The Swarming Habits of Some Danish Mosquitoes.

By

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INDEX

A. GENERAL.

1. Introduction and Acknowledgements.

The work reported in this paper is a continuation of the studies on the behavior of mosquitoes, especially the swarming habit of the males, which has been carried out in Denmark (Nielsen & Greve 1950), Florida (Nielsen 1958, Nielsen & Haeger 1954, 1960, E. T. & A. T. Nielsen 1953, H. T. Nielsen 1961a, 1961b, H. T. & E. T. Nielsen 1961) and in Iraq (E. T. and H. T. Nielsen 1958).

The earlier studies in Denmark took place at a locality where one single species *(Aedes cantans)* was so much more abundant than other culicides that it completely dominated the swarming. The present investigation was intended to include observations of as many species as possible. Most emphasis was given to obtaining information about the habits of *Aedes caspius* which were previously investigated under much different conditions in Iraq (l. c.).

The present investigation was made possible by a grant from the Carlsberg Foundation to whom our most sincere thanks are due.

Although most of the actual work was done in the field we are very grateful to Professor, Dr. phil. P. Brandt Rehberg for permitting us to use the Zoophysiological Laboratory (A) of the University of Copenhagen as a base for the work, and we remember with gratitude the kindness with which everyone at the laboratory took care of our needs.

We would like to express our best thanks to Mrs. Nina Branch, Entomological Research Center, Florida State Board of Health, who by training the junior author made it possible for her to identify the collected specimens daily during the field work. Later Mrs. Branch verified the identifications by critical revision. We are much indebted to Dr. Alan Stone, U. S. National Museum, Washington, for his advice in a few especially difficult cases mentioned in the following. We are also very grateful to Dr. phil. S. L. Tuxen for having placed the collections of the Zoological Museum of the University of Copenhagen at our disposal.

We are indebted to the following for having facilitated our work: Dr. Arden O. Lea, Entomological Research Center, Florida State Board of Health, who helped us in many ways, especially

by placing his automobile at our disposal which highly facilitated the first exploratory part of the work; Mr. Ole Holst for permission to work at his estate, Nysø, where we found most of our observation places; many friendly citizens of Præstø; and Miss Kirsten Tetens Nielsen who occasionally participated in the observations and who took a number of photographs, some of which are reproduced in the following.

2. Description of Observation Places.

With few exceptions the observations were made around Præstø, a small town on the southeast coast of Zealand (55°08' n. lat., 12°06' e. long.). The Baltic Sea forms a bay, Fakse Bugt, between the peninsula, Stevns, in the North and Jungshoved and the island, Møen, in the South. In front of the bottom of this bay a narrow peninsula, Feddet, protrudes southward from Stevns, separating the innermost part of the bay, Præstø Fjord (fig. 1). Several brooks disembogue into Præstø Fjord, the largest of which, Tubæk Å, runs through the town of Præstø. The Baltic Sea has a low salinity (1.0 %₀ and lower) and in Præstø Fjord the shore line is often bordered by reeds (Phragmites). Behind

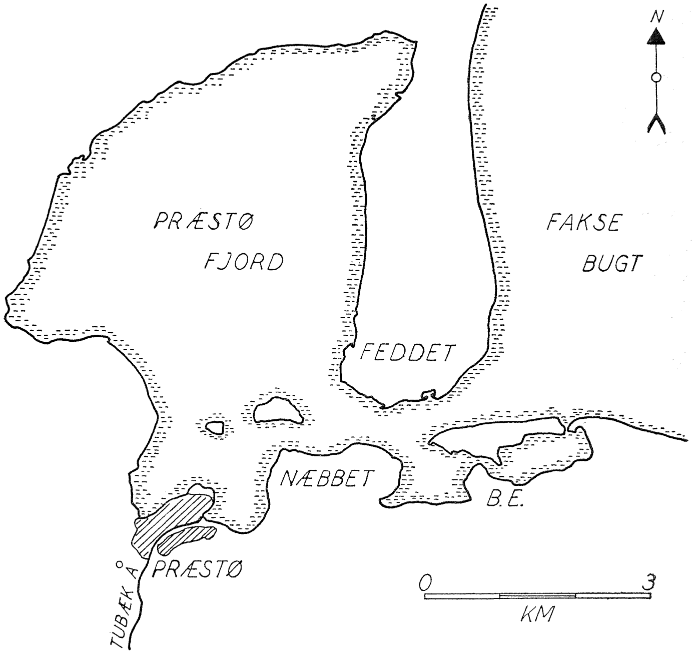

Fig. 1. Sketch map of the area around Præstø.

Fig. 2. Sketch map of the observation places East of Præstø.
(1): Skibbinge Hovedskov; (2): observation place for *A. geniculatus;* (3): Næbskoven; (4): Næbengen; (5): Rævsvænget; (6): Bøndernes Egehoved; (7): Hejreskoven.

the reeds — if present — there are usually seaside meadows, 50—100 meters wide. These are dry in the spring but become more and more wet as the summer progresses and by late fall they may be completely inundated.

Bøndernes Egehoved (fig. 1, B. E., fig. 2 (6)) was the easternmost place where observations were made. It is a slightly hilly part of the coast about 100 × 300 meters rising rather steeply a few meters above the seashore meadow which here is open to the water without Phragmites. It has probably been used as a pasture for centuries but thorny bushes have protected single trees or small groups of trees (fig. 3). The trees are mostly beech *(Fagus sylvaticus),* oak *(Quercus robur), Carpinus betulus,* and ash *(Fraxinus excelcior).* The thorny bushes are blackthorn *(Prunus spinosa),* whitethorn *(Crataegus oxyacantha)* and wild roses. Wild apple also occur. Between these "islands", which are frequently bordered by a low hedge of nettles and thistles, are open areas with grass which is cropped by cattle and horses roaming the area, thus preserving its traditional appearance.

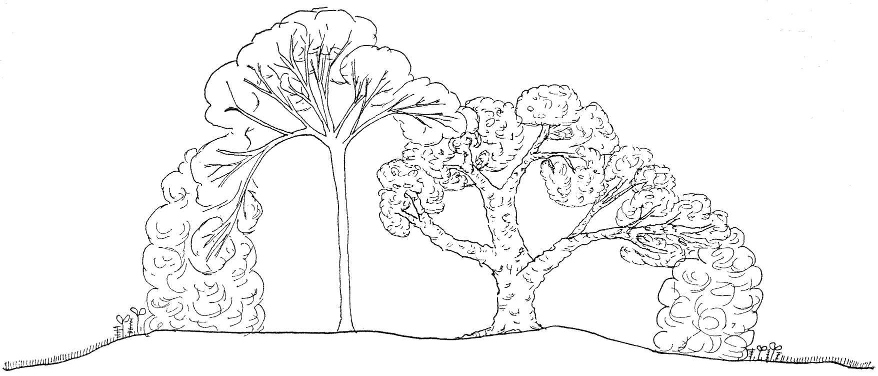

Fig. 3. Cross section through one of the "islands" at Bøndernes Egehoved. The canopies of the big trees form the ceiling of the rooms, the thorny bushes the walls. Weeds form a transition between the bushes and the grass.

In this locality nine species of *Aedes* were found: *cataphylla, rusticus, detritus, flavescens, punctor, dorsalis, cantans, annulipes,* and *vexans;* and two species of *Anopheles: maculipennis* and *claviger*. Usually the number of individuals was small, and the biting was never annoying. The main breeding place was a grassy pool in the middle of the enclosure. There was water in it all the time but it varied much in size. A ditch along the east side may have been a breeding place for some of the earliest species but was dry when we found it early in June. A creek which separates Bøndernes Egehoved in the southwest from the wood, Hejreskoven, overflowed in September and formed pools with larvae, mostly of *Culex pipiens*. In Hejreskoven, a typical Danish beechwood, were several localities for the breeding of such species as *A. cantans* and *A. annulipes* but these pools were dried out before we inspected them. Most of the observations in Bøndernes Egehoved took place during the first part of the investigation before the seaside meadow became flooded. In September larvae of both *Culex pipiens* and *A. caspius* were found here although the meadow mosquitoes mostly were observed elsewhere.

A description of Bøndernes Egehoved would be incomplete without at least a remark on the richness of the birdlife. A nightingale in each group of bushes and more than half a dozen other songbirds pleased the ears during the observations while the flights of herons, swans, eider ducks, swallows, and others delighted the eyes.

Næbengen (fig. 2, (4)). A small bay cuts in on the south side of Præstø Fjord west of Bøndernes Egehoved; it penetrates westward so much that the woods surrounding it on higher land form a "U", opening eastward. The bottom part of the "U" is a large meadow which we called Næbengen. Næbbet ('the beak') is the point north of the meadow with the woods, Næbskoven (3) and Skibbinge Hovedskov (1), while the wood south of the meadow is called Rævsvænget (5). A ditch runs in the middle of the meadow from west to east separating it into a North Meadow and a South Meadow. The latter is bounded in the east by a ditch draining Rævsvænget. Reeds, grasses, weeds, and one tree, an alder *(Alnus incana)* grow along this ditch. On the east side of the ditch is a meadow with an abundance of flowering plants, the Flower Meadow. Reeds grow everywhere along the shoreline.

Beldringe Kirkeeng is an inland pasture with scattered alder trees situated a few kilometers west of Præstø.

Kongelundsengen. This is a classical locality frequently mentioned by Wesenberg-Lund (1921). It forms the southwest point of the island, Amager, south of Copenhagen (55° 32' 30" n. lat., 12° 33' e. long.). It is also a seaside meadow between the water (Køge Bugt) and a wood, Kongelunden. There are a few pools and ditches with permanent water which inundate large areas after rain. Occasionally we made observations here but the frequent southwest wind often hampered swarming of the mosquitoes which were abundant both in number of species and of individuals.

A few other localities, where only single observations were made, will be described below.

3. **Ecological Factors.**

a. Time. All time indications are in M. E. T., one hour before Greenwich Mean Time. We corrected our watches every day shortly before the start of the observations by means of the time signal from the Danish State Radio received by a small transistor radio.

Sunset and sunrise, as used here, indicate the moments when the uppermost part of the sun appears to coincide with the horizon. It was rarely possible to observe this moment directly; therefore in all cases, it was calculated from the Air Almanac.

