor Erkki Kääriäinen of the Geodetic Institute. The error does not exceed ± 2 min. Considering the influence of local conditions the method is regarded as sufficiently accurate.

Air temperature. Air temperature in the shade close to the swarming site was measured with a mercury thermometer at the level of the underbrush and at 1.5 m. Unless otherwise stated, air temperature data refer to the latter values. When the effect of cloud shadows was studied, the temperature was also measured in sunlight (see Fig. 17).

Light intensity. Light intensity was measured with a Lunasix 3 exposure meter aimed towards the zenith. For determining the effect of cloud shadows, the meter was pointed first towards the zenith and then from a height of 50 cm directly at the ground (see Fig. 21).

Wind velocity. Wind velocity was measured with a Fuess 118 glowing wire anemometer. The instrument was placed as close to the swarms as possible without disturbing them, at the level of the lowermost individuals. Air temperature was always recorded simultaneously.

Humidity. In 1970 the effect of relative humidity was studied for *Siphlonurus linnaeanus.* Two thermo-hygrographs were placed in the shade 15 cm above the ground and at a horizontal distance of about 5 m from the swarm studied. The direct effect of rain was observed for each species, but the amount of rainfall was not recorded.

Experiments with artificial swarm markers. Swarming sites and the orientation of individual mayflies were studied by testing the effectiveness as markers of pieces of cardboard or plastic that varied in size, colour or brightness, or were striped or checkered. Tests were also made with cut trees.

Transfers of swarming individuals. L. marginata individuals were transferred from one site to another in gauze mesh frames measuring from about 10 × 10 × 15 cm to 15 × 15 × 40 cm. Before being released, they were marked on the ventral surface of the abdomen with a bristle dipped in nail polish (see Holopainen 1970).

III. Results

1. Mechanism of swarming

A. Distance of the swarms from the shoreline

Fig. 7 shows the distances of the swarms of each species from the shoreline at Tulisaari. The distances were similar at the other localities (Table 1). *Ephemera vulgata, Leptophlebia marginata* and *L. vespertina* swarmed only above land, usually above a shoreline belt about 10 m wide, but successively smaller swarms were observed up to 100—150 m from the shoreline. *L. marginata* avoided the shore zone, which at Matkonsaari is about 5 m wide.

In *E. vulgata* the distances of the swarms from the river were studied about 500 m from the Syrjäjoki rapids in an area measuring 50 × 100 m (the shorter side parallel to the river), where the vegetation was fairly uniform (trees 1.5—6 m high; a dense stand of tall spruce beginning at 110 m). During the evening the swarming individuals were counted at 1-h intervals. Altogether six separate counts were made. As Fig. 8 shows, the number of swarmers decreases with increasing distance from the river (Kruskal-Wallis H = 39.628, i.e. significant at a confidence level of 99.9 %). Only a single individual swarmed 100—110 m from the river.

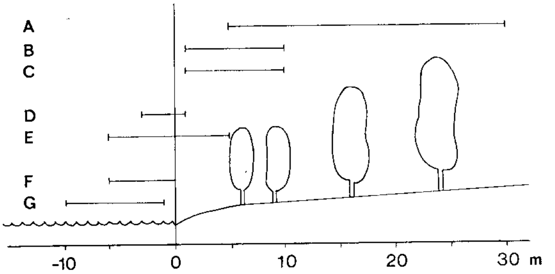

Fig. 7. The distances of swarms from the shoreline at Tulisaari. The line segments indicate the location of the majority of swarms of each species. No attention was paid to swarming height. A = *Leptophlebia marginata*, B = *Ephemera vulgata*, C = *Leptophlebia vespertina*, D = *Heptagenia fuscogrisea*, E = *Caenis horaria*, F = *Centroptilum luteolum* and G = *Siphlonurus linnaeanus.* The data are taken from Table 1.

Table 1. The distance of swarms from the waterline in metres. For species swarming over land only, the minimum gives the position of swarms closest to the waterline; for species swarming over water it gives the position of swarms farthest from the waterline. The maximum indicates the position of swarms over land farthest from the water. — = swarm above water, + or without a sign = swarm above land, n = number of observations. *L. m.* = *Leptophlebia marginata*, *L. v.* = *L. vespertina*, *E. v.* = *Ephemera vulgata*, *H. f.* = *Heptagenia fuscogrisea*, *C. h.* = *Caenis horaria*, *C. l.* = *Centroptilum luteolum*, *S. l.* = *Siphlonurus linnaeanus.*

	Locality	n	Minimum	Majority	Maximum
L. m.	Matkonsaari	15	1 – 5	5 – 30	All the way
	Tulisaari	10	1 – 5	5 – 30	150
L. v.	Syrjäjoki	10	0 – 1	1 – 10	100
	Tulisaari	5	0 – 1	1 – 10	100
E. v.	Syrjäjoki	20	0 – 1	1 – 10	130
	Tulisaari	20	0 – 1	1 – 10	100
H. f.	Syrjäjoki	20	Above the river		30
	Tulisaari	5	–5 – –7	–3 – +1	3
C. h.	Lammi	15	–10	–5 – +5	40
	Tulisaari	5	–15	–5 – +5	10
C. l.	Lammi	10	–12 – –10	–5 – 0	Not over land
	Tulisaari	10	–10 – –7	–5 – 0	Not over land
S. l.	Tulisaari	20	–20	–1 – –10	Not over land

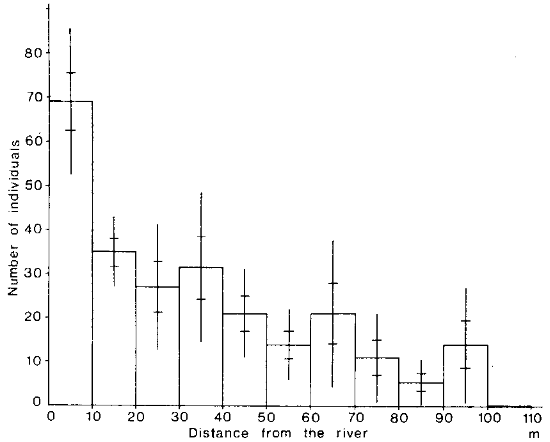

Fig. 8. The average numbers of *Ephemera vulgata* swarmers observed at Syrjäjoki on 17–19 June over different zones parallel with the river. Number of observations = 6, bars = standard deviations and cross-bars = standard errors of the mean.

Caenis horaria and *Heptagenia fuscogrisea* swarmed close to the shoreline over both land and water (Table 1, Fig. 7), the site and its distance from the shore depending on the swarm marker. *C. horaria* swarmed above light patches in the terrain and *H. fuscogrisea* orientated either to thes hore or to the river (p. 26). At Syrjäjoki, *H. fuscogrisea* was seen swarming above the river; if the weather was calm and if swarmers were present in large numbers, the mayflies also spread over sedge belts and forest. Accordingly, in Table 1 the maximum figure, 30 m, refers to the edge of a continuous swarm. At Rikkavesi the swarms were usually above water and shore stones but, if the numbers were large, swarming individuals were seen over trees on the shore.

Siphlonurus linnaeanus and *Centroptilum luteolum* swarmed only above water (Table 1, Fig. 7), the former above light-coloured markers to about 20 m from the shore (e.g. above *Nuphar* leaves) at the mouths of the bays, the latter on the shore.

Mayflies may drift for long distances with the wind and then swarm far from the shore. During windy weather swarms of *Leptophlebia vespertina* were found about 250 m from the Syrjäjoki, and on one occasion three individuals of *L. marginata* were seen swarming at Maarianvaara about 600 m from the little lake Mietunlampi (Fig. 1). In such weather *L. marginata* may swarm right at the shoreline and *C. luteolum* may drift overland for distances of 40 to 50 m from the shore.

B. Swarming sites and swarm markers

Ephemera vulgata

E. vulgata swarmed above open terrain as well as above single trees and forested areas (Table 2). Swarms were regularly seen above sedge belts fringing shores, and also farther away from the shore, e.g. over fields and forest clearings, but not between trees in a forest. Small swarms were sometimes seen, however, between the crowns of the trees; then, during calm weather, the major part of each flight trajectory rose above the treetops. During gusts of wind swarms often took shelter on the leeside of trees. Trees rising above the surrounding forest were preferred. This was confirmed by bringing cut trees of different heights into open terrain. Next to a forest of short trees, and sometimes also beside tall trees, part of a large swarm rose above the trees while another part swarmed at a lower level beside the trees. Swarming sites were permanent and the swarms remained in the same place even when over a large uniform area. The swarmers therefore apparently orientate to particular features of the terrain. Their ability to recognize such features was studied in the following experiments.

Small horizontal markers. Artificial markers ranging in size from 0.35 × 0.35 to 1 × 1 m were tested several times both during the day and in the evening. Individuals in large swarms over uniform terrain did not react to small markers but, if the swarm was small and concentrated, individuals avoided a marker placed below the swarm and returned to the original site only if the marker was removed.

Large horizontal markers. A semi-transparent plastic sheet, 3 × 6 m, was tested for two evenings at Tuli-

Table 2. Swarming sites (+) of the species studied. A = beside or above trees, B = over open terrain, C = over land above light-coloured markers, D = above light-coloured markers in water and E = over open water.

	A	B	C	D	E
Leptophlebia marginata	+	–	+[1]	–	–
L. vespertina	+	+	+[2]	–	–
Ephemera vulgata	+	+	–	–	–
Caenis horaria	+	–	+	+	–
Heptagenia fuscogrisea	+	+	–	–	+
Siphlonurus linnaeanus	–	–	–	+	–
Centroptilum luteolum	–	–	–	–	+

[1] = at Munaharju only
[2] = at Inari only

saari during calm, warm weather. When the sheet was carefully slipped under the swarm, all the individuals shifted to form a swarm next to the plastic or above nearby trees. Immediately the sheet was removed, they began to return to their original sites.

Tests with trees. Cut trees were brought into open terrain several times at Syrjäjoki and Tulisaari. Regardless of the number, height (1.5 to 6 m), and spacing of the trees, some individuals always moved over the trees, swarming as they do within or at the edge of a forest, and would even follow when the trees were moved to and fro over the sedge belt. Similarly, when a boat of the same colour as the shore sand at Vesanto was rowed away from the shore, one individual followed the boat for a distance of 10 to 15 m.

These experiments show that light-coloured markers may influence the position of swarms, their effectiveness depending on their size and on the site. However, swarmers would also follow a marker the colour of the ground. They seemed to orientate visually to the sedge belt or other features of the terrain. Trees and continuous vegetation seem to serve almost equally well as swarming sites, since swarms hovering above trees may move to open terrain and vice versa.

On their offering flight (cf. SYRJÄMÄKI 1964a, HOLOPAINEN 1970) females may orientate to the swarming site in the same way as males. On three occasions observed at Vesanto a female made offering flights above a swarming site even though no male (twice) or only one male was present. The male and female showed no signs of interest in each other.

L. vespertina resembled *E. vulgata* in behaviour. When the numbers of individuals were very large, swarms were almost continuous over the forest, but denser around treetops (Syrjäjoki). At Inari (68° 43′ N, 25° 10′ E.) swarms were observed on a sedge fen above small markers paler than the environment (e.g. bush of *Salix lapponum* or an insect net).

Leptophlebia marginata

Observations at Matkonsaari and Syrjäjoki. In open terrain swarms formed beside single trees, but within a forest they formed alongside treetops, with the upper edge of the swarm at the level of the treetop. Exceptionally small swarms were observed in open terrain over or beside tussocks. A swarm near a single tree formed above the shadow of the tree and moved round the tree with the shadow (Fig. 9). Near single trees (1 to 8 m tall) small swarms (1 to 20 individuals) formed at about the end of the shadow, i.e. the taller the tree, the farther from it the swarm. Large swarms were usually elongated, with the leading edge of the swarm close to the tree and the rear edge over the end of the shadow (cf. Fig. 9).

The establishment of a swarm over a site thus depends on trees. The following tests were made to study the mode of orientation. (Experiments 1—4 were repeated several times each summer).

1. When all trees were removed from a site of regular swarming, only a few mayflies swarmed above the site.
2. If trees were erected in open places, where no regular swarming occurred, swarms usually appeared by the newly erected trees and would follow them if they were moved slowly and steadily.
3. These mayflies also swarmed near vertical black-and-white plastic markers measuring 50 × 160 cm (Fig. 10) and near the observer. They followed these markers.
4. No swarming was observed over artificial markers ranging in brightness from pure white to pure black and of various sizes, from 25 × 25 to 100 × 100 cm, placed horizontally over low vegetation. No individuals moved over the markers if they were placed next to swarms or used to lengthen the shadow of a tree.

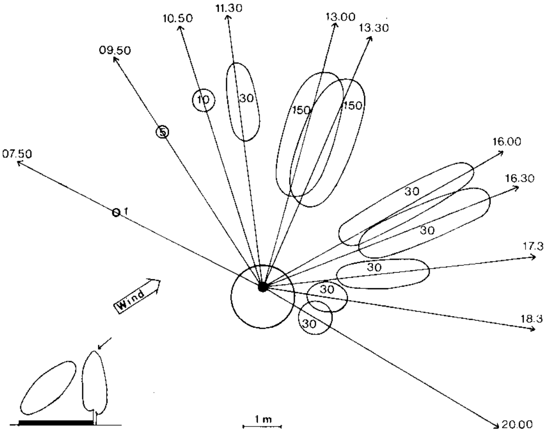

Fig. 9. The movements of a single *Leptophlebia marginata* swarm on 4 June 1968 at Matkonsaari beside a tree 6 m tall. The arrows indicate the direction of the sun's rays at a given time. The numbers inside the ovals or circles (illustrating the position of the swarm) denote the numbers of swarmers. The circle in the centre with the black dot inside it represents the foliage and stem of the tree. The small figure at the lower left corner shows the relationship between the swarm and the tree. The slanted column represents the swarm, the thick line below it the shadow of the tree, and the arrow the direction of the sun's rays at noon.

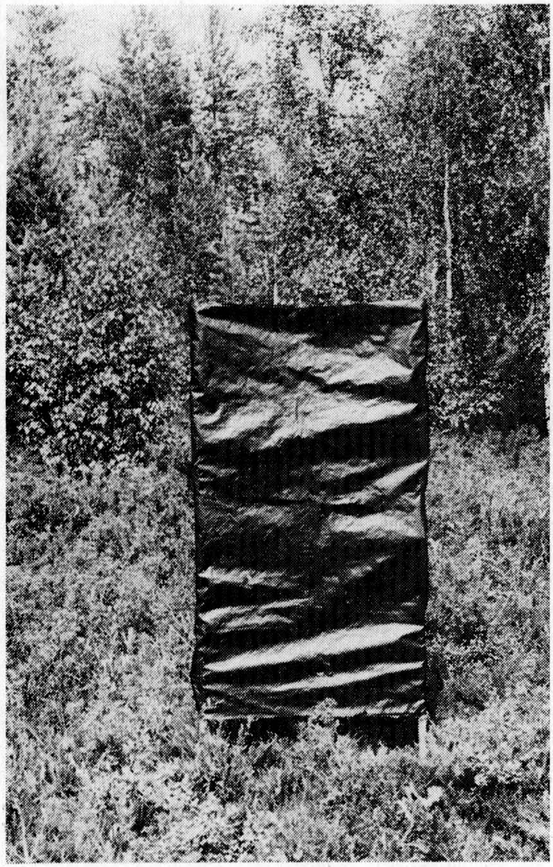

Fig. 10. The black vertical marker used in attracting *Leptophlebia marginata*.

5. A large horizontal marker appeared to inhibit swarming. A black and white marker, 1 × 1 m, placed by a pine 1.5 m tall, another light grey marker, 1.5 × 3.5 m, and a black marker, 1 × 3.5 m, placed beside a pine 6 m tall under the swarm caused it to disperse, and swarmers did not return if driven away from the tree by a gust of wind.

These tests show that in this species the marker is a vertical object. Possibly to these mayflies, which always swarm above land, the horizontal marker appeared as water.

If a short and a tall tree were near each other, the taller one gradually attracted a larger swarm.

Observations at Munaharju. L. marginata exhibited two different modes of behaviour with regard to swarming sites and swarm markers: some swarmed beside trees, and some even inside the forest at a low level (0.2 to 1.5 m) above markers paler than the environment, such as stones, patches of lichen and pieces of grey-and-white cardboard. Swarming took place only above markers exposed to direct sunlight. The readings of light intensity reflected by the actual markers were consistently higher than simultaneous readings taken from adjacent underbrush exposed to direct sunlight.