The duration of civil twilight is the period from sunset to the moment when the sun's center is 6° below the horizon or, in the morning, the period from the sun's altitude is —6° until sunrise. As the half diameter of the sun-disc is 16' and the refraction in the atmosphere is likely to cause an error of 34', sunset and sunrise are given as the moment when the sun's altitude is —50'. Twilight is therefore the number of minutes it takes for the sun to change the altitude 5° 10', from —50' to —6° 00'.

During our observations the duration of twilight varied from 60 minutes at midsummer to 36 minutes in the last part of September. Our observations in Iraq were made during twilights lasting 25 to 26 minutes. In Florida we have observations made in twilight lasting from 23 to 26 minutes.

It has previously been shown (Nielsen & Greve 1950, Nielsen & Nielsen 1953, Nielsen & Nielsen 1958) that the duration of twilight is a highly significant factor in the swarming of mosquitoes, and presumably also for much other twilight activity. In order to facilitate the analysis of such activities is has been proposed (Nielsen 1961) to introduce a time unit called crep (for crepuscular). This unit is the duration of civil twilight under given conditions, and having the value of zero at sunset and sunrise. Crep values are positive between sunset and sunrise, negative when the sun is above the horizon.

The simple indication of time in hours and minutes is of limited value in a work of this kind. If the commencement of the swarming of a mosquito at one place, A, is at 18h40' and at place B is at 21h30' there appears to be considerable difference between the two observations. If the sunset at point A is at 19h00', and at point B is at 22h00' the beginning of swarming could have been given as 20 and 30 minutes before sunset, resp. If, however, the twilight lasts 40 minutes at point A, and 60 minutes at point B it will be seen that the swarming at both places began at —0.5 crep, half of the duration of twilight before sunset.

The crep values are found by dividing the difference between a certain moment and sunset (or sunrise) by the duration of twilight under the given conditions. Even if it is a little troublesome to change the conventional time indications into crep values, we have found that it is well worth the time it takes. Further justification for the introduction of crep is found in the following; a more thorough discussion of the problem is given elsewhere (Nielsen 1963).

b. Illumination. When nothing else is indicated illumination in this paper is understood to be the diffused light from the unobstructed sky incident to the horizontal plane. When the sky is clear the illumination depends on the altitude of the sun. As the crep values mentioned in the preceding chapter approximately express the altitude of the sun, it follows that by a clear sky a certain value of crep corresponds to a certain illumination. Our investigation in Iraq (Nielsen & Nielsen 1958) made us aware of this relationship but we felt that renewed investigation of swarming during long twilights was needed to justify the introduction of crep. The relationship between crep and illumination was compiled from all data available to us and from these data we drew a smoothed curve. A table based on this curve showing the illumination in log lux for each tenth crep from —2.0 to +2.0 together with more detailed tables of illumination, crep and the altitude of the sun are given elsewhere (Nielsen 1963). The illumination at sunset and sunrise is 2.60 log lux and at +1.00 crep (the end of twilight in the evening and the beginning of dawn in the morning) it is 0.55 log lux. (The illumination of one lux (0.00 log lux) occurs at +1.226 crep). The zenith light, when the full moon has an altitude of +30°, is 0.90—2 log lux which is the normal illumination at +1.775 crep. Starlight on a moonless night is 0.95—4 log lux corresponding to 4.3 crep.

When the sky is clear, as it was during our observations in Iraq, no essential error would have been committed if, instead of measuring the light intensities, we had referred to the table to find the illuminations at any given time. It is more surprising that even during the varied weather of the Danish summer a serious error would only have been committed on six of 49 evenings by having used the standard illuminations instead of the ones actually observed.

On evenings with little or no cloud cover an easy way to measure the light is to have a correct watch. But in cloudy weather and for precise measurements a lightmeter is, of course, necessary.

The crep-log lux table is useful for the calibration of lightmeters. All that is needed is to read the instrument in arbitrary units on one or a few clear evenings and in the table find the illuminations corresponding to the moments of the readings. During this investigation we had to limit ourselves to our privately owned equipment; we used a Polaroid Land Camera exposuremeter calibrated and used with the film sensitivity indicator set on ASA 100. It rendered excellent service except that it was not quite sensitive enough to be used below +0.8 crep.

The principle of measuring the illumination as diffused sky light incidental to a horizontal plane is, of course, not the correct way to learn about the influence of light on animals which might be resting in dark places. It was found that while the illumination in the open was 3.40 log lux, it was only 2.29 log lux at the darkest place in the grass where the mosquitoes were resting. The first illumination corresponded to —1.0 crep, the other one to +0.2 crep. As the twilight lasted 55 minutes, this meant that when the illumination in the open is the normal one of nearly one hour before sunset, the animals are actually exposed to light which usually occurs more than ten minutes after sunset. In connection with the observations of *Aedes caspius* swarming under the canopy of an alder tree (see below) it was noticed that the swarms close to the trunk, at the darkest place, were formed earlier than at the lighter places towards the perifery. During five nights the illumination at two such places was measured as soon as possible after the measurement of the light in the open (fig. 4 and 5). At the outer place (B) only a single branch shielded the meter from the light from the sky and a slight movement of the meter changed the reading considerably, causing more dispersion of the points for curve B than for

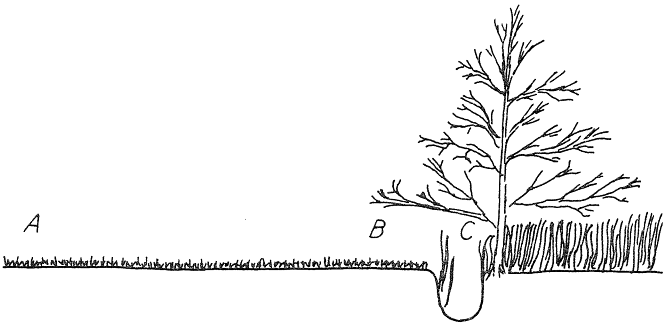

Fig. 4. The three locations for light measurements. A in the open, B and C under the canopy of the alder on Næbengen.

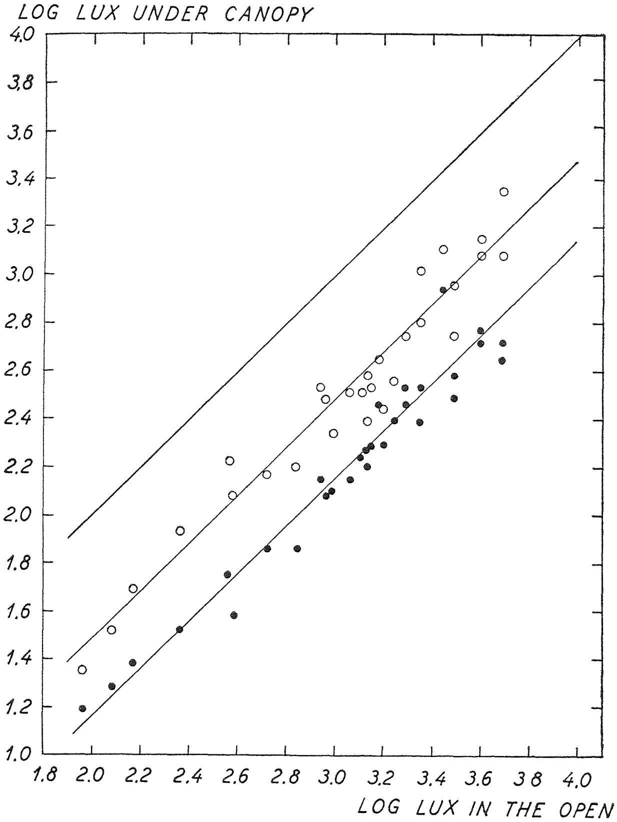

Fig. 5. Relation of the illumination at two places (B and C) under a canopy to the illumination in the open (A; see fig. 4).

curve C. Even if there is considerable difference between the illumination at different places there seems to be a simple correlation between them and the illumination measured in the open.

c. Temperature and Other Climatic Factors. The meteorological measurements were kept at a minimum, partly because our modest equipment was inadequate for a complicated study, and partly because the observations did not leave us time enough for more measurements. In Iraq the swarming occurred in a very similar way day after day, and the weather changed very little, always completely calm with a clear sky. During the observations in Denmark species of mosquitoes succeeded one another continually, and each species varied the behavior presumably in agreement with the highly varied meteorological conditions. These variations allowed us less time for measurements than in Iraq.

The standard observations which we tried to make every 15 minutes were usually started at about —2 crep and continued to the end of swarming at about +1 crep. They included the following measurements:

(a) Illumination.
(b) Temperature and humidity by means of a Lambrecht sling-psychrometer.
(c) Wind direction and force.
(d) Clouds: types movements, and tenths of complete cover.

Attempts were made on several occasions to measure the difference in vertical temperature distribution between an open area where free swarms and marker swarms were observed and in the foliage of higher vegetation over which topswarms were found. A couple of these observations, based on measurements

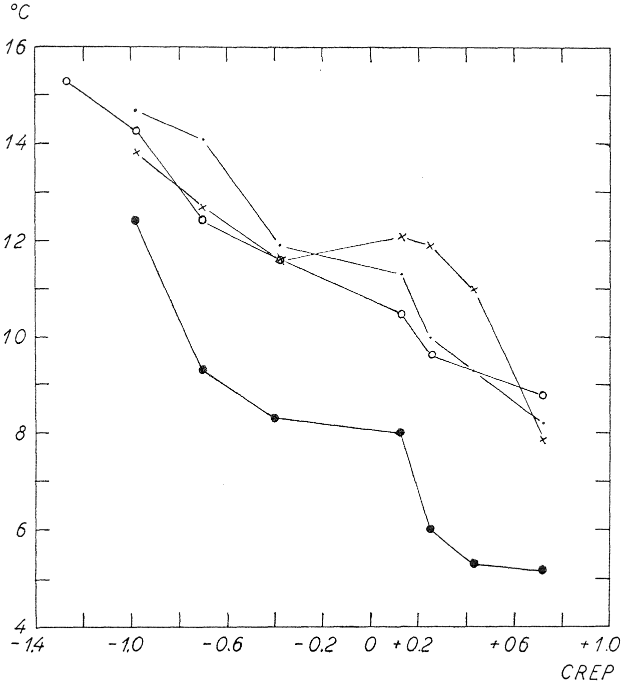

Fig. 6. Temperatures at Beldringe Kirkeeng.
○ 200 cm above the ground in the open.
· 350 cm above the ground in the canopy of an alder tree.
x In the grass under the tree.
● In the grass in the open.

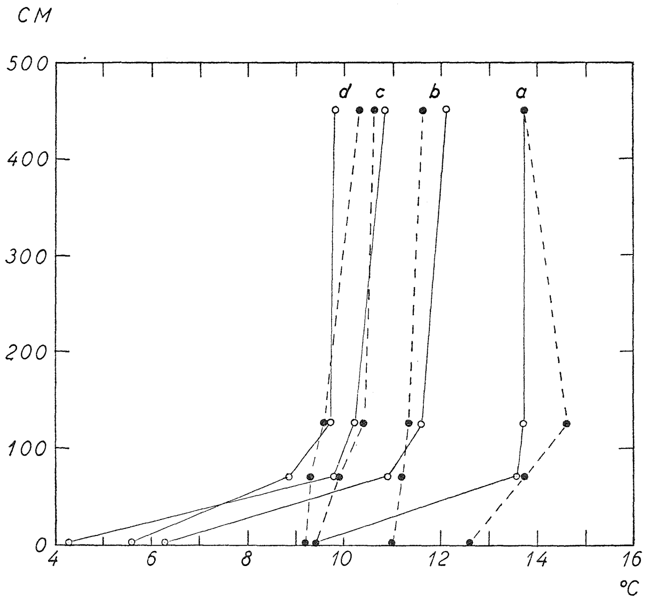

Fig. 7. Temperature tautochrones from Bøndernes Egehoved. The fully drawn lines represent the temperatures in the open, the broken lines those in and above a whitethorn bush over which *A. annulipes* swarmed. The measurements are those from —0.90, —0.14, +0.37, and +0.88 crep (a, b, c, and d, resp.).

with small mercury thermometers are given as figs. 6 and 7. There is, of course, considerable difference in temperatures at lower levels but at the levels where mosquitoes swarm the differences are so slight as to be rather insignificant.

The temperature of water in the breeding places was sometimes measured, especially during the development of *Aedes caspius*; but as the water was in constant interchange through ditches with the bay, the temperatures varied in such a chaotic way that a much more detailed study was needed than it was possible for us to make.

Rainfall was measured during the investigation on Næbengen in the hope of gaining an understanding of the changes in water level of the ditches, but this was given up because it was obvious that the water level depended much more on water from Fakse Bugt being forced into the smaller bays and ditches by wind than on rainfall.

Barometric pressure changes were regularly observed but only as an aid to weather prognosis.

4. Photography.

The camera used was a Samoca 35 mm camera with a 50 mm Fuji lens, f: 3.5. For night pictures a small pocket-type flashgun with fan-shaped reflector and miniflash bulbs was used.

B. OBSERVATIONS.

The observations on the different species are arranged in the order in which the species were found.

1. **Aedes (Ochlerotatus) leucomelas** Meigen.

Very little seems to be known about this species. Martini (1931) mentions it as one appearing very early in the season.

We have only two observations on *A. leucomelas,* one from the very first evening in Præstø, May 15. Three small swarms were observed close to the western border of the wood, Rævsvænget. The animals were flying about one to one and a half meters above the ground; one of the swarms was situated over a patch of grass but nothing could be identified as a swarm marker for the other swarms. They were very sensitive to light colors: even a white net waved some distance from them was enough to scatter the swarms. They were also sensitive to a man's voice but not to that of a girl. The first swarms was noticed at —1.02 crep, which might have been shortly after it began. The weather was calm (the wind was ESE and not felt among the trees); there was less than 1/10 clouds, mostly at the western horizon, so that the sun had disappeared at —0.55 crep. Shortly before sunset the temperature was 10.0° and relative humidity 93 %. The illumination at the swarming site under the tall trees was 2.14 log lux at sunset. Most of the swarming males disappeared at +0.12 crep and the last swarmer ceased at +0.23 crep. At this time the illumination was 1.75 log lux, the normal illumination in the open at +0.5 crep.

The fibrillae on the antennae of specimens caught in the swarm for identification were extended when caught, but were retracted during the transportation to our quarters. One of the specimens extended its fibrillae again when narcotized by tobacco smoke.

We may have seen this species forming a top swarm over a birch tree on Kongelunden June 1—2, but we cannot be sure because the specimens were so badly rubbed that it is impossible to decide whether they belong to *A. leucomelas* or *A. cataphylla* (see below).

2. **Aedes (Ochlerotatus) rusticus** Rossi.

Callot and Ty (1945) found this species swarming in sunshine 1½ to 2 meters above trails and roads. There seem to be no other reports on the behavior of the imago.

Wesenberg-Lund (1921) found that it hibernates as larva and therefore appears very early in the year. This is in good agreement with our findings: it was the first mosquito we found in numbers on the first afternoon we visited Bøndernes Egehoved (May 16). They were especially numerous in the grass downwind (on the west side) of the grassy pool from which they evidently had emerged. Larvae and pupae were found in the pool but the breeding appeared rather well synchronized and had lasted only a few days. The swarming that evening (May 16) was different from those on the following evenings (see below) with but few participants; it gave the impression of being the first evening of swarming. By May 19 most of the individuals were found some distance from the pool.

On the evening of May 16 most of these mosquitoes were in the grass, although quite a few were found in the bushes, especially in the white flowers of the blackthorn. We did not see any of them feeding and none had the abdomen swollen. All had recumbent fibrillae.

From —0.92 crep provoked swarms occurred, and a few minutes later, at —0.82 crep a low free swarms was observed

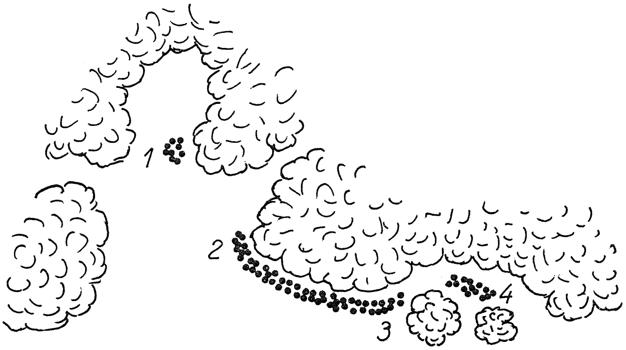

Fig. 8. "Hedge swarm" of *A. rusticus* in a "cove" at Bøndernes Egehoved.

Fig. 1. Grassy pool at Bøndernes Egehoved. Flowering blackthorn. Oak in background not yet in leaves.

Fig. 2. The largest of the "rooms" inside the tree groups at Bøndernes Egehoved.

Fig. 1. Beldringe Kirkeeng.

Fig. 2. The meadow at Kongelunden. The wood is to the left, the sea to the right. *A. dorsalis* swarmed over the depression in front of the fence. To the left of the fence toward the background were breeding places for *A. dorsalis* and *A. flavescens*. Preliminary swarms of *A. flavescens* were over these waterholes (see Plate III, fig. 1 and 2).

Fig. 1. *A. flavescens* swarming at Kongelunden.

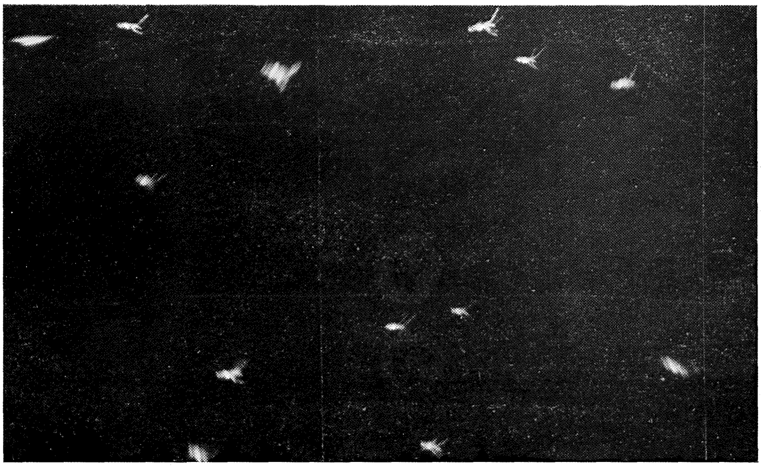

Fig. 2. *A. flavescens* swarming at Kongelunden.

Fig. 1. Bøndernes Egehoved. Note the "hedge" of thistles and nettles bordering the tree groups — a favorite resting place for *A. annulipes*.

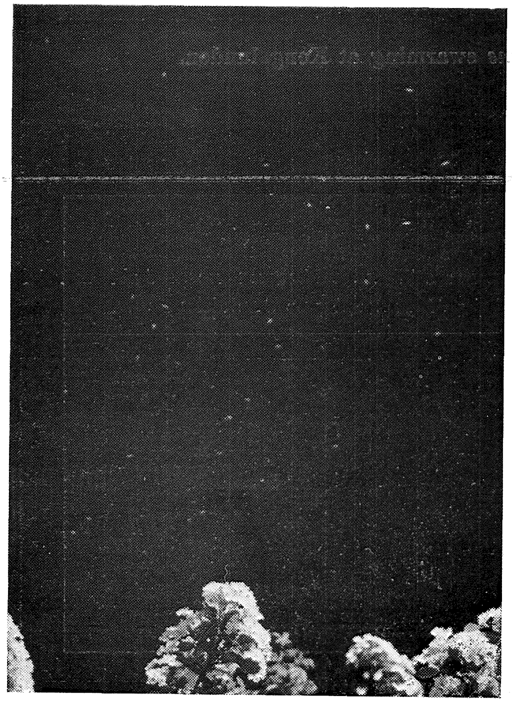

Fig. 2. *A. annulipes* swarming over whitethorn bush in flower.

Fig. 3. *A. annulipes* copulating venter-to-venter.

Fig. 1. Swarming tipulids and *A. geniculatus.*

Fig. 2. *Culex* swarming around the tip of a branch of the alder on Næbengen.