These differences in behaviour were studied by transferring individuals from one locality to another. Of the individuals orientating to horizontal markers at Munaharju 87 were marked and transferred to Matkonsaari and 144 to the shore of Nälkölampi, a pond on a bog (see Fig. 1); 25 of the former and 9 of the latter were recaptured from pale horizontal markers. Marked specimens from Matkonsaari (75 + 118 individuals) were transferred to Munaharju; 7 of the former and 2 of the latter were recaptured, all from swarms high up beside treetops.

The occurrence of two types of swarming, one related to horizontal and the other to vertical markers, is interesting because this behaviour persisted even when the individuals were transferred to a new environment. Whether the two types merit taxonomic separation is still uncertain. However, they possibly represent separate species.

Siphlonurus linnaeanus

Individuals of *S. linnaeanus* swarmed only above markers paler than the environment and located in water or at the waterline (Table 2), usually stones or floating leaves of water plants. They behaved in the same way to stationary or moving artificial markers; over stretches of water they followed such markers for over 1 km (in certain experiments), but above dry land they did so for a few metres only. Females, during their offering flights (even before swarming), used the same markers as males.

Experiments with swarm markers. Artificial markers of different sizes and shades were positioned near the N shore of Kalliolahti before the onset of the evening swarming. Some markers were uniform in colour, others striped or checkered. The markers were mounted horizontally about 50 cm above the water surface on poles standing in a line parallel to the shore and 1.5 m from the shoreline. Plants with floating leaves were removed; the distance between any marker and the nearest plant was at least 10 m. The markers were not moved during a swarming period, but each marker was positioned once on each pole, so that all combinations were tested. Records were kept of the onset and cessation of swarming at each marker, and swarming individuals were counted at intervals of 15 to 20 min.

Markers of different sizes. The markers were sheets of white cardboard with sides of 6.5, 9, 13, 18, 25, 35 and 50 cm. The results are given in Table 3 and Fig. 11. In general, the larger the marker, the larger the swarm above it (W = 0.672, $P < 0.01$). Swarming always began above one of the three largest markers (W = 0.525, $P < 0.01$) and ceased over one of the two largest markers. Cessation of swarming depended on the size of the marker and the size of the swarm. The last swarmers were seen more often above the 50 × 50 cm marker than above the one measuring 35 × 35 cm, and swarming mostly ceased above the marker which had attracted the largest swarm. The lowest point of an individual flight trajectory was usually 1 to 2 m above the marker, but above the two smallest markers it was slightly lower (0.7 to 1 m).

These experiments show that the smallest marker attracting a swarm was 9 × 9 cm. A marker measuring 6.5 × 6.5 cm attracted a swarm only if placed at the tip of a tongue of land. The linear regression (Fig. 11) indicates that, to be effective, a marker must have a minimum length of about 8 cm (when $x = 7.89$, $y = 0$).

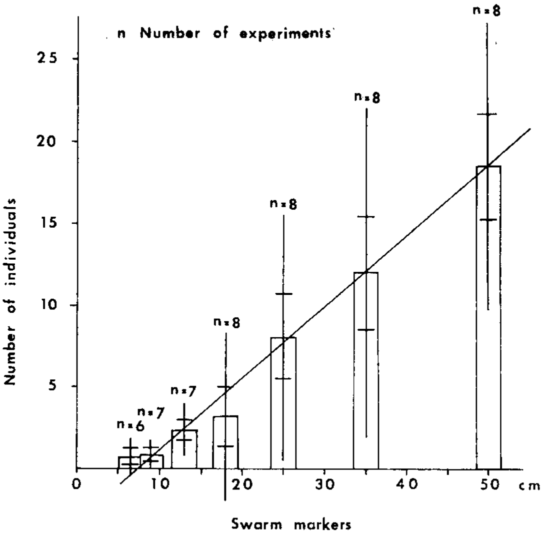

Fig. 11. The correlation between marker size and the size of *Siphlonurus linnaeanus* swarms. The symbols are as in Fig. 8. The data are taken from Table 3.

The sites and order of markers affected the size of the swarm and the time of onset of swarming. The mayflies preferred the sites at the end of the line of poles and in the middle (where the shoreline is slightly curved). When a small and a large marker were near each other, the swarmers moved from the small to the large one.

A single observation was made with sheets of white plastic 1 m wide and of various lengths.

Table 3. The effect of marker size on swarming in *Siphlonurus linnaeanus*. — = no data available, 0 = no swarming individuals, Roman numerals = order of onset of swarming above the four largest markers. Swarming continued longest above the markers underlined. The values in the table denote the maximum number of swarmers. On the evening of 9 August, only four markers were employed, and the marker 6.5 × 6.5 cm, which was not used as a marker, has been omitted from the calculations.

Date (1969)	Time	Size and order of markers	50	35	25	18	13	9	6.5
9 Aug.	21.15	50, 35, 25, 18	30,I	20,II	20,III	15,IV	—	—	—
10 »	21.05	9, 13, 18, 25, 35, 50	30,I	4,IV	1,II	5,III	4	2	—
11 »	21.15	6.5, 13, 9, 25, 18, 50, 35	15,I	30,II	15,III	1,IV	5	1	0
12 »	21.12	13, 9, 6.5, 35, 50, 18, 25	12,III	20,II	15,I	2,IV	1	0	0
14 »	20.40	50, 35, 25, 18, 13, 9, 6.5	5,I	4,III	2,IV	1,II	3	2	2
15 »	20.45	18, 50, 35, 25, 9, 6.5, 13	24,I	3,II	1,IV	0,III	2	0	0
16 »	20.37	25, 18, 50, 35, 6.5, 13, 9	17,I	9,III	6,II	1,IV	2	1	0
17 »	20.45	35, 25, 18, 50, 13, 9, 6.5	15,I	7,II	5,III	2,IV	0	0	3
		Mean	19	12	8	3	2	1	1

Kendall coefficient of concordance (W): — number of swarmers 0.672**
— order of onset 0.525**

If the sheet was more than 2 m long a swarm formed above each end, but shorter markers induced only a single swarm.

Markers of different brightness. White, light grey, dark grey and black cardboard markers measuring 35 × 35 cm were used. Table 4 and Fig. 12 show that swarm size depended on the brightness of the marker (= the difference in reflectivity between the marker and the environment), i.e. the lighter the colour of the marker, the larger the swarm (W = 0.345, when the black marker is excluded, since it did not appreciably attract swarmers; W = 0.751, when the black marker is included. These values are significant; for the former $P < 0.05$, and for the latter $P < 0.01$). The brightness of the markers did not influence the order of the onset of swarming (W = 0.079, n.s.). The order of cessation of swarming was not observed. During other tests made in a single evening swarming started earlier and ceased later above a lighter marker than above a darker one.

In evaluating these results one must consider the influence of the effects of the site and the order of the markers (p. 24). In addition, wind (velocities from 0.3 to 1 m/s) may have interfered with swarming on 23, 26, and 27 July, and 3 and 5 Aug.

Striped and checkered markers. The effects of a pattern were studied with cardboard markers

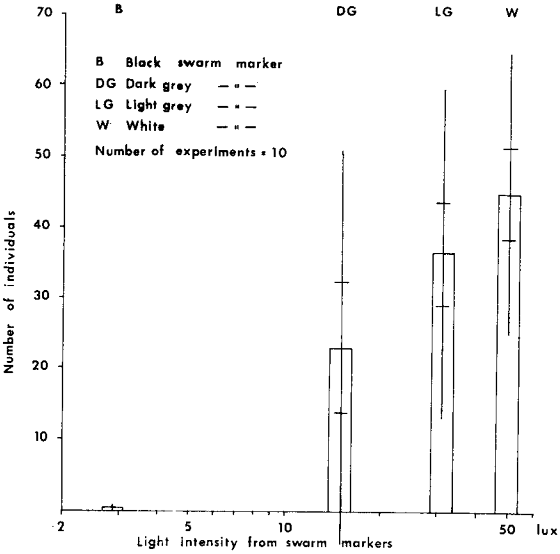

Fig. 12. The correlation between size of *Siphlonurus linnaeanus* swarm and the contrast of brightness between the marker and the environment. The markers are arranged on a scale from left to right according to the lux values measured from them on 31 July 1970 at 21.50 (= at maximum swarming intensity). For explanation of symbols see Fig. 8. The data are taken from Table 4.

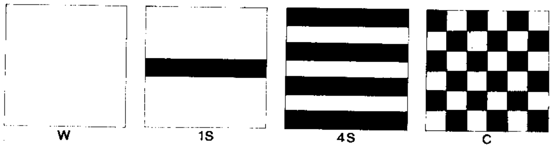

Fig. 13. The striped and checkered markers used with *Siphlonurus linnaeanus*. Each marker is designated by a symbol.

Table 4. The attractiveness of markers of different degrees of brightness to *Siphlonurus linnaeanus*. W = white, LG = light grey, DG = dark grey and B = black. Other symbols as in Table 3.

Date (1970)	Time	Order of markers	W	LG	DG	B
23 July	21.35	B, DG, LG, W	40, II	20, I	20, III	0
24 »	21.50	DG, LG, W, B	80, III	100, II	100, I	1
26 »	22.10	LG, W, B, DG	30, III	35, I	15, I	0
27 »	22.08	W, B, DG, LG	70, I	30, II	19, II	1
28 »	21.55	B, LG, W, DG	30, III	40, I	20, II	0
31 »	21.50	LG, W, DG, B	50, I	40, II	6, III	1
1 Aug.	21.40	W, DG, B, LG	60, I	25, I	8, III	0
3 »	21.45	DG, B, LG, W	25, II	30, III	30, I	0
4 »	21.35	W, DG, B, LG	40, II	20, I	8, III	0
5 »	21.35	LG, B, DG, W	25, I	25, II	5, III	0
		Mean	45	37	23	0

Kendall coefficient of concordance (W): — number of swarmers (black marker included) 0.751**
— — » — (black marker excluded) 0.345*
— order of onset of swarming 0.079

measuring 35 × 35 cm (Fig. 13). Table 5 shows that after addition of a pattern (or stripes or checkerboard) swarm size did not change (W = 0.031, n. s.).

In evaluating the results one must consider the effects of the site, the order of the markers (p. 24) and, above all, the few repetitions of the tests. Therefore, these results are only suggestive.

Table 5. The attractiveness of white (W), checkered (C) and striped (1S and 4S) markers to *Siphlonurus linnaeanus*. Other symbols as in Fig. 13 and Table 3.

Date (1971)	Time	Order of markers	W	1S	4S	C
24 July	21.43	W, 1S, 4S, C	100	35	12	35
25 »	22.10	1S, 4S, C, W	60	150	50	17
29 »	21.45	4S, C, W, 1S	21	35	70	30
30 »	22.00	C, W, 1S, 4S	40	12	13	50
		Mean	55	58	36	33

Kendall coefficient of concordance (W): 0.031

Heptagenia fuscogrisea

Cloud-like swarms of *H. fuscogrisea* formed above the Syrjäjoki, and during calm weather they spread over the sedge belts and even over the trees (Table 2, Fig. 14). No swarming was observed between the forest trees or above the river where trees growing on the banks hung over the water. At Rikkavesi most swarmers were over the water, but some were seen over land 2 to 3 m from the edge of the water and even above the nearest trees.

C. Shape, size and density of swarms. Swarming height

Shape

The shape of the swarms varied with their size, site and marker and with wind velocity.

Small horizontal markers. Swarms of *Leptophlebia marginata* were either spherical or slightly higher than broad. Swarms of *Siphlonurus linnaeanus* and *Caenis horaria* were columnar, during calm weather narrow and vertical, but in winds lower and broader, and veering into the wind.

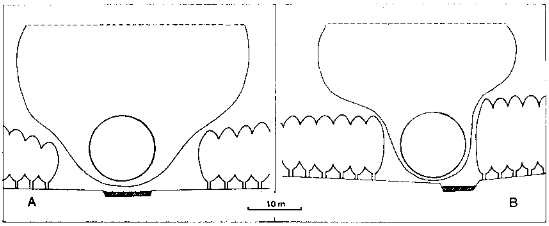

Fig. 14. Diagrammatic cross-section through a *Heptagenia fuscogrisea* swarm at Syrjäjoki in calm weather (A) at the location studied and (B) over the rapids. The black area = the river, the circle the densest part of the swarm, the dashes = the swarming height of the highest individuals.

Swarms of *C. horaria* often became momentarily spherical or changed to a cluster of irregular shape.

Trees. Small swarms of *Leptophlebia marginata* near single trees were either spherical or slightly higher than broad. Near tall trees large swarms were columnar with a large diameter and the columns were usually slanted (cf. Fig. 9), but near short trees even large swarms were spherical. Inside a forest the swarms were spherical or broadly columnar, or else flat, with most individuals swarming side by side, probably because adjacent treetops acted as markers.

Small swarms of *L. vespertina* (10—100 individuals) were observed both near and above trees, being columnar or, more frequently, rather narrow in shape. Sometimes the swarm became momentarily spherical or irregular.

Large swarms of *Ephemera vulgata* above trees were spherical. In small swarms the individuals were side by side; the height of the swarm then depended on individual flight trajectories, the clusters being broad and shallow.

Continuous vegetation. In small swarms the individuals of *Ephemera vulgata* were side by side and the swarms were often flattened, but in large swarms the individuals congregated one above the other, some swarms being spherical and others clusters of various shapes, often elongated in the direction of the wind or along a narrow swarming site. At a forest edge and near single trees large swarms would be elongated or slanted, the swarm extending from above a tree to near the ground.

Small swarms of *Leptophlebia vespertina* were columnar or spherical. Over open terrain extensive swarms composed of hundreds of individuals formed a shapeless cluster, often high above the ground.

River or waterline. During the peak of swarming *Heptagenia fuscogrisea* formed continuous "clouds" above the river or shore; these clouds stretched all the way to the forest.

Size, density and height of swarms

The mean numbers of individuals, dimensions of the swarms, swarming heights and densities are given in Table 6.

Ephemera vulgata. The dimensions of a swarm depend on the swarming site and on the number of individuals (newcomers did not appreciably increase the density). Above trees the swarms tended to be smaller but denser (max. 50 to 60 individuals, diameter 1.5—2.5 m, distances between individuals, 0.1—0.5 m) than over open terrain. Above a tree the swarming height of the lowest individual was 0.3—0.6 m and of the highest 1—2.5 m above the tree top.

In open terrain swarming usually started at a height of 0.3 to 2 m. At its peak the lowermost individuals were 0.5—3 m (average 1.2 m) above ground level. The larger the number of individuals in a swarm, the higher were those at the top (3—10 m). The swarms were densest at the centre (2—5.5 m). When swarming ceased during daylight, the last swarmers were at about the height at which swarming started, but in the evening the last swarmers were usually those at the centre of the swarm. High in the air, evening swarming ceases because of vertical differences in air temperature (Brodskii 1973).

Leptophlebia marginata. Next to single trees, swarm size was proportional to the number of individuals. Next to tall trees the swarms were tall columns, but next to short trees they were broad, flat columns. The lowest individuals always swarmed at 0.5—1 m, but the taller the tree, the higher was the maximum swarming height. Over horizontal markers at Munaharju the swarms were smaller and denser (largest swarms 20—40 individuals, diameter 20—50 cm, intervals between individuals 5—15 cm) than next to trees. Over horizontal markers the swarms were low, the lower edge being only 0.1 to 1.5 m above the marker, even inside a forest.

Caenis horaria. The swarms were compact, and smaller than in the other species. Swarming height varied; even during apparently calm weather a swarm might shift from 2 to 10 m.

Leptophlebia vespertina. The swarms were larger than in the other species studied. Kjellberg (1972) reported that in Sweden this species does not form swarms.

Table 6. The size, swarming height and density of mayfly swarms. Height = distance from the lower to the upper edge, n = number of observations, Lower and Upper = distances of the respective edges of the swarms from the ground, A = majority of swarms, B = largest swarms. Density = average distance (m) between individuals.