Fig. 1. Næbengen towards south.

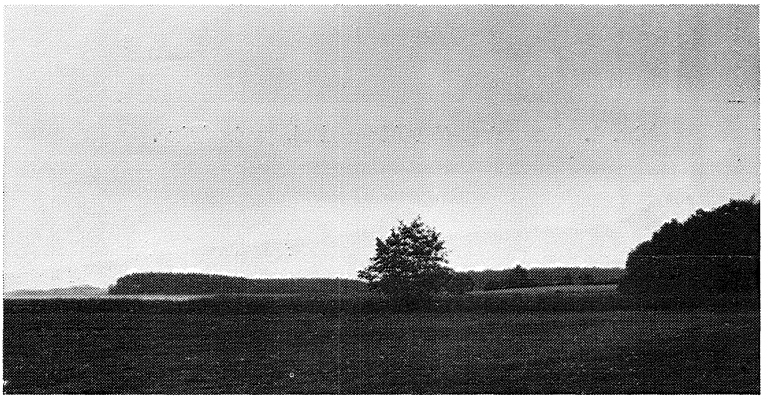

Fig. 2. Næbengen towards east. The south meadow with the alder at which *A. caspius* and *C. pipiens* swarmed.

Fig. 3. The alder on Næbengen.

Fig. 1. Swarm of *A. caspius* under the alder on Næbengen.

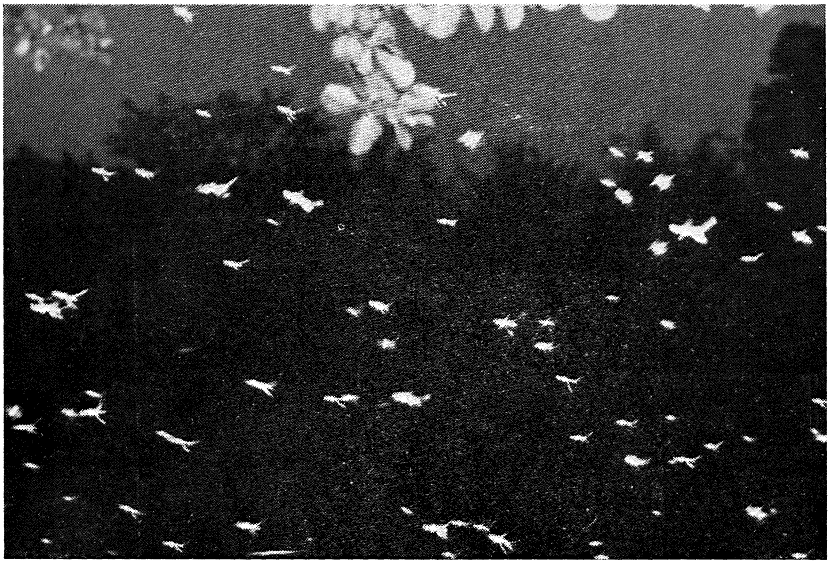

Fig. 2. Swarm of *A. caspius* under the alder on Næbengen.

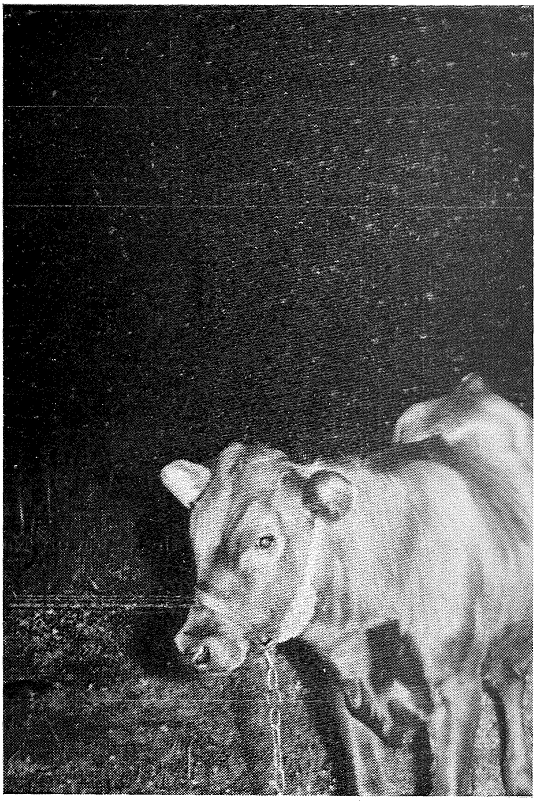

Fig. 1. Swarms of *A. caspius* over a calf.

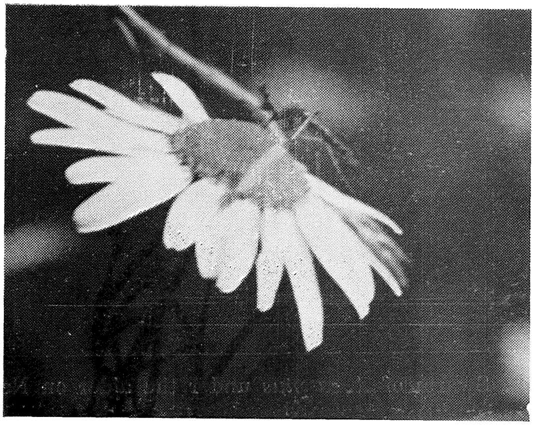

Fig. 2. Male *A. caspius* feeding.

in a small open space with bushes towards the west, north, and east — a "cove", 8-10 meters deep, 5 m across the mouth and a couple of meters wide at the bottom (fig. 8). The swarm was very loose and occupied most of the inner part of the cove. The flight was only a meter or less above the grass. The swarm had a weakly developed nucleus in the middle. The evening was chilly with temperature dropping from $10^1/_2{}^0$ to 9^0 during the observation period. At —0.10 crep there were fewer swarming, and at +0.35 crep there were only 4-5 left in the nucleus. The height above the ground in which the swarming took place decreased and at +0.41 crep it was below $^1/_2$ meter. The flight was then so slow that the animals sometimes seemed to hover in the air. The last one disappeared at +0.63 crep. The swarmers seemed to have the fibrillae extended but all others had them closed. No other swarms was observed this evening but four times (—0.10, +0.08, +0.18, and +0.20 crep — in other words, close to sunset) single individuals made attempt to start a high free swarm.

The following evening (May 17) it was 8/10 cloudy and the temperature remained at about 10^0. There were many more mosquitoes, especially females. The swarming began in the cove at —0.90 crep but as late as at —0.67 crep only the swarmers had extended fibrillae. Some in the low bushes had the fibrillae out at —0.57 crep. At —0.33 crep there were many males resting in the grass close to the swarm, all of which had extended fibrillae; when disturbed they took part in the swarming.

At —0.16 crep a top swarm was formed over a bush west of the entrance to the cove. We succeeded in catching only one individual *(A. rusticus)* at the outskirts of the swarm. Although at least some of the topswarmers looked like culicides most of them were, perhaps, one of the two species of chironomids which also swarmed that evening. Some of the *A. rusticus* males flew high in the air after swarming and disappeared, but most of them came to rest in the bushes. Many fed on blacktorn, all of them had recumbent fibrillae. It was completely calm in the cove but the swarming was again rather low over the ground, $1—1^1/_2$ meters. The swarm ended at +0.35 crep and the topswarm at +0.67 crep.

The next evening it rained until —0.71 crep. It was so dark that the illumination at —0.67 crep was the same which normally prevails at +0.05 crep. The temperature was then 11.3° and dropped to 9.4° before sunset. Everything was dripping wet. For a few minutes, between —0.16 and —0.10 crep, a few individuals were swarming.

In the following days many swarms were seen, especially in the "rooms" under the canopy of the big trees (see fig. 3). Swarms, such as *A. rusticus* made in the first days in the open coves, were later made by *A. cataphylla* which, during the following evenings, developed such swarms in all the open spaces. The *A. rusticus* swarms were usually found in the middle of the rooms, where the sunrays penetrated the foliage, especially where there was a mixture of sun and shade. The swarms were always low, usually about half a meter and never more than one meter above the ground. There was often a swarm of small fast-flying flies above the *A. rusticus* swarms in the "rooms".

The other type of swarm was new to us. It has already been mentioned that the wooded "islands" had walls of thorny bushes and at the foot of the walls was a low hedge of nettles and sometimes thistles following the rounded contour of the thorny bushes. *A. rusticus* flew over these nettles in a manner called a "hedgeswarm". Fig. 8 shows the first cove mentioned above and the hedgeswarms along the east side. The flight was different from the usual movements in a swarm: the head was not turned towards the wind but in the direction of the flight which carried the individuals from one end of the swarm to the other where it turned around and flew back, more like a kind of promenade or patrolling than the usual dancing flight. However, the presence of a large number of participants gives the swarm a more irregular appearance than that. Occasionally a swarmer stopped its flight and hovered a few seconds and then either proceeded or turned around. The flight was easiest to see in the swarm between "2" and "3" in the figure. It occasionally happened that an individual continued the flight past "2" to "1" or vice versa. There was no connection between point "3" and "4" probably because there was a low (40 cm high) blacktorn bush in blossom between tho points. It was repeatedly found that the flight was discontinued by areas of strong contrast on the ground. Both a white net and a black coat placed halfway between "2" and "3" interrupted the flight so that two separate swarms were formed. However, on May 22 at —1.53 crep and before the hedgeswarms were fully developed (—1.47 crep) a swarm occurred just over the same small blackthorn bush; but while the hedge-swarms usually flew 20—50 cm above the top of the nettles, this swarm kept about two meters above the ground.

The "corkscrew" flight, during which the mosquito flies in a spiral around the flight direction as if it were following the edge of a corkscrew, was sometimes seen in the hedge swarm, especially on long flights. This flight is also performed by other mosquitoes and is mostly seen in free flight through the air. We have no explanation of this habit.

Towards the end of the swarming *A. rusticus* moved away from the bushes and formed a low free swarm as on the first evening but not at the same place; however, by that time (about —0.5 crep) the number of swarmers was decreasing.

A few matings were seen in the swarms in the "rooms" very early in the evening of May 22 at —3.26 crep, mostly when the females were stirred up by the approach of the observer. The following day one mating was seen when we arrived. It was obvious that the vast majority of matings occurred at times other than during swarming.

This species swarmed very early in the evening, especially in the "rooms" where the illumination could be 1.0 log lux lower than outside. This will be further discussed in the general part of this paper.

Close to the swarm, males were often seen resting in the grass with extended fibrillae; they could easily be provoked to join the swarm. The fibrillae of animals resting farther away were sometimes opened and sometimes closed. The animals in the bushes had them closed.

Animals feeding on the flowers of blackthorn were seen repeatedly, especially during the first days. These always had the fibrillae closed.

The last swarm of *A. rusticus* was seen on June 12 on the southwest side of Bøndernes Egehoved; there were only a couple of individuals.

Another male was seen the same evening, he seemed to be very old; nearly all its hairs were rubbed off, and it had lost both hindlegs and some segments of one of the palps.

3. **Aedes (Ochlerotatus) cataphylla** Dyar
syn. **A. (O.) prodotes** Dyar

Dyar (1920) observed swarms of this species fairly high above the ground between spruces and willows at White Horse in the Yukon Valley in Canada, and Frohne and Frohne (1954) found a swarm in Alaska as late in the year as July 18. Wesenberg-Lund (1921) found that *A. cataphylla* formed swarms together with *A. communis* but the former appears earlier in the year than the latter. He described the swarms as low, in open spaces between trees in a wood. They took place before sunset.

The first swarming of *A. cataphylla* observed during this investigation was on May 19, during an inspection in the morning at about 10 h. *A. rusticus* which had swarmed the preceding days (see above) were resting in bushes and in the grass. The grass was still wet from the rain which had fallen May 18 when there had been hardly any swarms because of the rain and wind. However, under a tree a few very dark mosquitoes were performing a swarming flight low over the ground. When two of them were caught, the remainder stopped the flight and went to rest with fibrillae still extended. No swarm was seen in the early afternoon but the animals seemed unusually active and were provoked to flight by the approach of even a bee or a fly (later this was also observed in resting *A. annulipes,* p. 129). At —1.60 crep there were free low swarms at all open areas, at the borders and partly over the surface of the water in the grassy pool (see above). The flight was similar to that of *A. rusticus*: long flights back and forth with zig-zag flights at the turning points. Towards —1.0 crep the low swarms began to dwindle and single individuals were seen leaving the swarm and fly up in the air. Some disappeared, some seemed to come to rest in the top of the bushes, some began to swarm high in the air. From —0.40 crep top swarms were formed, and there were also large free swarms. To what extent *A. cataphylla* contributed to these swarms is unknown. One swarm which was low enough to be caught consisted of *A. detritus* but some of those swarming were undoubtedly chironomids. The high swarming continued until after +0.5 crep, and possible until after +0.7 crep. Several matings were seen, the last one at +0.12 crep. Only a couple of mosquitoes (one of them a female) were seen feeding on flowers this night.

The following evening *A. cataphylla* swarmed in the same way. On May 23 it was noticed that the low swarms ended in the dark coves at +0.33 crep while they went on at the higher illumination on the open plains until +0.47 crep.

On May 24—27 it was so cold (below 8°) that no swarming took place and May 28 to May 31 the evening observations were made at Beldringe. On June 1 on Kongelundsengen a swarm of *A. cataphylla* and *A. flavescens* was seen at the border of the woods over a dark spot in the grass.

When we returned to Bøndernes Egehoved, *A. rusticus* was much reduced in numbers and there were also fewer *A. cataphylla* while *A. annulipes* had become the dominating species. It has a definite ascent phase of the activity before the true swarming, and *A. cataphylla* often took part in this or formed the usual type of free swarms over open places. They were never found in the topswarms of *A. annulipes* but it is quite possible that there might have been some.

The sites for the low free swarms of *A. cataphylla* changed from day to day without any reason apparent to us: one day they would be at one place, the next day at another. On June 12 there was no swarm of this specics to be found anywhere but on June 14 and 18 they were swarming again. At that time there were so few mosquitoes at Bøndernes Egehoved that we moved to Næbengen. A small swarm was found here in the wood close to the meadow on June 22, and another one right outside the wood on July 6.

4. **Aedes (Ochlerotatus) detritus** Haliday

Although this is a common sea-shore mosquito in northern Europe not much is known about its habits. Haliday (see Marshall 1938) observed large columnar topswarms which appeared as smoke. Horsfall (1955) quotes for this species the observations of Bro Larsen (1948) on *A. caspius*. Wesenberg-Lund (1921) mentions it as having only one very late generation in Denmark.

We found this species occasionally during the whole period of observations: the first one was seen on May 19, the last one on September 20. The most regular swarming was in May at Bøndernes Egehoved on May 19, 21, and 23. The swarms were at different places all three days but they were all near the top of bushes not always over the top but sometimes in "niches" between the uppermost branches of the bushes. On May 31 a free swarm of this species was found over the grass on the sea shore meadow on the north side of Næbbet close to a stack of seaweed. At Bøndernes Egehoved a topswarm appeared on June 4 over a small "island". It reacted easily to a girl's voice. It is unlikely that this swarm has been overlooked previously and it did not return the following day. On Kongelundsengen August 6 there were many swarms of *A. detritus:* rather low (2-3 meters) free svarms, topswarms and especially one or two enormous swarms which filled up the space between a couple of trees close to the edge of the wood. The flight in the swarm was mostly long, fast sweeps. It was a calm evening with 10/10 cloud cover, mostly alto-stratus. At +0.20 crep the illumination was 2.41 log lux, not much lower than the standard illumination (2.57 log lux). Temperature fell from 15.5° to 15.2°, relative humidity was about 90 %. No swarming of *A. detritus* occurred at sunrise the following morning, but more surprisingly, the next evening the only swarming of this species seen was a little low swarm over a patch of nettles at the outskirts of the wood. The temperature ranged from 16.8° at —1.69 crep to 14.6° at +1.24 crep. Cloud cover 3-4/10 mostly along the horizon. The illumination was nearly normal, and the wind though rather strong from NNW was hardly felt in the observation area. During the evening the relative humidity rose from 86 % to 94 %. At the site for the swarming the preceding day large numbers of *A. detritus* were resting and feeding on flowers. They rose to a kind of ascent from about —0.42 crep but made hardly any swarming flight; they disappeared, most of them before +0.47 crep when *Culex pipiens* had started to swarm at the trees where *A. detritus* swarmed the day before. In September no true swarms of this species were seen but several individuals were found among the migrants on Næbengen (see below under *A. caspius*). Females in these flights sometimes had large eggs visible, and sometimes they were bloodfilled.

5. **Aedes (Ochlerotatus) cantans** Meigen

Callot and Ty (1945) and Nielsen and Greve (1960) appear to be the only investigators to have studied the habits of the imagines of this species. The Danish authors found that it performed several different types of flight: Provoked swarms, ground swarms as part of the ascent, high free swarms, top swarms, and ceiling swarms. Whether the high free swarms were really free or formed over markers, contrasting areas on the ground, is not known. The idea of marker swarms first conceived by Cambournac and Hill (1940) and brought into prominence by Downes (1955, 1958), was unknown to Nielsen and Greve.

During the present investigation we often met with *A. cantans* but only on three evenings did we observe swarms believed to have been of this species alone. The first one was a high free swarm in the cove at Bøndernes Egehoved where *A. rusticus* and *A. cataphylla* swarmed. Whether these species participated in the higher swarming after the low flights described above is not known but in a similar svarm on May 23 one *A. rusticus* was found in the swarm of *A. cantans.* At Kongelunden the seashore meadow is separated from the wood by means of a rather irregular embankment. On June 1 over a hollow part of this grass-clad slope there was a low flight of *A. cantans* which later disappeared, undoubtedly a kind of ascent flight; the true swarm was perhaps over a birch tree nearby where there was a very large swarm of *A. leucomelas* or *A. cataphylla.*

On June 9 a pure swarm of *A. cantans* was found over the gate in the fence around Bøndernes Egehoved. Fence gates seemed to attract this species as we found another swarm over the gate into Beldringe Kirkeeng May 31 at sunrise. It was mixed here with *A. flavescens.* A third case was on Næbengen where the swarm was mixed with *A. annulipes.*

On Beldringe Kirkeeng *A. cantans* and *A. flavescens* were found in about equal numbers. In the evenings of May 28, 29, and 30 and in the morning of May 31 we observed several swarms, both over tree-tops and over dark areas on the ground; unfortunately both species occurred in both swarm types, and as they are of about the same size it was not possible to distinguish between them during the observations.

At Bøndernes Egehoved quite a few *A. cantans* were observed in June when the closely related *A. annulipes* dominated the swarming. *A. cantans* probably occurred in some of the swarms but as *A. annulipes* was so much more abundant it would have been necessary to catch a very large number of swarmers to find an *A. cantans* among them. One exception was a swarm at a flowering whitethorn bush seen June 10, 11, and 13, but not on June 12. It was rather loose although well defined, and extended over the top of the white bush to the top of a taller bush behind it. This is not typical of *A. cantans* but the possibility that the top part of the swarm was formed by other mosquitoes cannot be excluded.

Nielsen and Greve found that *A. cantans* usually swarmed at sunrise if the temperature was above 8°. On the first morning that we found it necessary to make observations at sunrise, June 6, neither *A. cantans* nor *A. annulipes* swarmed, although the temperature was 11.4—12.1°, calm, 3/10 clouds, 99 % relative humidity.

6. **Anopheles plumbeus** Stephens.

On May 28 about —1.30 crep, along the little road between Beldringe Church and the meadow, a few mosquitoes formed a small swarm over some tall weeds. They were male *An. plumbeus*. The swarm was probably provoked by our arrival.

7. **Aedes (Ochlerotatus) flavescens** Müller
syn.: **A. (O.) lutescens** F.
A. (O.) fletcheri Coquillet

Wesenberg-Lund (1921) found this species breeding in open meadow close to lakes or the seacoast. The emergence is in the latter part of May, and imagines remain on the wing all summer. He describes the swarms as the largest culicide swarms he observed. He gives a very clear description of the swarming at Aalholm Castle on the island Lolland; it is of the ascent type and many matings occurred. Hearle (1929) studied this species at Indian Head, Saskatchewan. He confirmed Wesenberg-Lund's observation except that the copulating females had not had a bloodmeal before the mating as found in the Danish individuals. We are able to corroborate the observation of Wesenberg-Lund: we have seen cases of females of this species copulating while they had the abdomen distended by blood; the same was also seen in *A. annulipes* and *A. caspius*.