				Size of swarm			Height above ground		
		n	Individs.	Height	Length	Width	Lower	Upper	Density
Ephemera vulgata	A	20	5–20	1.5–5	1–6	1–5	0.5–2.5	1.5–6	0.1 –1.5
Above open ground, Tulisaari	B	10	60–200	4–9	6–12	4–10	0.5–1	4–10	0.1 –1
Leptophlebia marginata	A	50	5–20	0.5–2	0.5–1.5	0.5–1.5	0.5–2	1–6	0.1 –0.3
Matkonsaari	B	20	150–200	1.5–6	1–2	1–2	0.5–2	2–7	0.05–0.2
L. vespertina	A	20	5–100	0.5–8	0.5–2	0.5–2	0.5–2.5	2.5–9	0.05–0.5
Above open ground, Syrjäjoki	B	10	300–2000	2–9	1–6	1–6	0.5–2.5	2.5–10	0.05–0.5
Siphlonurus linnacanus	A	50	5–20	6–10	1–2	1–2	1–3	7–13	0.1–1.5
Tulisaari	B	10	100–200	8–13	1.5–3	1.5–3	1–1.5	10–15	0.1 –0.5
Caenis horaria	A	20	5–50	1–4	0.5–1	0.5–1	0.5–5	2–10	0.05–0.15
Lammi	B	10	100–200	1–5	0.5–1	0.5–1	0.5–5	2–10	0.03–0.15

Heptagenia fuscogrisea. Continuous swarms were seen above the Syrjäjoki, the swarm continuing about 100 m upstream to lake Syrjäjärvi and along the lake shores. Swarm width was determined by the confines of the river with its fringes of sedge. During calm weather some swarmers also spread above the forest (Fig. 14). The swarm is 5 to 60 m wide (average 10 to 20 m) and swarming always started at a low height (0.5 to 1 m), but as the numbers increased, the swarmers rose sometimes during calm weather to more than 30 m above the ground. Above a forest the lowest individuals were some metres above the treetops. The swarm was densest at 1 to 7 m above the river, the spacing between individuals being 0.2—0.8 m. Higher up and towards the periphery the swarm was less dense; above the forest and at the upper levels of the swarm, the individuals were sometimes several metres apart.

In *H. fuscogrisea,* in contrast to the other species, the density of the swarm increased with the number of individuals, probably owing to the width of the swarm marker. When the numbers were low, the swarmers were well spaced above the marker (with clusters here and there). The last daytime swarmers were observed at a height of 0.5 to 2 m. During calm weather, evening swarming ceased at 6 to 12 m (cf. *E. vulgata*).

The number of individuals was very large. At Syrjäjoki, below the rapids, a single swarm was made up of hundreds of thousands of individuals. At Rikkavesi the swarms were smaller, the largest swarms were some tens of metres long, 5—10 m wide and high, comprising some thousands of individuals. Distances between individuals ranged from 0.5 to 2 m.

Centroptilum luteolum. In 1969 the shores at Lammi were covered by continuous swarms several km long. These swarms were 8 to 12 m high and equally wide, with distances between individuals of 0.2—1.5 m. During other summers the swarms at Lammi and Rikkavesi consisted of only a few hundred individuals. These swarms had a diameter of only 2—5 m, the lowest individuals swarming at 0.5 to 1 m and the highest at 10 to 13 m.

2. Swarming seasons of the different species

At Maarianvaara, the earliest swarmer was *Leptophlebia marginata.* At Munaharju swarming began in late May, and at Rikkavesi in early June (3 June 1969 at Matkonsaari). At Rikkavesi swarming ceased in mid-June, on the Syrjäjoki still later. In *Ephemera vulgata* swarming commenced on the Syrjäjoki in mid-June (14

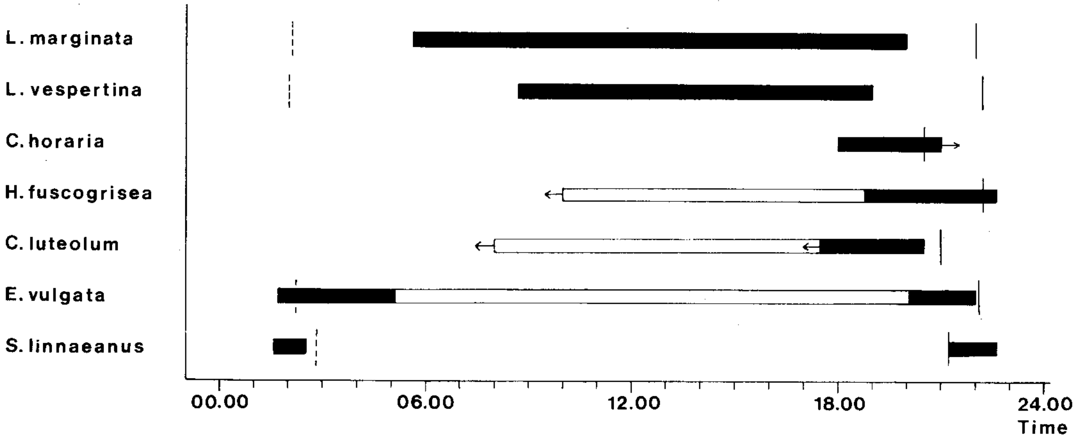

Fig. 15. The daily swarming times. Dashes = sunrise, solid line = sunset, arrow = no observations available on the onset or cessation of swarming, black horizontal column = actual swarming time, white = only when sky overcast. The sunrise and sunset times are means for the observation periods and the onset and cessation times are also averages. The data are taken from Tables 7—10, 12—14 and 16. There was only one observation each for *Leptophlebia vespertina* and *Caenis horaria.* The onset and cessation times were determined independently. The observations on *C. horaria* and *Centroptilum luteolum* were made at Lammi; the other species were studied at Maarianvaara.

June in 1969) and the number of individuals declined towards late June; at Rikkavesi swarming began some days later (16 June in 1970), numbers did not fall until mid-July, and swarms of a few individuals were seen until the end of August. *L. vespertina* and *Heptagenia fuscogrisea* swarmed from June to July, *Centroptilum luteolum* from June to August, and *Siphlonurus linnaeanus* from July to August.

3. Effects of illumination and weather on swarming

A. Light and air temperature

Diel periodicity of swarming

Fig. 15 shows the diel swarming periods for the species studied.

In *Siphlonurus linnaeanus* swarming took place in three ways:

1) The basic type was separate evening and morning swarming (Fig. 16A).

2) At the start of the season in early July swarming began in the evening and did not cease till morning (Fig. 16B), because at these northern latitudes the illumination was high enough throughout the night. Even then, the diel swarming periods were occasionally separate when the weather was unfavourable or the swarms were small. At midnight the number of swarmers was always low.

3) In late July (26—27 July 1970, 24—25 July 1971) and August (9—13 Aug. 1969, 1—2 Aug. 1970) swarming was observed only in the evening (Fig. 16C). On these occasions the morning temperature had been low or the evening swarms were small.

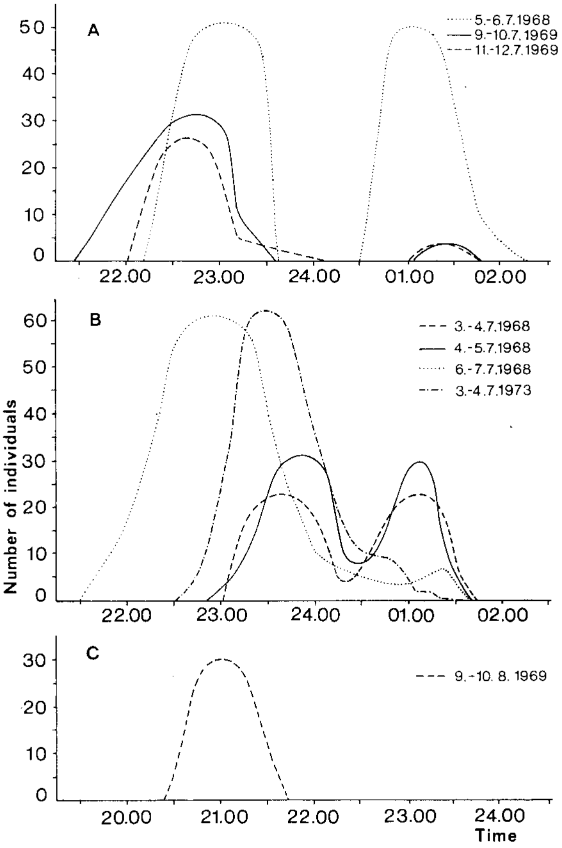

Fig. 16. The daily swarming periods of *Siphlonurus linnaeanus*. B = swarming continued throughout the night, A = separately in the evening and in the morning and C = in the evening only.

Leptophlebia marginata

Observations were made mainly at Matkonsaari (Table 7). Even when the sky was cloudless and the weather warm, swarming began only after sunrise at high light intensity. When the weather was cloudy and chilly, swarming did not begin until the sun came out. Swarming ceased between 18.36 and 21.16, 37—199 min before sunset, when the light intensity was still 5 500—61 000 lux, the time depending on wind, cloudiness and air temperature. The cooler the air, the earlier swarming seemed to cease (Table 7), but swarming ceased at a light intensity so high that there was no correlation between this and the air temperature. Occasionally, after swarming had already ceased, some individuals briefly resumed a swarming flight, either spontaneously or when disturbed. When they stopped, some of these swarmers then flew straight from one place to another.

In cool weather swarming was interrupted by gusts of wind and especially by clouds covering the sun. In chilly weather swarming occurred only during sunshine, including that filtering through thin clouds (Fig. 17). When the sun began to shine, the number of swarmers rose rapidly, but when clouds appeared the numbers fell more slowly.

Table 7. The onset and cessation of swarming in *Leptophlebia marginata* at Matkonsaari. T_1 = air temperature (°C) at 1.5 m, T_2 = at the level of the underbrush, L = light intensity (lux) measured towards the zenith, D = difference (min) between cessation of swarming and sunset.

	Date		Time	T_1	T_2	L		Cloudiness in the morning
Onset	6 June	1970	5.35	17.5	16.4	30000		Clear
	5 »	1968	10.00	14.5	14.9	88000		Overcast, rain
	6 »	1969	10.25	12.0	12.2	260000		» »
	7 »	»	9.37	11.8	12.7	270000		» »
						L	D	Cloudiness
Cessation	5 June	1968	20.23	19.8	19.5	27000	90	Clear
	4 »	»	20.35	19.0	18.1	10200	76	»
	5 »	1970	21.16	18.2	17.8	5500	37	»
	7 »	»	20.33	16.9	16.3	12700	84	»
	3 »	1968	20.14	16.2	15.1	11000	95	»
	9 »	1969	19.47	16.1	15.9	25000	133	Partly cloudy
	7 »	»	19.34	16.0	16.0	41000	143	» »
	8 »	»	19.29	16.0	16.0	61000	150	» »
	31 May	1973	19.46	14.7	14.0	25000	116	Clear
	6 June	1969	18.36	13.7	14.8	41000	199	»
Mean				16.7	16.4	25940	112	

The Spearman correlation coefficient (r_s): cessation of swarming

- between L and T_1 − 0.596
- between L and T_2 − 0.284
- between D and T_1 0.839*
- between D and T_2 0.644

At air temperatures above about 16 °C, this species swarmed in both sunny and cloudy weather; but during cloudy weather the swarms were smaller. Even in warm weather sunshine caused a rapid increase in numbers. The lowest temperature at which swarming was observed was 11.8 °C.

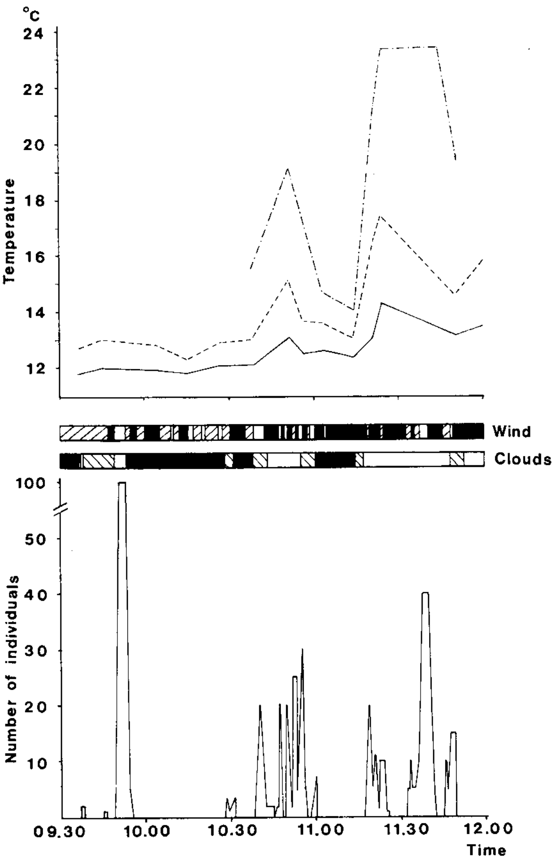

Fig. 17. The swarming of a single *Leptophlebia marginata* swarm on 7 June 1969 between 9.30 and 12.00 at Matkonsaari. Cloudiness is indicated as follows: black area = sky heavily overcast, shaded area = sun behind thin clouds, open area = sun shining. Wind velocity: open area = under 0.5 m/s, shaded area = 0.5 — 1 m/s (swarming disturbed) and black area = over 1 m/s (swarming prevented). Air temperature: dashes = at the level of the underbrush, solid line = at 150 cm and solid line interrupted with dots = measured in sunshine at the level of the underbrush.

Heptagenia fuscogrisea

Daytime swarming was observed only when the sky was overcast (Fig. 18); however, in a brief period of sunshine swarming did not totally cease. Before noon swarmers were not numerous even in cloudy weather, but in the afternoon there were as many as in the evening.

In the evening swarming was seen even if the weather was cloudless. And before the evening swarming proper, clouds in the afternoon often induced swarming, which then continued after the cloud had passed.

Swarming began between 18.15 and 19.25, 167—230 min before sunset, at light intensities of 25 000—35 000 lux (Table 8). No significant correlation was observed between temperature and onset of swarming, nor was there a correlation between air temperature and light intensity.

During the period when observations were being made on the cessation of swarming, the time of sunset hardly changed (between 22.07 and 22.11). Swarming ceased between 20.56 and 00.11, 73 min before to 124 min after sunset, at lux values ranging from 175 to 13 500. There seemed to be a threshold when the air temperature (measured at 1.5 m) was 11 °C. (The actual temperature at the height

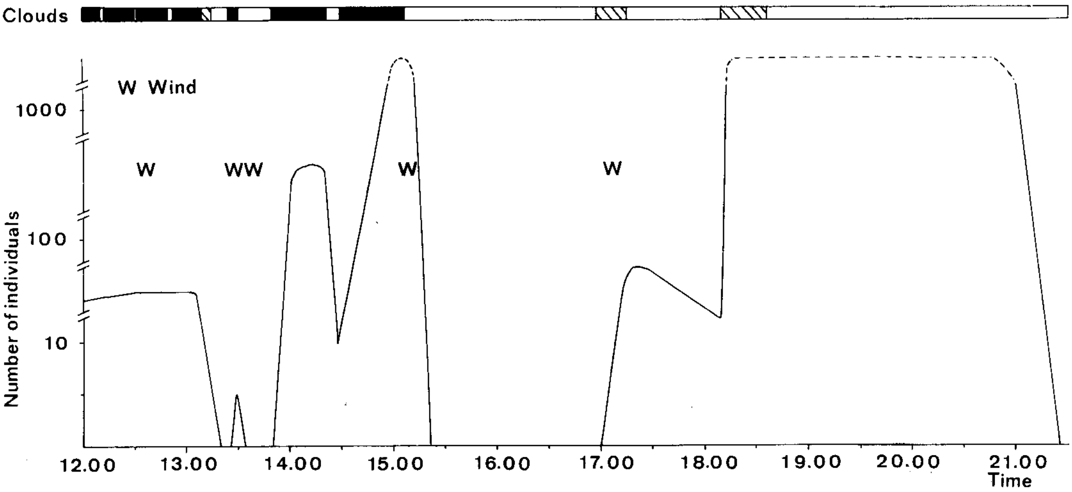

Fig. 18. Swarming of *Heptagenia fuscogrisea* on 15 June 1969 between 12.00 and 21.30 at Syrjäjoki. The number of individuals gives the approximate number over a stretch of the river 10 m long. W = a gust of wind disturbing swarming. The symbols for cloudiness are as in Fig. 17.

Table 8. The onset (in cloudless weather) and cessation of swarming in *Heptagenia fuscogrisea* at Syrjäjoki. D = difference (min) between onset or cessation and sunset (— = before, + = after sunset). Other symbols as in Table 7.