During the present work we repeatedly had opportunity to observe this species. The first time was on May 23 at Bøndernes Egehoved where it swarmed in a "niche" near the top of a bush, very much the same way as described above for *A. detritus* the same day but in another bush. It has been mentioned already that on the inland meadow Beldringe Kirkeeng *A. flavescens* and *A. cantans* swarmed together. The first evening (May 28) only a few were seen but there were many on the following days. The swarms were normal, fully developed topswarms and marker-swarms and we did not see anything like the low ascent swarms described by Wesenberg-Lund. However, at Kongelundsengen June 1 and 2, several kinds of low swarms occurred early in the evening from —1.20 crep to sunset and perhaps later at the edge of the wood, over a dark spot in the grass, and over the water in a ditch or pool with permanent water. They were not observed closely enough later on to see whether they flew higher because a large free swarm of *A. dorsalis* demanded our full attention (see below) from —0.18 crep. However, it was noted that in several cases *A. flavescens* swarmed over the heads of the observers, following them around. The next evening many swarmed low over the pool (plate 3, fig. 2). Matings occurred when females flew up through the swarm. Matings were also seen in the open over the meadow where there was no swarming.

Both larvae and pupae of *A. flavescens* were found in the pool mentioned above, as was the case June 30 in the ditches on Næbengen.

At Kongelundsengen on August 6 *A. flavescens* flew in one of the high swarms together with *A. detritus*, and like that species it took part in the ascent the following evening but no swarms were formed by either species. Our last note of this mosquito is that a female was biting as late as September 15.

8. **Aedes (Ochlerotatus) punctor** Kirby

This species has repeatedly been observed in North America (Dyar 1920, Twinn et al. 1948, Hocking et al. 1950, Jenkins and Knight 1952, Frohne and Frohne 1952). From Canada high free swarms have been reported after sunset; from Alaska swarming occurs earlier in the evening with numerous copulations in the swarms.

Wesenberg-Lund (1921) had collected only one specimen in Denmark; Nielsen and Greve (1950) found a few among large numbers of *A. cantans.*

During the present investigation we found this species several times at our observation places around Præstø, but the number was usually low. The first time was on May 22 when a few individuals participated in a free swarm of chironomids at —0.31 crep.

On the meadow Beldringe Kirkeeng a water pump was covered by a boxlike house, over which a few *A. punctor* swarmed at +0.08 crep. Rather high above them swarmed a few more which we were unable to catch for identification. Earlier in the evening (—0.75 crep) a biting female was found at another part of the meadow.

May 31, on the seashore meadow on the northside of Næbbet a male was caught in the grass at —1.35 crep, and later on, at —1.15 crep, a few individuals flew in ascent-like flight towards the edge of the wood.

At Bøndernes Egehoved there were several swarms in June. Early in the evening of the third of June, at —0.93 crep, they formed a high free swarm while *A. cantans* was still ascending.

Both on June 9 (at +0.29 crep) and June 10 (at —0.33 crep) we had swarms of *A. punctor* over our heads, first one individual, eventually three or four. The swarm was dispersed when a white net was held under it. On June 13 there were a few small swarms over the meadow down to the dried-out part of the grassy pool. One swarm here was made up of *A. punctor,* the others of *Anopheles maculipennis.* Only one swarm was followed from commencement to cessation. It was on the meadow on the east side of Næbbet on June 21, formed rather close to the edge of the wood over a patch of high grass. It began at —0.42 crep, and at +0.42 crep one was left; it finished at +0.53 crep. The next day we tried to repeat the observation but only very few individuals appeared and they split up in two or three swarms. The swarming began with a single individual at —0.61 crep, at —0.36 crep there were two, at —0.14 crep, three, and at —0.10 crep five individuals. Around sunset more individuals came forth apparently from the reeds at the edge of the water, a distance of about 60 meters. Most of the flight was a couple of meters above ground but especially at +0.15 crep the swarming animals went much higher. The two other swarms were found at +0.24 and +0.41 crep. All three swarms of *A. punctor* were tested by a white net placed under them and they all dispersed (contrary to *A. dorsalis* which swarmed at the same time, see below).

Only once, later, did we see *A. punctor*: it was as late as September 13, in the garden of the inn "Svend Gjønges Kro" which is situated between the main street of Præstø and Tubæk Å. Males participated here in the ascent of *Anopheles claviger* (see below) but the swarms were not found.

9. **Aedes (Ochlerotatus) dorsalis** Meigen

It is a species with a very large area of distribution. Although found over most of the Eurasian continent most of the knowledge of its habits has been collected in North America. According to Quayle (1906) and Rees (1945) it is migratory. Rees and Nielsen (1947) found it swarming over a soil bank 1-3 meters above ground. Earlier descriptions (Dyar 1917, Segen 1924) indicated the swarming to be topswarms over bushes.

To us the species offered particular interest because it is very closely related to *A. caspius*; some authors consider it to be a subspecies of *A. caspius*; and Wesenberg-Lund (1921), failing to find any reliable difference between them, referred his observations only to *A. caspius*. Most authors, however, consider them distinct. Natvig, in his authoritative tome (1948) so considers them, even though he qualifies his conclusion by stating that there are cases which hardly support such a division and refers (p. 107) to them as sibling species. Although at first it was feared that the difficulty of distinguishing between the two species living in the same places would be an obtacle, the fear was unfounded. Individuals which were not too badly rubbed were not difficult to distinguish, and the junior author had no difficulty in distinguishing them alive in a glasstube or even before catching them. The correctness of such identification was, of course, later verified. The easiest way to distinguish swarms of the two species is by placing a white net under the swarms: *A. caspius* males will disperse at once while *A. dorsalis* males will concentrate over the net and may be moved around with it. We never found any exception to the fleeing-reaction of *A. caspius;* but in two of the scores of times the attraction of *A. dorsalis* was tested, the swarmers reacted by dispersal. Further comparison of the swarming habits of the two species will be found under *A. caspius* and in the general part of the paper.

The first *A. dorsalis* we saw was on May 22 at Bøndernes Egehoved when a male took part in the ascent and flew up to the top of a bush. The next day two females were found at the grassy pool. Two males were found resting in the grass with closed fibrillae at —0.70 and —1.06 crep on May 31 on the meadow on the north side of Næbbet but we did not see any swarming of them that evening.

Miss Kirsten Tetens Nielsen called our attention to the presence of mosquito swarms on Kongelundsengen, and hoping that it would be either *A. caspius* or *A. dorsalis* we inspected the locality on June 1. It was a clear evening with mist at the horizon; there was a fresh E-SE wind but the meadow was sheltered against the wind and it was calm where we made the observations. Temperature varied between 11.5° and 12.5°, and the relative humidity between 88 % and 90 %.

Most of the mosquitoes were found in the grass at the most sheltered place right outside the edge of the wood. Besides *A. dorsalis* there were some *A. flavescens,* and *A. cataphylla* (or *A. leucomelas* — see above). At —0.52 crep a male with recumbent fibrillae ascended and flew together with a swarm of tipulids. At —0.21 crep single individuals started swarming at several places on the meadow. Finally at —0.04 crep a full-fledged swarm was found over a little depression rather close to the fence between the meadow and the wood. The grass was slightly lighter in color here than the surroundings. The swarm was large, consisting of approximately a hundred males; the number slowly tapered off; at +0.41 crep there were clearly fewer, and at +0.82 the swarming stopped.

The following evening (June 2) there was a very thin cirrus veil over the sky but the illumination completely followed the standard curve. The wind was weak, from the east, and was not felt in the observation area. The temperature dropped during the observations from about 16° to 10.8°, and the humidity rose from 78 % to 93 %. At our arrival at —1.02 crep, males were already found resting with extended fibrillae and flew up easily and formed small, very low swarms, probably provoked. Between —0.84 and —0.70 crep the swarming started at the same place as the preceding day, over the discolored grass. Just before the beginning of the swarming many males, when disturbed at their resting place in the grass, close by the swarming site, flew up and towards it. An inspection of the meadow showed several swarms over discolored spots in the grass, especially if the spots were not too large and the contrasting color was not too light. Over places with white sand there were swarms of chironomids but not of *A. dorsalis*. Close to the border of such places were sometimes small culicid swarms but all attempts to catch them were unsuccessful. *A. dorsalis* finished swarming at +0.81 crep, practically at the same time as the day before.

We returned to Kongelundsengen on June 7 but the weather was unfavourable. The wind was from SW straight in from the water at a force of 5 rising to 6. By means of soap bubbles the wind was found to be 5.6 m/sec at —2.60 crep and 6.5 m/sec at —1.11 crep at a height of 1-2 meters. There was 10/10 cover of nimbus, and it was so dark that sunset illumination prevailed at —0.67 crep, or 38 minutes before sunset. The temperature dropped from 19.4° at —3.47 crep to 17.2° at sunset. Relative humidity rose from 84 % to 88 %.

There were but few animals in the grass, mostly females of *A. dorsalis* and *A. flavescens*. Most of the mosquitoes were found at sheltered places. At —2.95 crep all males had closed fibrillae. They seemed to have fed; this was most clearly apparent in *A. flavescens*. Females of both species were biting. At —0.84 crep all but two male *A. dorsalis* still had the fibrilliae recumbent; the two with open fibrillae were found in the shelter of some tall and dense grass. Males caught at —0.58 crep opened the fibrillae in the net or in the vials. At —0.49 crep rather suddenly all males at the resting place had the fibrillae extended. Shortly after (—0.40 crep) an ascent began at sheltered places. When they had come to a potential swarming site they were carried away by the wind. No swarming took place, and at sunset the biting of the females decreased.

Again at Kongelundsengen, on June 15, the weather was windy from NW 2.4—3.1 m/sec one to two meters above the ground. There was 2-4/10 strato-cumulus clouds. The illumination was oscillating around the normal values, sometimes a little too high, sometimes a little too low according to the fast changing cloud cover. It was a fairly warm and dry evening, from 15.0° to 13.8° and from 71 % to 79 % relative humidity.

The males resting in the grass around the first-found swarming place unfolded the fibrillae as did *A. caspius* in Iraq (E. T. and H. T. Nielsen 1958): for further discussion see the general part. At —1.00 crep to —0.93 crep the males could be provoked into flying up to a distance of three meters but there was no provoked swarming. First at —0.23 crep, mosquitoes were seen flying around. From —0.15 crep, one mosquito after another made attempts to fly up from the grass and started swarming at the place where the first swarm was seen, but they drifted away with the wind. At +0.20 crep, a small swarm formed over the head of the observer; and finally at +0.30 crep, a swarm was formed of first two individuals, then four, and later more, but it was difficult to count them because all the while the wind caused them to make irregular movements. Between gusts there seemed to be more than ten. Several females were biting. The swarm dispersed at +0.40 crep and was not formed again that evening. It lasted only 0.10 crep (six minutes). Another swarm was found at +0.54 crep over a dark humid depression in the bank which formed the borderline between the meadow and the woods. Sweeping the net caused the swarm to disperse but it formed again soon after and lasted to about +0.90 crep. It is noteworthy that this swarm was formed over a dark area (at least dark to the human eye) because *A. dorsalis* usually swarmed over light-colored markers.

After the swarming was finished at +1.02 crep, chironomids came drifting with the wind from the water, very much as newly emerged *Glyptotendipes* drift to the shore from the lakes in Florida (Nielsen 1962).

The following day observations were made both at sunrise and at sunset. In the morning, at 12° temperature with 85 % relative humidity, the cloud cover was reduced from 5/10 to 0/10 during the observations but the wind increased from force 4 to force 5; it was from NW as the preceding evening. Between +1.12 crep and +1.03 crep we saw one female. At +0.27 crep a male with closed fibrillae flew up to the top of a bush on the sheltered side.

In the evening the wind had turned toward WSW and was at force 5. The illumination decreased to the sunset value at —0.42 crep, 25 minutes ahead of time. Male *A. dorsalis* were found deep in the grass, after —0.92 crep they extended the fibrillae but no other sign of activity was observed.

At Præstø the first *A. dorsalis* was seen July 4, having emerged from a mixed brood of *A. caspius* and *A. dorsalis*. The former was more numerous and the first to finish development. As early as the following day a male was swarming over the head of the observer. During the following period (July 10, 11, 13, and

15 in the evening, and July 13 in the morning) several swarms of *A. dorsalis* were seen, most of them over the observers' heads. In several cases these head swarms were mixed with *Culex pipiens* or chironomids. Free swarms were also seen but it was not always possible to identify the marker. One of these swarms between +0.61 and +0.56 crep in the morning of July 13 did not react to white net.

On August 6, at Kongelundsengen, there was a very large swarm of *A. dorsalis* at the same place as on June 1. It was a calm evening with 10/10 altostratus clouds, 15.5°—15.2° and 90°/$_0$ relative humidity; the illumination was slightly below standard. At sunrise the following morning, at very nearly the same weather conditions (15.0°—14.9°, 96—97°/$_0$, 10/10 alto, NW-1) there was again swarming at the same place. It was a very high swarm and the few individuals caught were all chironomids. No other free swarm was seen but they participated in a swarm around and above a birch tree. It is possible that the swarm at the top consisted mostly of *Aedes* but in the lower part of the swarm where we could catch specimens $^3/_4$ of them were *Culex pipiens* and $^2/_3$ of the rest were *A. dorsalis* and $^1/_3$ *A. caspius*. In the evening of August 7 when *A. detritus* disappeared (see above) there were huge swarms at the three and also the usual *A. dorsalis* swarm which however was rather loose, perhaps because this place was not protected against the wind (NNW, 3-4). One of the free swarms close to the fence was dispersed by placing a net below it.

During the observations on Næbengen at Præstø in September several swarms were seen (September 6, 9, and 10); the free swarms were often mixed with chironomids especially during the first part of the daily period of swarming. September 9 at +0.08 crep three small single swarms united with a swarm of chironomids over the head of the observer. The chironomids gradually disappeared and at +0.62 crep only eight *A. dorsalis* were left and they finished the swarming at +0.95 crep.

10. **Aedes (Ochlerotatus) annulipes** Meigen

According to Wesenberg-Lund (1921) this species overwinters in the egg stage, as does the closely related *A. cantans*. Callot and Ty (1945) observed matings which took place in swarms above trails in forests or along park roads, the same place in which they found *A. rusticus* and *A. cantans*. The description indicates that the flight ”est de grand amplitude”; it seems to be the same type of swarming flight we found in *A. rusticus* (see above).

Early in June, when this species became the dominating mosquito at Bøndernes Egehoved, it appeared so much like *A. cantans*, both in appearance and in behavior, that at first we thought it was *A. cantans* which the senior author has previously observed. Both species rest in the daytime in low vegetation from which they rise when the observer approaches; towards late afternoon provoked swarms eventually become the low groundswarms of the ascent to the high part of the trees, the females directly, the males after having performed the typical swarms, either high free or over the tree tops. Before entering into the details of the phases of the swarming the differences between the two species should briefly be mentioned:

1. *A. annulipes*, especially after the first days, mostly rested in bushes during the daytime, while *A. cantans* were found mostly in the grass.
2. *A. cantans* mated equally well in the daytime and in the ascent swarms and practically never in the typical swarms; *A. annulipes* mated mostly during the ascent and less during the daytime rest. A few copulations occurred during the typical swarming.
3. The topswarms of *A. cantans* are intermediate passage swarms in which each single individual remains for only a fraction of the duration of the swarm; the swarms of *A. annulipes* are perpetual, most of the time consisting of the same individuals.
4. *A. cantans* forms true topswarms over or close to the top of elevated objects but *A. annulipes* always swarms over a light contrasting area.
5. *A. cantans* swarmed both at sunset and at sunrise; *A. annulipes* only at sunset.
6. The late appearance 2-3 weeks after *A. cantans* makes it appear likely that there is a difference in the rate of development of the two species.

At the resting places the males already had the fibrillae extended in the afternoon at —5 crep. On June 6 most of the males were, as usual, in the lower part of the bushes with extended fibrillae but the few which were found in the grass still had them closed —1.60 crep. It was a warm, calm evening with clear sky; humidity was low (20°, 66 % r. h.).

The first sign of the evening activity (the provoked swarming) was seen when the males, which were chased up by the approaching observer, remained flying for a little while before settling down again. The first swarms of this type occurred at times which varied from day to day: on June 12 there were provoked swarms at —2.22 crep but the preceding day there was none until after —1.31 crep.

By means of a stopwatch a number of measurements of the duration of the swarms provoked by the observer were made; they varied from 9 seconds to 2 minutes and 45 seconds but it was not possible to correlate the duration with external factors except in one case where it was found that swarms in sunshine were shorter (9—13 seconds) than in the shade (29, 75, and 86 seconds). In a group of males provoked to swarm, some will, of course, stop earlier than others: on June 10 at —2.79 crep, in a swarm with 10-12 individuals, half of them stopped after 15 seconds, 2 or 3 after 20 seconds, and one individual continued 35 seconds. Similarly, on June 12, at —2.20 crep, 4 of a swarm of 8 stopped after 12 seconds, 3 after 20, and one after 25 seconds. In some cases we tried to provoke the same group of resting mosquitoes to swarm with an interval of ½—5 minutes and in all cases we found that the second swarming was considerably shorter than the first one.

Besides those which are provoked to swarm there are always some individuals which fly a straight course up into the higher foliage; the swarmers will usually come to rest in the lower vegetation such as nettles.

It is not always possible to know whether a swarm is provoked or spontaneous; a moth flying around at a resting place has been seen not only to chase the mosquitoes up but also to start the males swarming, as it has also been observed in *A. cataphylla* (see p. 116).

The activity during the ascent is difficult to describe as there is much variation from one evening to the next. There are two main types of flight: the horizontal ground swarms, and the "climbing" which ascends up along the foliage. The ground swarms are characterized by being performed so close to the surface that it often looks as if the bottom of the swarm is touching the ground. Further, the flight movements have large amplitudes, long flights uninterrupted by the sudden changes in direction found in higher swarms; the head often faces the direction of flight rather than toward the wind. There is great similarity between the swarming of *A. rusticus* and *A. cataphylla* as described above and the ground-swarms of *A. annulipes* and, as known from previous investigations, of *A. cantans*. Actually, *A. annulipes* frequently swarmed in the low free swarms of *A. cataphylla,* which usually commenced shortly before the beginning of the ascent of *A. annulipes.* Later in the evening, *A. annulipes* disappeared from the *A. cataphylla* swarms and began their typical higher swarms which lasted until long after the *A. cataphylla* swarming had ended.

The climbing consists of smaller flights from one resting place to another, the new place being each time somewhat higher than the preceding. When a large number of individuals participate in this type of flight it appears as a continuous stream up along the foliage. This type of ascent has previously been observed in *A. cantans, A. taeniorhynchus,* and *A. caspius* (E. T. Nielsen and H. T. Nielsen 1958, p. 299—300).

High free swarms were seen a few times, and also swarms over the head of the observer, which probably were an occasional entr'acte between ascent and the final swarming. In *A. cantans* high free swarms normally occur during the first part of the top swarming but swarms over the head of people were never observed in this species.

At Bøndernes Egehoved the final swarms appeared as top swarms over the tops especially of whitethorn. They corresponded clearly to the final topswarms of *A. cantans* but due to the rather large number of individuals in the swarms it appeared unlikely that they were intermediate passage swarms.

Rather soon it became evident that the swarms of *A. annulipes* were formed over whitethorn bushes at a time when they were in bloom and covered profusely with white flowers. Usually a few days difference separates the blooming of individual bushes, each bush blooming for 5 to 10 days. After the first days' observations some of the bushes shed the white petals and became dark brown and green while a neighboring bush came into bloom. In such cases — two or three were observed — the swarm moved to the bush which had become white. One observation showed that mosquitoes started to swarm as usual over a tree that had lost its white bloom, and then one individual after another left it and flew to the new site so that the old swarm more or less disintegrated.