	Date	Time	T_1	T_2	L	D
Onset	19 June 1967	19.03	19.9	18.2	35000	— 189
	19 » 1969	19.25	19.8	18.0	25000	— 167
	19 » 1973	18.28	18.5	17.0	31000	— 224
	3 July 1967	18.15	17.5	15.0	35000	— 230
	17 June 1967	18.25	17.1	15.8	35000	— 226
		Mean	18.6	16.8	32200	— 207
Cessation	13 June 1968	00.11	17.1	15.2	175	+ 124
	26 » »	23.12	15.3	14.1	290	+ 61
	18 » »	22.56	13.5	13.0	350	+ 45
	17 » »	22.28	10.9	9.7	1400	+ 17
	16 » »	20.56	10.6	10.6	13500	— 73
	14 » 1969	22.10	10.4	9.3	1400	+ 2
	15 » »	21.25	9.8	8.8	4900	— 43
	13 » »	21.13	9.5	8.3	6000	— 54
	18 » »	22.09	9.4	8.8	2000	— 2
	17 » »	21.46	9.2	8.4	3400	— 25
		Mean	11.6	10.6	3342	+ 5.2

The Spearman correlation coefficient (r_s):

	Onset	Cessation
— between L and T_1	−0.335	−0.711
— between L and T_2	−0.335	−0.720
— between D and T_1	0.800	0.721
— between D and T_2	0.900	0.723

at which swarming ceased — 10 m or more — could not be measured.) At temperatures above this threshold, swarming was influenced by temperature and light intensity. The higher the temperature the later swarming ceased, and the lower was the light intensity at the cessation (Table 8). But if the air temperature fell below this threshold swarming ceased without regard to illumination or time of day, which accounts for the nonsignificant r_s values in Table 8. Accordingly, the minimum temperature for onset of swarming was between 9 and 11 °C.

Centroptilum luteolum

The actual swarming period was in the evening, but in cloudy weather this species swarmed in daytime also, and occasionally even in sunshine. When the sky was cloudless, swarming began at Lammi between 17.00 and 18.00 at a high light intensity. Swarming ceased at similar light intensities at Maarianvaara and Lammi (Table 9).

Ephemera vulgata

Spontaneous swarming by day. Spontaneous daytime swarming depended on cloudiness and air

Table 9. The cessation of swarming in *Centroptilum luteolum* in the evening. Symbols as in Table 7.

Date		Locality	Time	T_1	T_2	L
4 July	1967	Matkonsaari	22.47	13.7	11.8	500
10 Aug.	1968	Lammi	20.34	13.6	13.0	1720
18 June	1967	Tulisaari	22.15	12.9	11.2	1720
8 Aug.	1968	Lammi	19.53	12.4	12.4	13500
11 June	»	Matkonsaari	20.56	11.9	11.7	11000
19 July	»	Lammi	20.58	11.4	9.5	4200
			Mean	12.7	11.6	5440

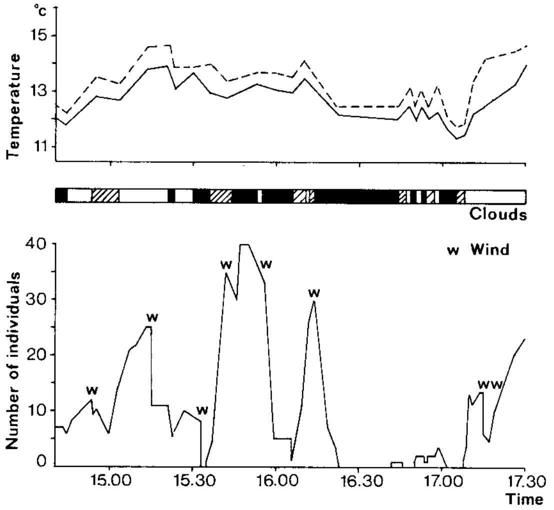

Fig. 19. The swarming of *Ephemera vulgata* on 24 June 1969 between 14.15 and 17.30 at Päivälahti above the sedge belt. For symbols see Figs. 17 and 18.

temperature as follows (+ = swarming observed, — = not observed):

Temperature at 1.5 m, °C	Sunshine	Cloudy
<12—13 (Fig. 19)	+	—
12—15 (Fig. 19)	+	+
15—20 (Figs. 20 and 21)	—	+
>20—22	—	—

When the air temperature was 15—20 °C, swarmers were abundant only in cloudy weather, both before noon and in the afternoon (Figs. 20 and 21). When the sun was behind a cloud, swarming began immediately, and the numbers of swarmers rose quickly. But when the clouds disappeared the numbers fell slowly; hence a brief spell of sunshine did not cause swarming to cease.

The number of swarmers did not remain constant when the sky was overcast. Fig. 20 shows two such cases. In one the sky was cloudy between 14.15 and 16.45; swarming began at 14.15 and ceased at 15.45, to begin again at 15.54. On another occasion the sky was clouded over from 10.37 to 11.43; swarming began even earlier at 10.29, but did not become abundant until the sky was cloudy. The size of the swarm began to decline about 35 min after the onset, and swarming ceased at 11.48, after the clouds had disappeared. Similar cases were observed at Vesanto and Lammi.

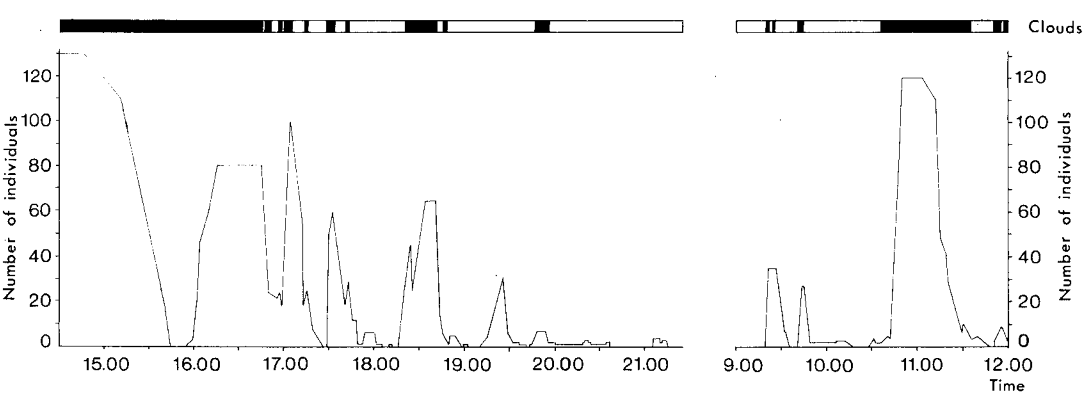

Fig. 20. The swarming of *Ephemera vulgata* from 29 June 1968 at 14.15 to 30 June 1968 at 12.00 at Päivälahti above the sedge belt. For symbols see Figs. 17 and 18.

Even on cloudy days swarming was periodic. The following observations were made at Kalliolahti on 2 August 1969:

Onset		End		Period	Quiescence
Time	T_1	Time	T_1	min	min
12.00	13.4	14.20	13.8	140	about 7 (2 ind. still swarming)
14.27	14.4	15.55	13.6	88	11
16.06	13.5	18.13	13.4	127	

At temperatures above 20—22 °C daytime swarming was seldom seen, but passing clouds sometimes induced flight in some individuals or small transient swarms.

Provoked daytime swarming. During periods when normally no swarms would occur, swarming was sometimes provoked by an observer walking in the sedge. Mayflies taking wing from their resting sites usually alighted at another site, but occasionally they swarmed for a while in typical fashion.

In warm weather, moreover, single individuals sometimes swarmed in sunshine at a low level (0.5—1.5 m) above open ground but only for a short while. Swarming of this type may be released by internal factors (p. 47). As the time for evening swarming approached, single swarmers grew more numerous.

Evening swarming. If the air was warm enough, evening swarming occurred regardless of cloudiness. On a warm, cloudless evening these mayflies swarmed in large numbers, but in cloudy weather, when swarming had continued all day, the number of evening swarmers was small (Fig. 21). If cumulus clouds were common in the afternoon and evening, swarming often continued directly into the evening.

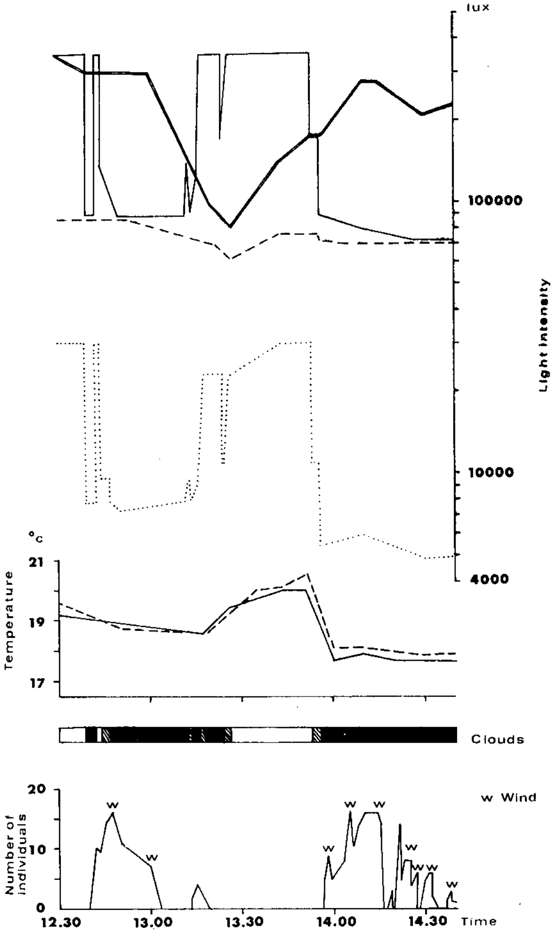

Fig. 21. The swarming of *Ephemera vulgata* on 4 July 1969 from 12.30 to 14.40 at Kalliolahti. The light intensity is measured from: double line = zenith, dashes = a white sheet of paper in the shade, solid line = a white sheet of paper in sunshine, and dotted line = a patch of sunshine in the sedge. For other symbols see Figs. 17 and 18.

Observations on the onset and cessation of swarming were made at Maarianvaara between June 13 and July 9 (Table 10). During this period the maximum difference between sunset times was 17 min (22.12 to 21.55), so the effect of this slight difference is negligible.

The onset of swarming was counted from the appearance of the first swarmer followed by continuous swarming. Swarming began between 18.19 and 21.13, 52 to 233 min before sunset, at light intensities ranging from 7 200 to 30 100 lux, and ceased between 20.16 and 23.35, 111 min before to 90 min after sunset, at light intensities ranging from 133 to 22 000 lux. The higher the temperature, the later swarming was observed and the lower the light intensity at which it ceased (Fig. 22). The observations on the onset suggest a correlation, but the values of r_s are hardly significant ($P <$ 0.1) (the r_s between lux values and T_1 is not significant). However, the time of onset of swarming was difficult to determine.

Swarming always began above open terrain, and some minutes elapsed before the first individuals were seen above trees. In calm weather the number of individuals then rose rapidly. In fine, calm weather swarming ceased earlier (10 cases, 1—36 min, mean 12.9 ±

Table 10. The onset (in cloudless weather) and cessation of swarming in *Ephemera vulgata* in the evening. S = Syrjäjoki, K = Kalliolahti. Otherwise as in Tables 7 and 8.

	Date		Loc.	Time	T_1	T_2	L	D
Onset	3 July	1972	K	21.08	23.3	22.6	9000	− 57
	4 »	1968	K	20.46	22.8	21.2	11800	− 78
	3 »	»	K	21.13	22.6	22.1	7200	− 52
	3 »	1973	K	19.57	22.5	21.6	26500	− 128
	2 »	1968	S	19.56	19.8	17.7	27000	− 130
	19 June	1969	S	19.16	19.7	18.0	25000	− 176
	19 »	1973	S	18.19	18.5	16.9	30100	− 233
	14 »	1967	S	19.15	15.3	13.5	27000	− 173
				Mean	20.6	19.2	20450	− 128
Cessation	3 July	1968	K	23.35	22.2	20.8	133	+ 90
	4 »	»	K	23.27	20.7	19.6	133	+ 83
	9 »	1969	K	21.53	19.2	18.7	700	+ 5
	2 »	1972	K	22.53	18.3	17.6	500	+ 47
	13 June	1968	S	22.38	18.1	16.0	870	+ 31
	5 July	»	K	22.31	17.2	16.8	800	+ 29
	25 June	»	K	22.34	16.6	15.5	580	+ 22
	27 »	»	K	20.24	15.8	14.8	11000	− 107
	18 »	»	S	21.47	15.4	14.6	1400	− 24
	4 July	1967	K	21.50	15.2	14.7	2800	− 14
	20 June	1968	K	22.12	14.6	13.8	2000	0
	6 July	»	K	22.02	14.4	13.7	1000	+ 1
	1 »	»	S	20.16	14.3	13.9	13500	− 111
	26 June	»	S	22.34	14.2	12.6	870	+ 23
	30 »	»	S	21.54	14.1	12.7	2800	− 14
	2 July	»	S	21.56	14.0	12.9	2400	− 10
	19 June	1967	S	21.07	13.8	12.9	22000	− 65
	4 July	1969	K	21.17	13.8	13.4	6000	− 47
	7 »	»	K	22.05	13.3	12.3	1850	+ 6
	24 June	1968	S	22.07	13.2	12.1	2300	− 5
	29 »	»	K	21.17	12.9	12.3	6800	− 52
	2 July	1969	K	20.16	12.9	12.5	18000	− 110
	16 June	1967	S	21.12	12.0	10.5	18000	− 57
	17 »	1968	S	21.37	12.0	10.9	4500	− 34
	15 »	1969	S	20.56	11.8	10.6	7400	− 72
	14 »	1967	S	20.45	11.5	11.5	13500	− 83
	16 »	1968	S	20.37	11.2	10.4	13500	− 92
	17 »	1967	S	21.35	11.1	10.0	11000	− 36
	19 »	1973	S	21.12	10.3	9.5	8400	− 64
				Mean	14.6	14.3	6025	− 23

The Spearman correlation coefficient (r_s):

	Onset	Cessation
− between L and T_1	−0.802	−0.770***
− between L and T_2	−0.862	−0.699***
− between D and T_1	0.857	0.688***
− between D and T_2	0.833	0.604**

3.46) above open terrain than above trees (1 case, 8 min earlier). In windy weather swarming ceased earlier above trees than above open ground. Above open ground the last individual swarmed alone for 0.5 to 14 min (16 observations, mean 6.4 min ± 0.85). Sometimes a few individuals reappeared to swarm for a while.

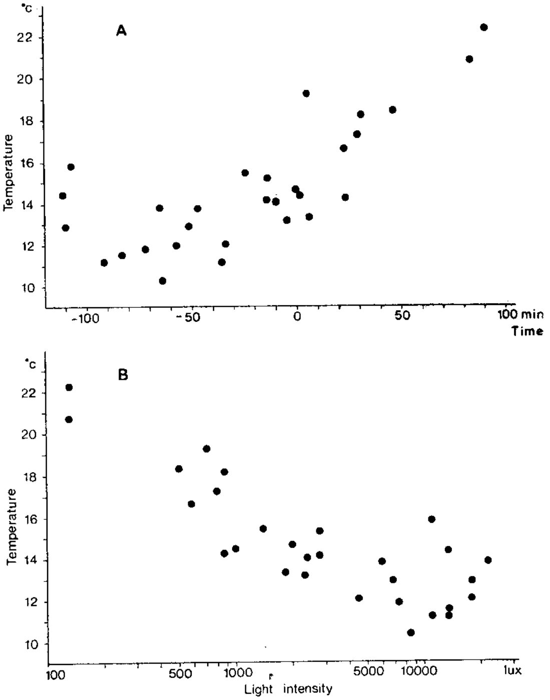

Fig. 22. The dependence of the cessation of evening swarming in *Ephemera vulgata* on air temperature (A) and the correlation between light intensity and air temperature at the cessation of the evening swarming (B). The data are taken from Table 10.

In fine weather evening swarming continued for 90 to 201 min (Table 11). Its duration did not depend on air temperature, which sometimes fell (by 0.4 to 8.2 °C) without affecting swarming. There were few observations, however, and the time of onset was difficult to establish.

Table 11. The correlation between the duration (min) of swarming in *Ephemera vulgata* and air temperature (°C) in the evening. TM = mean of the air temperatures at the onset and cessation of swarming, TD = the difference between the two.

Date		Duration	TM	TD
3 July	1968	142	22.4	0.4
4 »	»	201	21.8	2.1
2 »	»	120	16.9	5.8
19 June	1973	173	14.4	8.2
14 »	1967	90	13.4	3.8
	Mean	145	17.8	4.1

The Spearman correlation coefficient (r_s):

− between TM and duration	0.500
− between TD and duration	−0.100

Swarming in the morning. Regardless of cloudiness, morning swarms were numerous when the temperature was suitable, but consisted of 1—3 individuals only, and in general were seen above trees (Table 12). On three occasions (16.2—19.0 °C) swarming began before sunrise at about the same time and light intensity. On one occasion (15.5 °C) the morning was cool and foggy, and the resting mayflies were covered with water droplets which slowly evaporated as the temperature rose. Then swarming did not begin until 223 min after sunrise at a high light intensity. When swarming ceased, the light intensity was high (only two observations); it ceased earlier in warm weather (Table 12). No morning swarming was observed at temperatures below 11—13 °C.

Table 12. The onset and cessation of morning swarming in *Ephemera vulgata* at Rikkavesi. D = difference (min) between sunrise and the onset and cessation time, — = before and + = after sunrise. Other symbols as in Table 7.

	Date		Time	T_1	T_2	L	D
Onset	5 July	1968	1.35	19.0	17.9	800	— 41
	4 »	»	1.36	18.9	16.7	700	— 38
	10 »	1969	1.46	16.2	15.3	700	— 40
	30 June	1968	5.50	15.5	17.0	35000	+ 223
			Mean	17.4	16.7	9300	+ 26
Cessation	4 July	1968	5.05	22.2	22.1	41000	+ 171
	30 June	1968	8.15	17.0	18.4	38500	+ 368
			Mean	19.6	20.3	39750	+ 270

Siphlonurus linnaeanus

Evening swarming. S. linnaeanus swarms in the twilight. Observations were made at Kalliolahti in successive years between 3 July and 17 Aug. During this time interval the evening twilight slowly becomes earlier and the morning twilight later, the maximum difference in time of sunrise being 117 min and in time of sunset 119 min. Further, the total twilight period grows shorter towards late summer. In the beginning of the swarming season the twilight was a single long period (cf. Fig. 26), whereas at the end it formed two separate short periods, in the evening and morning. Because of the change in illumination conditions the observation period was divided into three periods with approximately equal differences between the times of sunset on the first and last evenings, viz.:

Period	Length, days	Maximum difference between sunset times, min.
I 3 — 21 July	19	36
II 22 July — 4 Aug.	14	38
III 5 — 17 Aug.	13	39

The onset of swarming began between 19.33 and 23.01, i.e. 140 min before and 56 min after sunset, at lux values ranging from 175 to 23 000 (Table 13). Swarming ceased between 21.03 and 00.04, 34—135 min after sunset, at lux values ranging from 4.2 to 500 (Table 14). The swarming period gradually became earlier because of the daily change in the time of sunset (Fig. 23). At a given temperature swarming began at approximately the same time in relation to sunset throughout the observation period. The higher the temperature, the later swarming began and the dimmer the light at the onset (Table 13 and Fig. 24). Swarming behaviour in the three periods did not differ with regard to the illumination at which swarming began or the interval between its onset and the time of sunset. The less significant r_s values of period II may have been due to slight differences in temperature during this period.

The warmer the weather, the later swarming ceased and the dimmer the light when it did so (Table 14 and Fig. 25). Further, the later the date, the earlier swarming ceased at a given temperature. But, as the sun then set

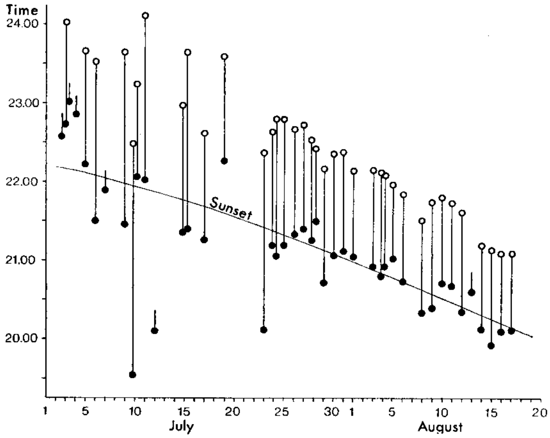

Fig. 23. The shift of the time of evening swarming in *Siphlonurus linnaeanus* during the summer on successive evenings. Black dot = onset and open circle = cessation of swarming. When cessation data are not given, either cessation was not observed or swarming continued throughout the night.

Table 13. The onset of evening swarming in *Siphlonurus linnaeanus* at Kalliolahti. Symbols as in Tables 7 and 8 (the periods are explained in the text).

Date	Time	T_1	T_2	L	D
Period I					
19 July 1970	22.16	23.1	22.1	175	+ 42
3 » 1968	23.01	22.0	20.7	370	+ 56
3 » 1972	22.43	21.5	21.3	660	+ 38
4 » 1968	22.52	21.2	19.8	430	+ 48
9 » 1969	21.28	19.4	18.7	940	− 27
3 » 1973	22.32	19.1	18.3	760	+ 27
11 » 1969	22.02	18.5	17.8	1050	+ 11
5 » 1968	22.13	17.2	16.8	1150	+ 11
10 » 1969	22.03	16.2	15.7	1850	+ 10
6 » 1968	21.30	15.5	15.0	2400	− 31
7 » 1969	21.54	13.9	12.5	2500	− 5
15 » 1967	21.20	13.4	12.1	5500	− 23
15 » 1969	21.25	13.4	13.0	4000	− 18
17 » 1967	21.15	13.2	12.0	4000	− 23
10 » 1968	19.33	12.7	12.4	23000	− 140
12 » »	20.05	12.3	12.5	16500	− 104
	Mean	17.0	16.3	4080	− 8
Period II					
28 July 1970	21.16	18.6	18.1	1150	+ 6
31 » »	21.10	18.6	18.2	940	+ 10
27 » »	21.45	18.0	17.2	1000	+ 12
3 » »	20.56	18.0	17.6	1600	+ 5
1 Aug. 1970	21.03	17.2	17.1	1400	+ 6
4 » 1971	20.47	17.2	16.9	2400	− 1
25 July 1971	21.13	16.9	16.2	2100	− 5
26 » 1970	21.20	16.8	16.1	760	+ 5
4 Aug. »	20.56	16.5	15.8	1400	+ 8
24 July 1971	21.04	16.3	15.5	3600	− 17
28 » »	21.32	16.2	16.1	700	+ 22
24 » 1970	21.12	15.9	14.9	2000	− 9
29 » 1971	20.45	15.6	14.9	4000	− 22
30 » »	21.04	15.3	14.8	1850	+ 1
23 » 1970	20.09	13.7	13.7	8400	− 75
	Mean	16.7	16.2	2220	− 4
Period III					
13 Aug. 1969	20.35	20.4	19.1	1000	+ 16
11 » »	20.41	20.2	19.1	870	+ 16
12 » »	20.21	18.6	17.2	2300	− 1
10 » »	20.43	18.2	17.2	1000	+ 14
5 » 1970	21.02	17.5	17.0	1050	+ 17
17 » 1969	20.07	16.9	16.4	1700	+ 1
6 » 1970	20.42	16.2	15.9	1650	0
9 » 1969	20.24	16.1	15.1	2400	− 8
16 » »	20.05	15.4	14.4	2300	− 5
14 » »	20.07	14.6	13.4	3400	− 9
15 » »	19.55	14.3	12.8	4900	− 18
8 » »	20.20	13.2	12.6	4900	− 15
	Mean	16.8	15.9	2289	+ 1

The Spearman correlation coefficient (r_s):

	I	II	III	All combined
− between L and T_1	−0.985***	−0.506	−0.879**	−0.868***
− between L and T_2	−0.947***	−0.569*	−0.905***	−0.881***
− between D and T_1	0.832**	0.582*	0.858**	0.792***
− between D and T_2	0.769**	0.646*	0.872**	0.793***

Kruskal-Wallis analysis of variance of ranks (H):

− Lux values between periods	0.254
− Differences between periods	0.048

Table 14. The cessation of evening swarming in *Siphlonurus linnaeanus* at Kalliolahti. Symbols as in Tables 7 and 8; the periods are explained in the text.

Date	Time	T_1	T_2	L	D
Period I					
19 July 1970	23.35	22.3	21.6	13	+ 121
3 » 1972	23.59	21.2	21.1	82	+ 114
9 » 1969	23.37	18.1	17.0	62	+ 102
12 » »	00.04	16.7	14.1	36	+ 135
5 » 1968	23.38	16.6	16.4	78	+ 96
10 » 1969	23.12	16.2	15.7	33	+ 79
15 » »	23.37	13.3	12.8	31	+ 114
7 » »	23.30	12.3	11.0	88	+ 91
15 » 1967	22.57	11.2	9.5	88	+ 74
17 » »	22.36	9.9	7.8	125	+ 58
10 » 1968	22.27	9.3	8.2	500	+ 34
	Mean	15.2	14.1	103	+ 93
Period II					
1 Aug. 1970	22.08	18.3	17.9	18	+ 71
3 » »	22.09	17.3	16.8	10	+ 78
27 July »	22.44	17.1	16.3	9	+ 91
31 » »	22.23	16.4	15.8	10	+ 83
28 » »	22.32	16.2	15.7	11	+ 82
4 Aug. 1971	22.07	16.2	15.9	11	+ 79
24 July 1970	22.38	16.1	15.9	25	+ 77
26 » »	22.40	16.1	15.4	11	+ 85
4 Aug. »	22.03	15.3	14.8	12	+ 75
25 July 1971	22.48	15.0	14.4	16	+ 90
28 » »	22.25	15.0	15.0	25	+ 75
30 » »	22.21	13.8	13.5	18	+ 78
24 » »	22.48	12.8	12.2	24	+ 87
29 » »	22.11	11.5	11.2	38	+ 64
23 » 1970	22.23	11.2	10.9	50	+ 59
	Mean	15.2	14.8	19	+ 78
Period III					
11 Aug. 1969	21.43	17.6	17.2	4.2	+ 78
10 » »	21.47	16.6	16.0	4.5	+ 78
5 » 1970	21.58	16.6	16.0	10	+ 73
12 » 1969	21.35	16.4	15.2	6.4	+ 73
17 » »	21.04	15.0	14.4	9.6	+ 58
6 » 1970	21.51	14.7	14.6	13	+ 69
9 » 1969	21.43	14.2	13.5	9.6	+ 74
16 » »	21.03	13.5	12.4	17	+ 53
15 » »	21.07	12.0	10.4	25	+ 54
8 » »	21.29	11.4	10.6	27	+ 54
14 » »	21.10	11.3	9.6	25	+ 54
	Mean	14.5	13.6	13.8	+ 65

The Spearman correlation coefficient (r_s):

	I	II	III	All combined
− between L and T_1	−0.706*	−0.757**	−0.888**	−0.448**
− between L and T_2	−0.697*	−0.629*	−0.888**	−0.454**
− between D and T_1	0.843**	0.275	0.818*	0.592***
− between D and T_2	0.733*	0.201	0.818*	0.541**

Kruskal-Wallis analysis of variance of ranks (H):

− Lux values between periods	18.122***
− Differences between periods	11.796**

earlier and the twilight was shorter, the lux value at which swarming ceased was lower. Accordingly, only a single lux value of period I was lower than the highest value of period III. The warmer the weather, the later swarming ceased in each period, and the dimmer the light when it ceased. The correlation between cessation time and air temperature is not significant during period II, probably because most observations were made at temperatures ranging from 15 to 17 °C.

Evening swarming lasted for 53—174 min (Table 15); the shorter the twilight, the shorter the duration of swarming (cf. Fig. 23). During period I (p. 35, Fig. 16) the duration of swarming was in some cases prolonged, lasting throughout the night (not included in the table). The duration of swarming was not correlated with air temperature.

Swarm size did not appear to be correlated with air temperature.

Morning swarming. Table 16 shows that in July swarming began at 1.02—1.05, 81 to 95 min before sunrise (36 to 82 lux) and ceased at 1.35—2.17, 1 to 64 min before sunrise (83 to 2 300 lux). On 5 August 1971, swarming began at 2.23 and ceased at 3.10, i.e. it was correlated with the later sunrise in August. Swarming time and illumination were not

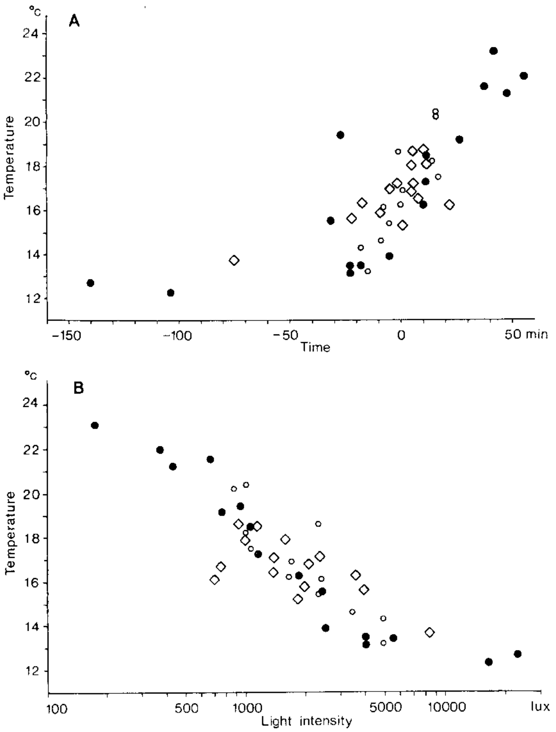

Fig. 24. The relation of time of onset of evening swarming in *Siphlonurus linnaeanus* to air temperature (A), and the correlation between light intensity and air temperature at the onset of swarming (B). Black dots = period I, lozenges = period II and circles = period III. The data are taken from Table 13.

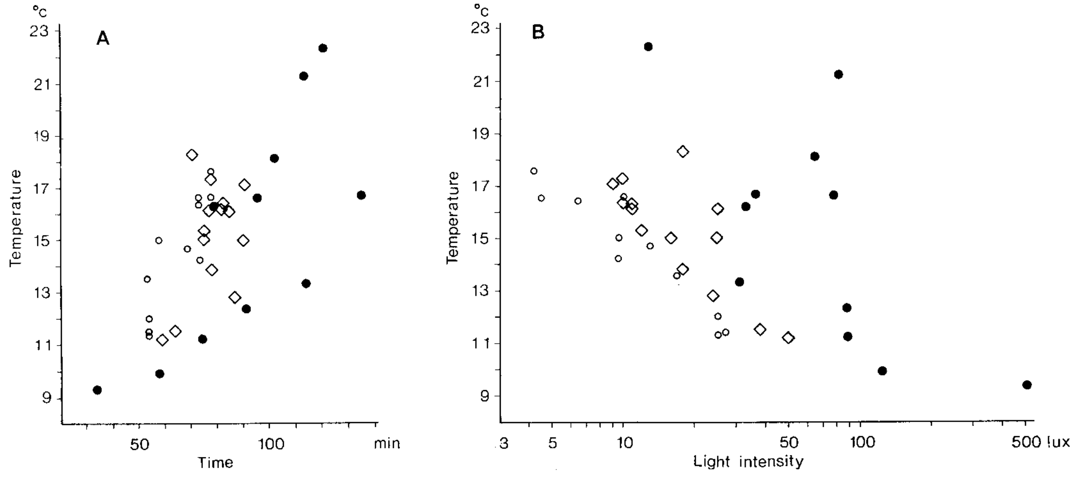

Fig. 25. The relation of the cessation of evening swarming in *Siphlonurus linnaeanus* to air temperature (A), and the correlation between light intensity and air temperature at the cessation of the evening swarming (B). The symbols are as in Fig. 24. The data are taken from Table 14.

Table 15. The correlation between the duration (min) of evening swarming of *Siphlonurus linnaeanus* and the air temperature (°C) at Kalliolahti. Symbols as in Tables 11 and 13.

Period I Day	Duration	TM	TD	Period II Day	Duration	TM	TD	Period III Day	Duration	TM	TD
19 July 1970	79	22.7	0.8	1 Aug. 1970	65	17.8	1.1	11 Aug. 1969	62	18.9	2.6
3 » 1972	76	21.4	0.3	3 » »	73	17.7	0.7	12 » »	74	17.5	2.2
9 » 1969	129	18.8	1.3	27 July »	79	17.6	0.9	10 » »	64	17.4	1.6
11 » »	122	17.6	1.8	31 » »	73	17.5	2.2	5 » 1970	56	17.1	0.9
5 » 1968	85	16.9	0.6	28 » »	76	17.4	2.4	17 » 1969	57	16.0	1.9
10 » 1969	69	16.2	0.0	4 Aug. 1971	80	16.7	1.0	6 » 1970	69	15.5	1.5
15 » »	132	13.4	0.1	26 July 1970	80	16.5	0.7	9 » 1969	79	15.2	1.9
7 » »	96	13.1	1.6	24 » »	86	16.0	0.2	16 » »	58	14.5	1.9
15 » 1967	97	12.3	2.2	25 » 1971	95	16.0	1.9	15 » »	72	13.2	2.3
17 » »	81	11.6	3.3	4 Aug. 1970	67	15.9	1.2	14 » »	63	13.0	3.3
10 » 1968	174	11.0	3.5	28 July 1971	53	15.6	1.2	8 » »	69	12.3	1.8
				24 » »	104	14.6	3.5				
				30 » »	77	14.6	1.5				
				29 » »	86	13.6	4.1				
				23 » 1970	134	12.5	2.5				
Mean	104	15.9	1.4		82	16.0	1.7		66	15.5	2.0

The Spearman correlation coefficient (r_s):	I	II	III	All combined
— between TM °C and duration	−0.391	−0.403	−0.114	−0.230
— between TD °C and duration	0.455	0.309	0.257	0.003

Kruskal-Wallis analysis of variance of ranks (H):	
— duration between periods	16.102***

Table 16. Onset and cessation of morning swarming in *Siphlonurus linnaeanus* at Kalliolahti. An asterisk after the date indicates cessation of swarming, which had continued through the night. Otherwise as in Tables 7 and 12.

	Date	Time	T_1	T_2	L	D
Onset	10 July 1969	1.05	16.9	15.6	82	− 81
	12 » »	1.02	15.6	14.7	66	− 88
	5 Aug. 1971	2.23	14.7	14.4	25	− 71
	16 July 1969	1.04	12.5	11.5	36	− 95
		Mean	14.9	14.1	52	− 84
Cessation	4 July 1968*	1.44	19.0	16.6	800	− 30
	5 » » *	1.45	19.0	17.9	800	− 31
	4 » 1973*	1.39	16.8	16.4	780	− 35
	10 » 1969	1.48	16.2	15.3	700	− 38
	12 » »	1.49	15.7	14.7	540	− 41
	5 Aug. 1971	3.10	14.4	14.1	760	− 24
	6 July 1968	2.17	13.2	12.9	2300	− 1
	16 » 1969	1.35	12.0	10.6	83	− 64
	7 » 1968*	1.45	10.2	9.6	800	− 35
		Mean	15.2	14.2	840	− 33

The Spearman correlation coefficient (r_s):	Onset	Cessation
— between L and T_1	0.800	0.153
— between L and T_2	0.800	0.153
— between D and T_1	0.400	0.176
— between D and T_2	0.400	0.167

correlated with air temperature, but the duration of swarming and the time of its cessation may have been correlated with swarm size. When the onset of swarming was observed in the morning, swarms of 2—5 mayflies swarmed for 31 to 47 minutes, but after continuous swarming all night, on 6 July 1968 morning swarming of a large number of individuals lasted for over an hour (Table 16, Fig. 16B).

No correlation was observed between duration of swarming and air temperature.

On some mornings there was no swarming. Such cases were observed both in cool and in warm weather. As a rule the number of swarmers was lower in the morning than in the evening, and when the number of individuals was low in the evening there was no swarming in the morning.

Swarming through the night. Continuous swarming all night long was observed three times in the very beginning of the swarming season in 1968 and once in 1973 (Fig. 16B and Table 16). On those nights the light intensity never dropped below 80 lux (Fig. 26). But swarming throughout the night cannot have been due to illumination alone (cf. Table 14). In three of the cases observed the air temperature was high throughout the night and in the fourth case it was low (Fig. 27). But even if the weather was warm swarming did not necessarily continue all night (cf. Table 14). The duration of swarming was correlated with swarm size. Therefore when the swarms were large (the largest swarms observed had 70 to 100 individuals), evening swarming may have continued long enough to overlap with morning swarming.

B. Wind

Table 17 shows the influence of wind on swarming in each species. The correlation between wind and temperature was not studied; the figures represent averages at different temperatures.

Wind had a certain influence on all aspects of swarming and its effects were roughly the same in all species. Swarmers always face the wind. In even the slightest breeze, individuals of *Ephemera vulgata* and *Siphlonurus linnaeanus* mostly faced into the breeze. The weakest breeze measured was 0.05 to 0.12 m/s for the former and 0.05 to 0.08 m/s for the latter species. In large swarms, many individuals changed direction without regard to the wind, because whenever two swarmers approached each other they started a copulatory chase (cf. Holopainen 1970).

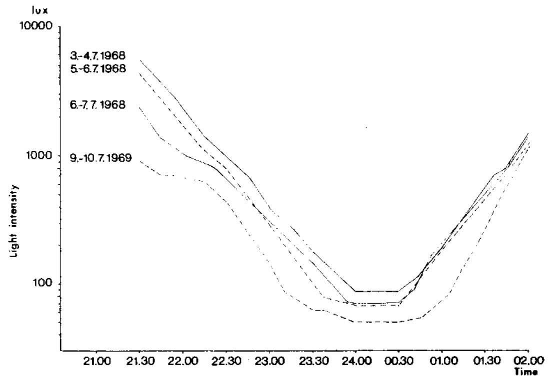

Fig. 26. Light intensity on four nights in the beginning of the swarming season of *Siphlonurus linnaeanus*. Solid line = swarming continued throughout the night, dashes = swarming was discontinuous.

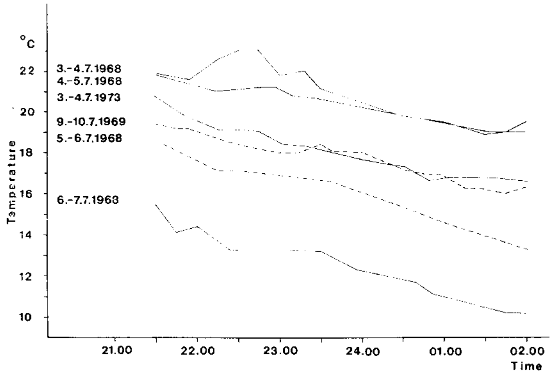

Fig. 27. Air temperature on six nights in the beginning of the swarming season of *Siphlonurus linnaeanus* at Kalliolahti. Solid line = swarming continued throughout the night, dashes = swarming was discontinuous.

Table 17. The effect of wind on swarming. The values for wind velocity (m/s) represent averages of observations, L = Lammi, P = Päivälahti, K = Kalliolahti, Ma = Matkonsaari, Mu = Munaharju and S = Syrjäjoki.

	Ephemera vulgata	*Siphlonurus linnaeanus*	*Leptophlebia marginata*	*Heptagenia fuscogrisea*	*Caenis horaria*	*Centroptilum luteolum*	*Leptophlebia vespertina*
Locality and no. of days	L, P, 15	K, 11	Ma, Mu, 7	S, 6	L, 5	L, 6	S, 2
Lowest and highest temperatures, °C	12.9; 22.1	16.0; 19.2	11.8; 20.8	16.2; 18.2	11.5; 19.0	11.5; 17.9	15.7; 17.8
Swarmers orientated against the wind	0.05 - 0.2	0.05 – 0.08	–	–	–	–	–
Swarming still occurred at normal height	0.2 – 0.5	0.2 – 0.5	0.2 – 0.3	0.4 – 0.5	0.3 – 0.4	0.4 – 0.6	0.2 – 0.5
The uppermost swarmers descended somewhat	0.5 – 1.0	0.5 – 1.0	0.3 – 0.5	0.6 – 1.0	0.5 – 0.7	0.6 – 1.0	0.5 – 0.7
Number of swarmers decreased, swarmers close to the ground	1.0 – 1.5	1.0 – 1.5	0.5 – 1.0	1.5 – 2.0	1.0 – 1.3	1.0 – 1.7	–
Swarming ceased	1.7 – 1.8	–	1.0 – 1.5	2.0 – 2.1	1.4 – 1.5	1.7 – 2.0	–

If the wind was weak (below 0.5—0.8 m/s), the individuals of *Leptophlebia marginata* faced the wind, and thus individual swarmers might be orientated in almost any direction instead of to the marker. At wind velocities exceeding 0.8 m/s the swarmers faced into the wind; during gusts they sometimes moved from the shadow to the leeside of the tree. No observations were made in completely calm weather.

At wind velocities of over 0.2 m/s swarming individuals of *Heptagenia fuscogrisea* faced the wind, although their horizontal flight (cf. HOLOPAINEN 1970) was directed along the river or shore. But if the wind was less strong they orientated parallel to the shore or river, some facing upstream, others downstream.

In calm weather the swarms were higher up, more typical in shape and larger both in number of individuals and in other dimensions than in windy weather. In windy weather the swarms at lower altitudes may be dense. At Syrjäjoki, for instance, swarms of *H. fuscogrisea* sometimes rose to heights above 30 m in calm weather, with individuals scattered over the forest in a loose swarm, but at wind velocities of 1 to 1.5 m/s all swarmers were down in a dense swarm above the river. Gusts often carried individuals into dense congregations at the bends of the river. In these, the distance between individuals was sometimes only 1—10 cm. At wind velocities of over 1.5 m/s the number of individuals was small and the swarms were loose.

Mayflies carried with gusts of wind often returned to the previous marker or swarmed above a new marker. Thus swarmers might drift from one marker to another. Wind sometimes transported individuals for long distances and they might then swarm far from any shore. Wind sometimes delayed the onset of swarming or caused it to cease earlier than in calm weather.

Since *Leptophlebia marginata* swarmed by day, when winds were strongest, the time of swarming was shortened every windy day.

C. Rain and relative air humidity

Rain. All species may swarm during a spell of rain, if short, weak or moderate, provided the temperature is high enough. Torrential rain did not affect swarm size or flight in *Ephemera vulgata*, but reduced the number of individuals of *Caenis horaria*. During a long spell of rain at Lammi the number of swarmers of *Centroptilum luteolum* was small, but swarming continued.

Relative air humidity. In *Siphlonurus linnaeanus* (Table 18) swarming usually takes place in the evening, when the relative humidity is already 100 %. But as the onset of swarming did not occur immediately when the saturation point was reached, it probably does not depend on air humidity. Nor did swarming or the number of swarmers change when the relative humidity fell because of wind. Moreover, no swarming took place in the rain by day.

Table 18. Effect of relative humidity (RH %) on the swarming in *Siphlonurus linnaeanus*. RH % = the lowest value of the day. Light intensity (measured towards the zenith): Lux O = at onset of swarming, Lux C = at cessation of swarming.

Date 1970	RH %	Number of individuals	Lux O	Lux C
23 July	73	131	8400	50
19 »	68	–	175	13
6 Aug.	67	–	1650	13
26 July	65	150	760	11
31 »	64	172	930	10
5 Aug.	63	90	1050	10
1 »	62	154	1400	18
28 July	60	156	1150	11
27 »	58	210	1000	9
24 »	55	381	2000	25
4 Aug.	54	131	1400	12
3 »	52	146	1600	10
Mean	62	172	1793	16

The Spearman correlation coefficient (r_s):

– between RH % and number of individuals	−0.188
– between RH % and Lux O	−0.189
– between RH % and Lux C	0.364

IV. Conclusions and discussion

1. Swarming sites and swarm markers

Mayflies usually swarm near their breeding waters (e.g. EATON 1883—1888, SPIETH 1940, LYMAN 1944, GRIMELAND 1966, BRODSKII 1973). The swarms of each species dealt with in the present study were also near a shore. Most individuals swarmed over a belt 10 to 20 m wide or over the shore water, with occasional individuals as much as 30 to 150 m away from the shoreline, depending on the species. Mayflies transported with wind may swarm far from a shore, and even at atypical swarming sites (cf. FISHKIS 1955, ULFSTRAND 1969).

Mayflies can be divided into two categories according to their swarming sites: 1) those swarming on the shore and 2) those swarming above the water (e.g. BENGTSSON 1926, ARO 1928, TIENSUU 1935, BRODSKII 1973). The species swarming above trees or the ground, or both, belong to the first category. According to BRODSKII (1973), who carried this division further, some species keep in visual contact with water, whilst others do not. This second category comprises the species swarming above the shore waters of lakes and rivers.

This division is justified only for the typical behaviour even if only a single species is considered, since many species swarm either regularly or occasionally both on the shore and above water (cf. e.g. TIENSUU 1935, SPIETH 1940).

The species I have studied can be divided into three categories:

1) Species swarming above dry ground: *Baetis scambus* Etn.: Swarms above ground only (observed at Lammi). *Leptophlebia marginata*: Swarming by trees. *Ephemera vulgata* and *Leptophlebia vespertina*: Swarming both above ground and above trees.

2) Species swarming above water: *Siphlonurus linnaeanus*, *Centroptilum luteolum*, *Heptagenia sulphurea* (Müll.) and *Ecdyonurus joernensis* Bgtn (the two latter species were observed at Rikkavesi).

3) Species swarming above ground and above water: *Caenis horaria* and *Heptagenia fuscogrisea*.

The existence of swarm markers has been amply documented for Dipterans, and most species have been observed to orientate visually to a certain swarm marker (e.g. SYRJÄMÄKI 1964a, DOWNES 1969). Swarm markers can be divided into two groups:

1) Horizontal markers, i.e. features of the ground either lighter or darker than their surroundings, waterline (DOWNES 1969, BRODSKII 1973) and continuous, extensive vegetation (SYRJÄMÄKI 1964a, BRODSKII 1973).

2) Vertical markers, objects higher than the surroundings, e.g. trees, bushes, buildings and even animals and man (SYRJÄMÄKI 1964a, DOWNES 1969). Dipterans react to different markers in a species-specific fashion; some species swarm above light markers only (e.g. NIELSEN & NIELSEN 1963), and others orientate to dark features of the ground (e.g. SYRJÄMÄKI 1965). Some species, however, swarm above dark as well as light markers (see e.g. NIELSEN & NIELSEN 1963).

Few studies have been concerned with the swarm markers of mayflies. EATON (1883—1888) mentioned that conspicuous "objects" (e.g. light-coloured rocks) attract mayflies, and according to ARO (1928) individuals of *Siphlonurus linnaeanus* often follow a boat. RAWLINSON (1939) stated that *Ecdyonurus venosus* (Fabr.) always swarmed close to the shore, above treeless grass belts (see also GRANDI 1973). DOWNES (1969) and HOLOPAINEN (1970, 1973) mention that mayflies orientate to a swarm marker. BRODSKII (1973) considered that in order to remain in a constant site mayflies orientate visually to certain features of the ground.

In this study each species was found to orientate visually to a swarm marker of a particular kind. The orientation to the marker was as follows:

1) To light-coloured horizontal markers: *Siphlonurus linnaeanus*, *Caenis horaria*, *Metretopus norvegicus* Etn. (at Vesanto), *Baetis scambus* (at Lammi), some of the individuals identified as *Leptophlebia marginata* (at Munaharju) and *L. vespertina* (at Inari).

2) To extensive vegetation, e.g. sedge: *Ephemera vulgata* and presumably *Leptophlebia vespertina* (at Maarianvaara).

3) To a river and/or water line: *Heptagenia fuscogrisea*, *H. sulphurea*, *Centroptilum luteolum* and *Ecdyonurus joernensis*.

4) To vertical markers: *Leptophlebia marginata*, *L. vespertina*, *Ephemera vulgata* and *Caenis horaria*.

Swarmers orientating to horizontal markers always swarm above the marker. Swarming midges orientating to vertical markers may be above (see e.g. NIELSEN & NIELSEN 1963), beside (see e.g. SYRJÄMÄKI 1963, KOSKINEN 1969, SAVOLAINEN & SYRJÄMÄKI 1972) or below (see e.g. WENK 1965) the marker. Mayflies have also been observed swarming above trees (e.g. BENGTSSON 1926, LYMAN 1944). *Ephemera vulgata* and *Leptophlebia vespertina* regularly swarmed above trees at Maarianvaara, and *Caenis horaria* occasionally did so at Lammi. *E. vulgata* and *L. vespertina* may also swarm beside trees. Except at Munaharju *L. marginata* always swarmed beside trees. None of the species studied was observed to swarm below a marker.

In what follows I shall summarize the observations made in this study.

Siphlonurus linnaeanus. Experiments with artificial markers showed that these mayflies form swarms above markers lighter than the background, such as stones or floating leaves of water plants. The attractiveness of the marker (cf. CHIANG 1961) depended on its darkness and size, and possibly on the distance from the waterline, but was independent of any striped patterns. The lighter the colour of the marker, the larger the swarm attracted by it, and the larger the marker, the larger the swarm. Above a larger marker swarming also began earlier and ceased later than above a smaller one. When markers were near each other, swarmers moved from a small marker to a larger one. A striped or checkered pattern on the marker did not increase its attractiveness. These results may, however, need confirmation.

According to CHIANG (1961), the minimum size of the swarm marker depends on illumination, i.e. the higher the light intensity, the smaller the marker still attracting a swarm. Probably this holds true for *S. linnaeanus*, since the smaller the marker, the earlier swarming ceased and, correspondingly, the higher the light intensity at which it ceased. The smallest marker which regularly attracted a swarm measured 9 × 9 cm. Only occasional swarmers were seen above the marker measuring 6.5 × 6.5 cm. The minimal size for an effective marker would be about 8 × 8 cm (cf. Fig. 11). Mayflies orientated to the ends of large (over 2 m long) markers (cf. DOWNES 1969).

Whether the distance of markers from the waterline affected their attractiveness was not tested separately. Swarming was not usually observed above dry land. Only a few individuals swarmed above white markers 1.5 m from the waterline. A marker well away from the shoreline and visible above the water seemed to be the most effective marker. The largest swarms were always at the mouths of bays above stones projecting from the water.

Caenis horaria. Swarming depended on markers lighter than the environment. Their attractiveness depended on their size and the contrast with the environment, as in *S. linnaeanus.* The mayflies orientated to the ends of a very large marker.

Ephemera vulgata. Swarm markers were trees or, in open terrain, continuous vegetation. On successive evenings swarms formed above the same features of the terrain. The swarms did not move even if the swarming site was large, but congregated above certain spots. Sometimes, however, individuals did move from one swarm to another. The swarms could be dispersed and the congregation of mayflies above certain sites prevented if the light markers were large enough. The swarmers followed moving trees or a boat serving as a horizontal marker. According to RAWLINSON (1939), *Ecdyonurus venosus* constantly swarmed at certain sites above treeless grass belts.

Leptophlebia vespertina. Marker experiments at Maarianvaara indicated a mechanism of orientation similar to that seen in *E. vulgata.* At Inari swarms were observed above light-coloured horizontal markers.

L. marginata. At Munaharju individuals identified as this species orientated to horizontal sunshine markers lighter than the environment at the beginning of the swarming season. In the other localities studied swarms were not seen above horizontal markers. In general these mayflies swarmed beside trees, above the shadow of the tree, and thus they orientated towards the sun. The swarm moved according to the movement of the sun, being in the same place at a certain time each day. That the tree, not its shadow, serves as a marker is supported by the following observations: In a dense forest, where the shadow is continuous, these mayflies swarm beside treetops. When the sun is low in the evening, the ground is entirely in shadow, even round an isolated tree, and yet the mayflies swarm beside the tree. Swarms may also occur inside a forest beside tall trees, close to the top but far from the shadow of the tree. When a large and a small tree stand near each other, the larger is a more attractive marker and draws individuals away from the smaller. These individuals fly towards the tree instead of to its shadow. Horizontal markers, however, if put under a swarm, inhibit swarming, perhaps because these mayflies do not swarm above water.

This is the only species that never swarms above but only beside trees, the swarms usually being entirely below the level of the treetops and above the shadows of trees. MCALPINE and MUNROE (1968) observed a similar orientation of the swarms of some Dipterans.

Heptagenia fuscogrisea. Swarms always formed at the same sites, above shores of lakes and rivers. In calm weather the individuals flew along the river or the shore. In a weak breeze they faced into the wind when swarming, but still flew parallel to the river or the shore. The individuals thus probably orientate visually to the river or shoreline. Experiments with *Centroptilum luteolum* and *Heptagenia sulphurea*, which swarm above shore water, revealed that the swarmers followed a moving boat. DOWNES (1969) and BRODSKII (1973) also mention that the waterline may serve as a marker.

Several authors have discussed whether swarming is a form of gregarious behaviour, i.e. whether individuals have to react to one another in order to remain in the swarm (see e.g. DOWNES 1950, 1955 and 1969, NIELSEN & NIELSEN 1958, HADDOW & CORBET 1961, SYRJÄMÄKI 1964a, 1964b). The following aspects of swarming have been used to support the hypothesis of gregarious behaviour:

1) Swarming in the darkness (see e.g. BURRILL 1913, COOKE 1940, BRITT 1962, LINDEBERG 1964, SAVOLAINEN & SYRJÄMÄKI 1972) and high up in the air (see e.g. EATON 1883—1888, SPIETH 1940, LINDEBERG 1964) are difficult to reconcile with the limitations imposed by the ability to see. At Lammi I observed *Caenis horaria* swarming so late in the evening that the swarmers could not be seen in the darkness, and in calm weather individuals of *Heptagenia fuscogrisea* rise above 30 m. Yet the hypothesis of gregarious behaviour does not explain why the swarm remains immobile. SYRJÄMÄKI (1964a) presumes that individuals swarming high up may orientate to a large marker which is distinguishable only from high up in the air. This is suggested by the swarming of *H. fuscogrisea*, too, since single individuals may swarm at altitudes exceeding 30 m. In the absence of fellow-swarmers they must be orientating to some marker down below.

2) Certain midge swarms move to and fro above open ground (FROHNE & FROHNE 1954). A comparable phenomenon was observed for *Caenis horaria*: sometimes these mayflies swarmed down above the marker, sometimes so high up that they could not be seen with the naked eye. Yet the swarm remained together, even though its form varied. There was no evidence of whether these different swarming levels were due to air currents or to some other phenomenon.

3) Swarming readiness is higher in large than in small swarms, i.e. swarming continues longer if the number of individuals is large (NIELSEN & NIELSEN 1958, CORBET 1964; *Ephemera vulgata* and *Siphlonurus linnaeanus* in this study) and individuals fly faster in large swarms than in small ones (GIBSON 1945, SYRJÄMÄKI 1965). DOWNES (1955) and CHIANG (1961) assume that swarming individuals attract others to swarm.

Yet each swarmer orientates to the marker individually, since single individuals behave as if they were in a swarm (e.g. SYRJÄMÄKI 1964a). Single swarmers were common in the species I studied. Further evidence against the hypothesis of gregarious behaviour is that individuals of *E. vulgata* often move from one swarm to another. Likewise, a mayfly may move out of its swarm and start swarming at a different site, often close to the swarm.

The females of species with female swarming (cf. TUOMIKOSKI 1939, GIBSON 1945, DOWNES 1958, HADDOW & CORBET 1961, DAHL 1965, RÖMER 1970, BRODSKII 1973) also orientate to the swarm marker (DOWNES 1955 and 1958 and RÖMER 1970). On the other hand, opinions are divided on the orientation of females in those species whose females make offering flights only (for a definition of the term see SYRJÄMÄKI 1964a). According to ROTH (1948), some Culicid females orientate by auditory clues. According to SCHOENEMUND (1930) and ILLIES (1968), Ephemerids orientate visually to swarming males, and according to SAVOLAINEN & SYRJÄMÄKI (1971) the Limoniid *Erioptera gemina* Tjeder orientates to the swarm marker. HOLOPAINEN (1970) observed *Ephemera vulgata* females making offering flights in the absence of males. In the present study such behaviour was observed in females of *E. vulgata* and *Siphlonurus linnaeanus*; the females of the former often made offering flights beside a swarm without approaching it. Probably the females of at least these two species orientate to the swarm marker only. BRODSKII (1973) came to the same conclusion. My observations support the conclusion that the purpose of swarming is to bring the sexes together for copulation (see DOWNES 1958 and 1969, HASKELL 1966, SAVOLAINEN & SYRJÄMÄKI 1971).

Swarming is optomotoric behaviour in relation to the swarm marker (see e.g. HASKELL 1966). Therefore, during wind the swarmers face into the wind. In apparently calm weather certain Dipterans (see e.g. KNAB 1906) and certain mayflies orientate against an air current. In calm weather swarming individuals of certain species, e.g. *Allochironomus crassiforceps* Kieff. (Chironomidae) (SYRJÄMÄKI 1964a) and *Caenis undosa* Tiens. (Ephemeroptera) (TIENSUU 1939), face the dry land, certain Cecidomyids (CHIANG 1961 and 1963, CHIANG & STENROOS 1963) face the sun, likewise *Tanytarsus gracilentus* Holmgr. (Chironomidae) faces the brightest source of light, either the sun or its reflection on the water surface (PAASIVIRTA 1972) and *Culex pipiens pallens* Coquill. (Culicidae) faces a vertical swarm marker (CHIBA 1967). *Leptophlebia marginata* resembles the two latter species. In calm weather these mayflies probably face the swarm marker and the sun at the same time. *Polymitarcus ladogensis* Tiens. (TIENSUU 1935) and *Heptagenia fuscogrisea* swarming in calm weather align themselves with the swarm marker, a river or a shoreline, but when the wind is blowing, they face the wind.

Closely related species of Diptera may have markedly different swarm markers or swarming times (see e.g. NIELSEN & NIELSEN 1963, CHIANG 1963). Differences in swarming behaviour thus constitute an isolating mechanism. Similarly, in Central Europe *Ephemera vulgata* swarms in the morning and *E. danica* Müll. in the afternoon (MÜLLER-LIEBENAU 1960).

HARKER (1953) suggested that the short life span and swarming behaviour of mayflies impedes interbreeding between different populations. KOSOVA (1967) observed that three populations of *Palingenia sublongicauda* Tshern. in the delta of the Volga river have different flight periods. KJELLBERG (1972) reported that in Sweden *Leptophlebia vespertina* does not form swarms, but that single individuals swarm separately. My results on the same species do not agree with this. In each locality I studied, this species often had extensive swarms. In Inari *Leptophlebia vespertina* swarmed above small horizontal markers lighter than the environment, but only in sunshine even if the weather was warm. In other localities the swarms were above trees or over open ground above a continuous vegetation pattern, and in warm weather swarming sometimes continued through brief cloudy spells.

Some of the individuals identified provisionally as *Leptophlebia marginata* swarmed in a different fashion. At Munaharju two patterns of swarming were seen:

1) Dense spherical swarms were observed at a height of 0.1 to 1 m above small sunlit horizontal markers lighter than their environment, even in a dense forest. Swarming of this kind began and ceased earlier in the season than the second type.

2) Swarms with trees as swarm markers were also observed. In a forest the swarms beside treetops were less dense than those of the former type. The swarming season was simultaneous with that in other localities.

No morphological differences could be observed between the individuals that differed in swarming behaviour. Very probably, however, this is a case of two as yet unrecognized sibling species that have still to be evaluated taxonomically.

GRUHL (1955) distinguished three types of swarming on the basis of its probable origin and individual behaviour: 1) synhesmia, 2) synorchesia and 3) a combination of the two. MCALPINE & MUNROE (1968) suggested that synorchesia, a regular and fixed pattern of behaviour, evolved from synhesmia, a more irregular and loose pattern. I should include those mayflies which orientate to horizontal or vertical markers or to extensive patterns of vegetation as cases of synorchesia. Species orientating to a river or shoreline would seem to be a third type, since their scattered swarms are of indefinite shape, but otherwise all individuals exhibit a species-specific flight pattern (see e.g. HOLOPAINEN 1970, 1973).

2. Diel periodicity of swarming

On the basis of their diel swarming periodicity SYRJÄMÄKI (1964b) divided the Diptera into five groups:

1) Species swarming at dusk. Many mayflies swarm only in the evening (see e.g. NEEDHAM *et al.* 1935, SPIETH 1940, PLESKOT & POMEISL 1952, MÜLLER-LIEBENAU 1960). However, none of the species studied by me belong to this group.

2) Species swarming in the evening and morning twilight. This group includes *Siphlonurus linnaeanus* (see also PLESKOT & POMEISL 1952, MÜLLER-LIEBENAU 1960).

3) Species swarming in the morning twilight only (see e.g. HALL *et al.* 1975).

4) Species swarming by day only. This group includes numerous mayfly species (see SPIETH

1940, Müller-Liebenau 1960). The category comprises only species that swarm in warm weather even in sunshine and cease swarming before sunset. Of the Finnish species *Melanameletus brunnescens* Tiens., *Paraleptophlebia cincta* Retz., *Leptophlebia marginata* and *L. vespertina* swarm in sunshine (Tiensuu 1935). I observed the two latter species swarming by day.

5) Species which commence swarming by day and do not cease until twilight. This category includes many mayflies (e.g. Eaton 1883—1888, Tiensuu 1935, Rawlinson 1939 and Müller-Liebenau 1960). I place *Caenis horaria* in this group.

Certain species cannot be assigned to any of these groups, but form a sixth, with the main swarming period in the evening and in the morning, or in the evening only but, depending on air temperature and cloudiness, these species may also swarm by day. The following Finnish mayflies exhibit such a pattern: *Ephemera vulgata*, *Heptagenia fuscogrisea*, *H. sulphurea*, *H. dalecarlica* Bgtn, *Centroptilum luteolum* and *Cloeon inscriptum* Bgtn (Tiensuu 1935). I observed the same behaviour in the five first-mentioned species. Some Dipterans also swarm in this fashion (Nielsen 1964, Savolainen & Syrjämäki 1971).

The diel swarming activity of the species studied can be divided into the following categories:

1. Spontaneous swarming which continues from day to day according to air temperature, illumination and cloudiness.

A. Diurnal swarming. Swarming by day, seldom continuing uninterruptedly till evening. The swarming of the fourth (*Leptophlebia marginata* and *L. vespertina*) and the noon swarming of the sixth group (*Ephemera vulgata*, *Centroptilum luteolum* and *Heptagenia fuscogrisea*) are of this type.

B. Evening swarming. Dusk swarming (*Siphlonurus linnaeanus*) and swarming commencing in the afternoon and continuing till dusk (*Caenis horaria*, *Ephemera vulgata*, *Heptagenia fuscogrisea* and *Centroptilum luteolum*) fall into this category.

C. Morning swarming. Swarming in the dawn (*Siphlonurus linnaeanus*) and after dawn but not continuing to noon (*Ephemera vulgata*) fall into this category.

2. Provoked swarming. A temporary type of swarming, which occurs when swarming readiness is high enough, but external factors inhibit swarming. It is of short duration and only a few individuals swarm at a time.

A. Swarming released by an exogenous stimulus, e.g. an observer. Observed in *Ephemera vulgata* in response to sunshine in warm weather and in *Leptophlebia marginata* in the morning before the onset of swarming, in the evening after its cessation, and also in chilly, overcast weather.

B. Swarming released by an endogenous stimulus, probably by swarming readiness higher than usual for the time of day. Such swarming was observed in *Centroptilum luteolum* and *Ephemera vulgata*. Both types of swarming have also been reported for Dipterans (e.g. Nielsen & Greve 1950, Nielsen 1962, Syrjämäki 1965).

Ephemera vulgata and *Siphlonurus linnaeanus* swarmed both in the morning and in the evening. In the evening swarming continued longer than in the morning and the number of individuals was higher. In this respect they resemble many Dipterans, but certain Dipterans swarm more intensively in the morning (see e.g. Nielsen & Nielsen 1962, Syrjämäki 1967, Koskinen 1969).

Early in the swarming season *Siphlonurus linnaeanus* may swarm through the night. Then the number of swarmers may be equal in the morning and evening, but considerably lower at midnight. If swarming continues through the night, it has two peaks, at dusk and dawn. The partial overlap is simply due to the light night.

3. Timing of swarming

According to several writers (see e.g. Bates 1941, Nielsen & Greve 1950, Provost 1958, Nielsen & Nielsen 1962, Nielsen & Nielsen 1963, Chiang 1963, Chiang & Stenroos 1963, Nielsen 1964, Syrjämäki 1964a, 1965, 1966, 1967 and 1968, Dahl 1965, Jones *et al.* 1966, Provost 1968, Römer & Rosin 1971, cf. also Mikkola 1973), the timing of swarming in Dipterans is controlled by either exogenous or endogenous factors or both. The mechanisms controlling swarming of mayflies are poorly known. Spieth (1940) assumes that latitude and altitude, time of year, air temperature, air pressure, relative humidity and light intensity together determine the timing of swarming. In Central Europe, according to Pleskot & Pomeisl (1952), light intensity is the main factor controlling the flight of females of *Torleya belgica* Lest.; they fly in the evening at a light intensity of 3 900 to 150 lux. These authors also reported that, in the course of the summer, the dawn swarming of *Caenis moesta* Bgtn gradually becomes later according to the daily change in sunrise time. Müller-Liebenau (1960) observed the same for *Ephemerella ignita* (Poda) in Central Europe. According to Grimeland (1966), the flight of the females of *Caenis horaria* in Norway starts in the evening at 3 800 ± 1 700 lux and ceases at 20 ± 14 lux, the variation being due to air temperature and relative humidity. Solem (1973) has suggested the existence of two endogenous rhythms in *Leptophlebia marginata* and *L. vespertina* nymphs, one diurnal and the other nocturnal. The nocturnal rhythm is correlated with foraging behaviour. The diurnal rhythm develops as the nymph grows, and is correlated with eclosions. It was interpreted as a preliminary stage of the circadian rhythm found in the adults.

In this study exogenous control of swarming is indicated by the following observations:

Diurnal swarming. This depended on air temperature and illumination (*Ephemera vulgata* p. 32, Figs. 19—21, *Heptagenia fuscogrisea* Fig. 18, *Leptophlebia marginata* p. 29, Fig. 17). No swarming occurred at low (in *E. vulgata* also high) temperatures (either in sunshine or in cloudy weather). In *L. marginata*, the higher the temperature, the later in the evening swarming seemed to cease (cf. Table 7). Changes in illumination caused by clouds had a visible effect: swarming commenced and the swarms grew rapidly when the sun appeared (*L. marginata*, *E. vulgata* in cool weather) or when a cloud covered the sun (*E. vulgata* in warm weather). A very brief spell of sunshine (*L. marginata*) or a quickly passing cloud (*E. vulgata*) were enough to produce this result.

Evening swarming. This depended on air temperature and light intensity: the warmer the temperature, the later swarming occurred and the lower the light intensity at which it did so (*Ephemera vulgata* Table 10, Fig. 22, *Heptagenia fuscogrisea* Table 8, *Siphlonurus linnaeanus* Tables 13, 14, Figs. 24, 25; cf. Nielsen 1964, Syrjämäki 1966). The swarming of *H. fuscogrisea* seemed to cease without regard to light intensity when the air temperature fell below 9—11 °C. In calm weather the swarming of *E. vulgata* and *H. fuscogrisea* ceased higher up as compared with the onset of swarming (the former above the trees, the latter high in the air), probably because close to the ground level light intensity and air temperature fell sooner than at higher levels (Syrjämäki 1964a, Brodskii 1973). In *S. linnaeanus* the change in sunset time was followed by a corresponding change in swarming time (Fig. 23; Nieslen & Greve 1950, Pleskot & Pomeisl 1952, Müller-Liebenau 1960, Syrjämäki 1966, Römer & Rosin 1971), and the shortening of the twilight period caused a corresponding shortening in the swarming period (Table 15; e.g. Provost 1968).

Morning swarming. In *Ephemera vulgata* swarming occurred earlier in warm than in cool weather, and in *Siphlonurus linnaeanus* the timing of swarming shifted with the twilight period in the course of the summer (only a few observations on either species, Tables 12, 16).

In this study the following observations suggest the influence of endogenous factors:

Diurnal swarming. In *Ephemera vulgata*, *Centroptilum luteolum* and *Heptagenia fuscogrisea* swarming did not cease as rapidly after a cloud had passed as it had begun. During a long cloudy period *E. vulgata* might cease to swarm and then begin again without regard to environmental factors. When the sky was overcast all day swarming was periodical. *E. vulgata* and *Leptophlebia marginata* could be provoked to swarm at times when they did not normally do so (cf. Syrjämäki 1965, 1967). Even if unprovoked, some species, e.g. *E. vulgata* and in particular *C. luteolum*, sometimes swarmed (though not vigorously) in sunshine in warm weather, the former more commonly in the evening shortly before the onset of swarming than at noon. When the evening swarming ceased, certain individuals of *E. vulgata* and *L. marginata* sometimes swarmed for a while or flew straight from one place to another. In *L. marginata* and *L. vespertina* swarming began in the morning and ceased in the evening at a high light intensity; in *L. marginata* there was no clear-cut correlation between the cessation of swarming and light intensity (cf. Syrjämäki 1964a).

Evening swarming. In every species swarming sometimes began at a very high light intensity (particularly in cool weather), and in *Centroptilum luteolum* and *Caenis horaria* it always began when the sun was still high (cf. SYRJÄMÄKI 1964a). On cloudy days, when *Ephemera vulgata* swarmed by day, evening swarming was hardly noticeable. The swarming of *Siphlonurus linnaeanus* did not cease at any particular air temperature at the same light intensity, but the end gradually shifted during the summer towards a dimmer light. A possible explanation is that, with the shortening of the twilight period towards the autumn, light intensity decreased more rapidly than swarming readiness. The swarming of *S. linnaeanus* continued longer in large swarms and with a higher readiness than in smaller ones (cf. NIELSEN & NIELSEN 1958, CORBET 1964, SYRJÄMÄKI 1965). Therefore in the beginning of the swarming season, provided the temperature was above 12—13 °C, swarming seemed to cease without regard to air temperature at about the same light intensity (30—90 lux), probably because the light intensity remained sufficiently high for swarming all through the night. For the same reason swarming sometimes continued through the night in the beginning of the swarming season, large evening swarms with high readiness lasting so long that they overlapped with the morning swarms.

Morning swarming. In cool weather the swarming of *Ephemera vulgata* tended to be postponed until the light intensity approached that of the day. In warm weather swarming ceased when the light intensity approached the maximum. In *Siphlonurus linnaeanus* the duration of swarming depended on swarm size (see p. 38), and the species did not always swarm in the morning even when swarms had been observed the preceding evening. An unsuitable temperature was not the sole explanation; when the number of individuals had been low in the evening, there was no swarming in the morning.

Swarming readiness. Laboratory experiments led SYRJÄMÄKI (1965, 1967) to suggest that in certain Chironomids swarming is controlled by an endogenous rhythm. This physiological condition, swarming readiness, shows a circadian rhythm. At its peak it results in swarming, which is released by light intensity.

The swarming of mayflies is clearly influenced by exogenous factors, but there are several aspects which cannot be accounted for by such factors. Swarming is thus probably controlled by both exogenous and endogenous factors. Since different species swarm at different times of the day, the rhythms of swarming readiness are probably species-specific. Fig. 28 is a schematic presentation of the swarming readiness of the different types (see p. 44) at different times of the day.

In *Ephemera vulgata* swarming readiness is below the threshold level (A) at night, and there is no swarming. By day it rises above A and swarming will then be released, whether there is sunshine or cloud, provided the air temperature is low enough. The exogenous factor releasing the onset and cessation of

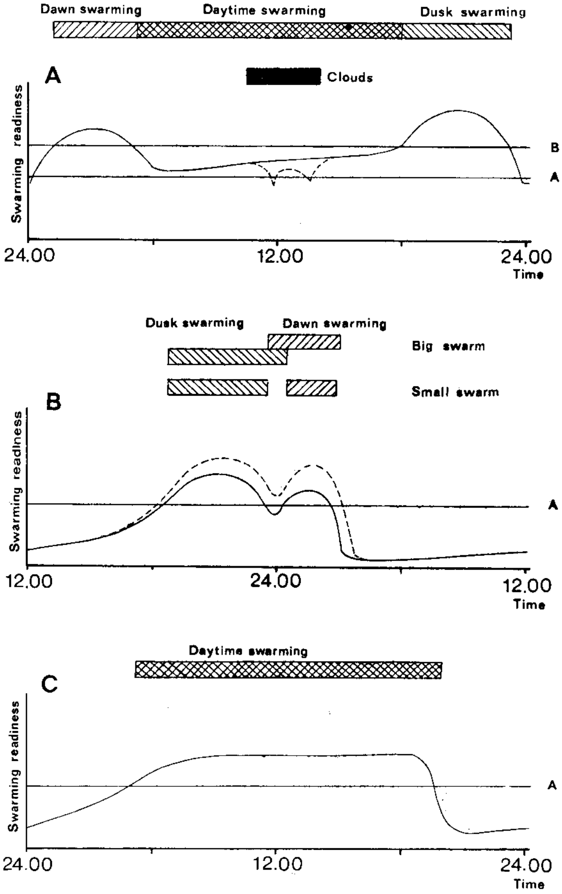

Fig. 28. The swarming readiness of *Ephemera vulgata* (A), *Siphlonurus linnaeanus* (*B*) and *Leptophlebia marginata* (*C*) at different times of day. A and B indicate the readiness levels. Clouds = Sky overcast. For explanation see text.

swarming is thus air temperature and light intensity which fluctuate when passing clouds cut off direct radiation. The effective components are probably both the change in the releasing factor and its maintenance at a certain level. In warm weather swarming commences rapidly when a cloud crosses the sun. During a long overcast period after continuous activity, swarming may cease and recommence, even though the releasing factor remains unchanged. Similarly, when the sky is continuously overcast swarming is intermittent.

The data on single swarmers in sunshine and on provoked swarming indicate that in sunny weather readiness to swarm increases towards the evening. At a certain time, swarming readiness reaches the second threshold (B). Above this level swarming occurs even in warm weather regardless of cloudiness, commencing when the readiness threshold is reached. This time depends on air temperature; light intensity is evidently less important, since swarming begins at a relatively high light intensity. As swarming proceeds, the readiness begins to decline, eventually falling below A. Then, at sufficiently low levels of light intensity and air temperature, swarming ceases. In the morning readiness is again maximal, above level B. The onset of swarming is probably released in warm weather by increasing light intensity and temperature, and in cool weather by a threshold in air temperature. Since swarming continues until the light intensity is high, its cessation is probably determined by a decline in swarming readiness and a rise in air temperature. Since the swarms are smaller in the morning than in the evening, readiness is evidently lower in the morning.

Swarming in *Heptagenia fuscogrisea* and *Centroptilum luteolum* is controlled in an essentially similar way. As yet, however, there are no data on cool weather or on cyclic swarming on a cloudy day. In addition, no morning swarming was observed, so swarming readiness does not rise above threshold B. In *H. fuscogrisea* swarming readiness seems to be low in the morning, since larger numbers of individuals swarm in the afternoon.

In *Siphlonurus linnaeanus* swarming readiness rises above level A at dusk and dawn, and swarming may then occur. Its onset is released by light intensity and air temperature as they rise in the morning and fall in the evening, interdependently reaching the threshold level. In the evening the readiness reaches level A relatively early, since air temperature has a strong influence on the time of onset.

The time when swarming readiness is above level A in the morning and in the evening depends on swarm size. Large swarms, which signify that readiness is higher, continue longer than small swarms. If light intensity and air temperature are sufficiently high, large evening swarms may overlap with morning swarms. A smaller number of morning swarmers indicates lower readiness in the morning. When the swarms have been small in the evening, there is no swarming in the morning.

In *Leptophlebia marginata* swarming readiness exceeds level A by day. Swarming begins in the morning and ceases in the evening at high light intensity, so this factor seems to have little, if any, effect on the control of swarming. Swarming readiness, which releases the onset and cessation of swarming, depends on air temperature. Whether the readiness remains above level A all day is not known. Since swarming occurs at the windiest time of day, gusts of wind interrupt swarming and readiness does not have time to fall below level A. Cloudy spells seem to inhibit swarming and sudden bursts of sunshine stimulate it.

The hypothesis on the control on swarming put forward above is based on field observations only. The individual exogenous factors contributing to the phenomenon are difficult to study singly in nature. Unknown deviations in the swarming of single individuals may increase the swarming time of a large swarm in relation to a smaller one. The hypothesis should be tested in laboratory experiments.

4. Effect of weather on swarming

Wind. Weather factors that reduce or inhibit swarming act synergistically, i.e. the effect of a single factor at a certain level is enhanced in comparison with the effect it would have alone. According to NIELSEN & NIELSEN (1966), the effect of wind on swarming is correlated with air temperature, wind having a greater influence when the weather is cooler.

For many Dipterans wind velocity thresholds disturbing or preventing swarming have been reported (e.g. KENNEDY 1939, DOWNES 1958, CHIANG 1961, CORBET & HADDOW 1962, Syrjämäki 1964a, Dahl 1965, Wenk 1965, Savolainen & Syrjämäki 1971 and 1972). The values vary with the species and the methods used for measuring velocity.

The influence of wind on the swarming of mayflies is poorly documented. Mayflies face even a slight breeze (e.g. Rawlinson 1939, Spieth 1940, Holopainen 1970), and in calm weather they swarm higher up than when the wind is blowing (e.g. Tiensuu 1935, Illies 1968). The flight path of individuals depends on wind (Holopainen 1970, 1973). In *Stenonema canadense* (Walker), according to Thew (1958), a wind of 4 beaufort disturbs but does not prevent swarming. A wind of 3 m/s does not affect swarming in mayflies but a wind of 6 m/s stops it (Tischler 1949). *Caenis horaria* still flies at 3 to 3.9 m/s (Grimeland 1966). According to Brodskii (1973), a wind of 5.6 m/s does not disturb swarming in *Caenis* sp. Neither is *Ephemera vulgata* affected by a wind of 4.3 m/s.

In this study the wind was measured close to the swarmers in the course of each bout of swarming. This gives a better idea of the effect of the wind than recordings from fixed heights. All species studied seemed to be equally sensitive to wind: a wind between 0.5 and 1 m/s limited and one between 1 and 2.1 m/s prevented swarming. *Leptophlebia marginata* was slightly more sensitive than the other species, while *Centroptilum luteolum* and *Heptagenia fuscogrisea* swarmed in a slightly stronger wind than the remaining species.

Air temperature. Among many Dipterans different species have different threshold temperature values for swarming. Species occurring in warm regions or during the warm season have higher threshold values than those of cool regions or seasons (see e.g. Syrjämäki 1964a, Dahl 1965, Nielsen & Nielsen 1966).

In mayflies the threshold values for swarming are poorly known. According to Eaton (1883—1888), mayflies seek shelter in cool weather. Cooke (1947) observed that *Hexagenia atrocaudata* McDunnough does not swarm below 18 °C. In *Ephemera vulgata* I observed swarming if the temperature was above 12—13 °C, but in the daytime a temperature above 20—22 °C inhibited swarming. *Heptagenia fuscogrisea* continued swarming in warm weather even at temperatures as low as 9—10 °C. The lowest temperature recorded at the onset of swarming in *Siphlonurus linnaeanus* was 12.3 °C, and swarming ceased at 9.3 °C. Studying *Caenis horaria*, Grimeland (1966) suggested that swarm size depends on air temperature, but my data on *S. linnaeanus* do not confirm this view. In certain Nematocerans, however, Syrjämäki (1964a) observed that swarm size depends on temperature.

For *Leptophlebia vespertina* the threshold value for swarming was 12—13 °C, but moulting to subimagoes was observed at still lower temperatures. Subimagoes of *Heptagenia fuscogrisea* likewise emerged in weather too cool for swarming. The same seems to be true of *Hexagenia* sp., since after weather conditions preventing swarming the swarms are unusually large (Lyman 1944). In *Ephemera vulgata* and *Siphlonurus linnaeanus* the duration of swarming does not depend on air temperature. The same was observed in *Chironomus pseudothummi* Strenzke by Syrjämäki (1966). In certain Dipterans the duration of swarming is correlated with air temperature (e.g. Nielsen & Greve 1950).

Humidity. Humidity does not usually influence swarming in Chironomids or Culicids (e.g. Nielsen & Greve 1950, Haddow & Corbet 1961, Nielsen & Nielsen 1963, Syrjämäki 1964a and 1964b). Even during light or moderate rain swarming proceeds as usual. In Trichocerids a low humidity seems to prevent swarming, and a high one that of young imagoes (Dahl 1965, 1969).

As the thin cuticle of mayflies makes them susceptible to dehydration (Spieth 1940), some have suggested that their swarming might be influenced by humidity (e.g. Spieth 1940, Müller-Liebenau 1960, Grandi 1973). Grimeland (1966) found that in *Caenis horaria* swarming was correlated with humidity. I did not observe a direct effect of relative humidity on swarming in *Siphlonurus linnaeanus*, which swarms in the evening when humidity has usually reached the saturation point.

According to Rawlinson (1939), *Ecdyonurus venosus*, which usually swarms in the afternoon sunshine, will also swarm during heavy rain. Grimeland (1966) observed that rainfall of less than 5 mm/day does not disturb the flight activity of *Caenis horaria*, and I observed that a short spell of rain did not appreciably influence swarming in this species. I saw *Centroptilum luteolum* swarming through a long spell of rain, but the swarms were small.

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