The final proof that *A. annulipes* actually swarms over a light marker was obtained after the swarming in Bøndernes Egehoved had stopped. On June 21 we found a swarm over a patch of light colored grass on the east side of Næbbet, the same place we observed *A. punctor* (see above). The swarm concentrated over a white net and could be moved somewhat around with it. The swarm lasted from —0.10 to +0.88 crep corresponding to the average of —0.17 to +0.93 crep for the swarms over the white bushes. The following day one more swarm was found also over a patch of pale grass; it lasted from —0.05 to +1.12 crep. The first swarm formed over a rather large marker, about 2 × 3 meters. This swarm would concentrate over a white net placed under it. If the net was moved around, the swarm followed it, but only within the limits of the pale area of the grass. The second swarm could be moved completely away from the natural marker by means of the net and could actually be taken for a walk of 5—10 meters.

The first day on which we saw *A. annulipes* swarms was June 3. These were believed to be the first swarms of this species as they were somewhat irregular. However, we cannot exclude the possibility that they had started as early as June 1 or 2 (on these days we were at Kongelundsengen).

There were many matings on June 3, and still more the next day. On June 5 there were somewhat fewer, and fewer still on June 6. Thereafter only two matings were seen on June 10, one on June 12, and the last one on June 13.

The copulation lasted a long time; 13 matings timed by a stopwatch lasted 21 to 57 seconds with an average of 34 seconds. Ten of them took place on June 5 at temperatures of 13.4° to 14.6° and lasted an average of 34.4 seconds with only one being less than 28 seconds. The three copulations timed on June 6 at temperatures of 18.6° to 19.3° lasted 23, 23, and 25 seconds. The copulation was always initiated venter to venter in the normal U-position (plate 4, fig. 3) but sometimes, especially in the longest lasting matings the couple changed to the end-to-end position.

It often looked as if the animals had difficulty in separating.

Usually the couple remained airborne, slowly drifting more or less with the wind but if they hit the ground, the female clung to a grass straw while the male flying from side to side seemed to try to get off by small jerks. The same couple may resume the copulation, in one case even three times.

Copulations at the resting places during the daytime were seen only a few times, but it occurred often among the animals chased up by the approach of the observer. By far most of the matings took place during the ascent between —1.5 and —0.2 crep.

Copulations, on the two evenings when maximum numbers occurred, continued until after the swarming had started, and quite a few matings were initiated in or near the swarms. On June 5 there were still many matings everywhere at sunset. Later on three were observed at +0.37 crep and two at +0.45 crep. The first three came from a swarm (the "photoswarm") over a rather low bush from where they drifted with the wind 12-15 meters out over the grass. Two of the males were seen to return to the swarm after separating from the females. In the third case three individuals whirled together to the ground. One of the matings at +0.45 crep was initiated in "high" swarm over a higher bush 8-10 meters behind and a little to the side of the "photoswarm". After the separation the male flew 15 meters to the photoswarm but right after reaching it he made a turn and joined the swarm he came from. The head of the male pointed downward during the last part of the copulation when the couple flew in the end-to-end position.

We made only one morning observation on June 6 and found that only a few made an occasional swarmlike flight of short duration. They closed the fibrillae as soon as they returned to the lower vegetation, around the sunrise. One mating was seen at —0.07 crep.

Of other animal activities noted at twilight during the *A. annulipes* observations in Bøndernes Egehoved, was the first appearance every evening of the bats, see table 1.

The reason for the early appearance the last two days is unknown, June 28, at +0.60 crep the bats caught may-beetles (*Melolontha*). One bat passed the observer so close that it was seen to have a beetle in its mouth. Its flight was straight instead of the usual twists and turns. On June 11, at +0.10 crep an owl began hooting while the cuckoo still was active.

Table 1.

The first appearance of bats.

Date	Appearance of first bat (crep)
June 3	+0.55
4	+0.46
6	+0.28
8	+0.49 (3 more at +0.61)
9	+0.41
10	+0.28
11	+0.34
12	+0.09
13	+0.02

11. **Anopheles (Anopheles) maculipennis** Meigen.

There is good reason to believe that the different varieties of this species differ in their swarming habits but there are too few observations to bear this out (Wesenberg-Lund 1921, Shute (Marshall 1938), and Cambournac and Hill 1940). During the present work a few observations were made mostly on single individuals which cannot be identified as varieties. Our observations of this species are therefore of little value and are only mentioned briefly for the sake of completeness.

On June 13 at —0.31 crep, a male was found swarming together with *A. punctor* at Bøndernes Egehoved at the dried-out part of the grassy pool. The following evening at +0.1 crep several single individuals made free swarms over the open grass. August 6 on the meadow at Kongelunden one male was caught in a huge free *A. dorsalis* swarm which also contained many *Culex pipiens* and a single *A. caspius*. September 8 at —0.24 crep on the seaside meadow at Bøndernes Egehoved close to the tree line a free swarm of chironomids was found in which was also an *An. maculipennis*. While this was caught and stored in a killing jar, a swarm of 20-30 individuals gathered over the head of the observer. At +0.68 crep, on the other side near the entrance to the enclosure, a swarm partly over and partly to the side of a bush was found. September 17, at sunset, also at Bøndernes Egehoved, a male was caught among a number of mosquitoes during an ascent; it was so windy that evening that there was no swarming. The following evening on Næbengen a few individuals swarmed with *C. pipiens* over a fencepost.

12. **Culex (Culex) pipiens** L.

The life-history of the common house mosquito has been known since Réaumur (1734—1742). Knab (1906) has described swarming in Illinois, and Wesenberg-Lund (1921) observed a huge free columnar swarm in a garden. Nielsen & Greve (1950) saw a couple of very small swarms in October in Denmark. It is so far unknown whether the different subspecies differ in the swarming.

During the present investigation this species was found so diversified in its behavior that we thought that the animals belonged to different subspecies but Dr. Alan Stone who has been so kind as to examine a representative collection of them, confirms that they are all of the subspecies *C. (C.) pipiens pipiens* L.

We saw the first *C. pipiens* on Kongelundsengen June 15 swarming behind some bushes, and on June 22 at Næbbet we saw a swarm over a white painted board at +0.36 crep. The next swarm was seen on July 5, and from that day to our last observation on September 21, this species swarmed at all observations wherever they were made. They rarely dominated the appearance of the swarming but were always present.

For many years Réaumur's description of the habits of *C. pipiens* was believed to cover the life history of all mosquitoes. Wesenberg-Lund and others in the years after the first world war found that most of the nordic-temperate species did not deposit their eggs as rafts in water during a season of continuous breeding but laid them singly on more or less dry ground from where one single generation is hatched by annual inundation. Naturally, and with good right indeed, *C. pipiens* was reduced to an exception instead of the paradigma of mosquito behavior, at least in Denmark and Northern Europe. It is the mosquitoes of the temporary pools which add their drops of wormwood to spice the enjoyment of bird song during the light nights of summer, and it is *A. caspius* which spoils the aim of the duck hunter in the fall; but during the present work we gained a strong impression that the house mosquito is part of the summer and fall everywhere in Denmark thanks to its adaptibility to a large diversity of conditions.

Although we found larvae in nearly all the mosquito-breeding places after the early temporary pools had dried out, we have nothing to add to the well-known facts of the natural history of the developmental stages.

Near human habitations the imagines, as well known, rest in sheds and similar dark places; in the field we saw only very little of them. And although we remember seeing them feed on thistle flowers we have actually no notes about their feeding; even when e. g. *A. caspius* was inferior in numbers during the swarming hardly any of the many individuals feeding on flowers were *Culex.*

On Næbengen, at the ditch separating the south meadow from the flower meadow (see above) grew an isolated alder (*Alnus incanna*). This tree was the center of swarming activity for *A. caspius* and *C. pipiens,* and from the 23 observations we made here a certain regularity of swarming was evident. There was a good deal of similarity in the swarming of the two species. Both had an ascent phase preceding the swarming consisting of "climbing" (see *A. annulipes,* above) but *C. pipiens* did not seem to have any swarming comparable to the ground swarms. When *A. caspius* began to form swarms at the tree, on an average at —0.80 crep, a rather confused situation usually occurred: *A. caspius* would swarm in the niches between the more or less horizontal branches of the alder through which *C. pipiens* climbed upwards and started to fly around until finally at an average of —0.23 crep, they began to swarm around the tip of the branches (plate 5, fig. 2). Not only the position but also the movement of the swarmers differed in the two species: *C. pipiens* flew with many more turns per time unit and with shorter amplitudes and closer together which gave the swarm the appearance of being more compact and the individuals of being more "excited" than *A. caspius.* Swarms of *Culex* followed the contour of a branch closely, but for a short distance (approximately 5 cm); when the branch swayed in the wind the mosquitoes tried to follow the tip of it, but there was usually a short moment of confusion before the swarm was formed again.

Over or close to the rather irregular top of the tree (it was actually a group of several trunks) there was a top swarm we could not sample but from both its appearance and the time it was observed it consisted at least mainly of *C. pipiens* although it might have been mixed with *A. caspius* and perhaps also chironomids. The midges swarming these evenings on Næbengen would usually stop the flights rather early, at +0.5 to +0.6 crep, while the average cessation of *A. caspius* was at +0.83 and that of *Culex* was at +1.06 crep. It was the latest swarming we observed in Denmark.

Branch-tip swarms of this species were also observed at other localities: at Kongelundsengen on some oaks, at Bækkebro north of Arresø around an alder; and in the garden of the inn, Sven Gjønges Kro, in Præstø, the branches of a birch tree were used. Similar swarms were observed earlier in the year mostly very high in beeches bordering the seaside meadow (e. g. May 31 on the north side of Næbskoven); some of these swarms were made by tipulids but some of them might have been *Culex*.

Another type of swarm which has been observed frequently is the marker swarm. While all other mosquitoes we know of either swarm over a light area contrasting with dark surroundings or over a dark spot on a lighter background, *C. pipiens* used both types of markers. As mentioned, one of the first swarms we saw was formed over a white board, and on Næbengen they often swarmed over the head of the observer or over the white net even if such swarms did not appear very regularly as did the swarms at the alder. On the other hand, close to the bridge connecting the north meadow and the south meadow the passage of the cows had worn of the grass and left spots of nearly black humid earth over which *C. pipiens* swarmed July 11 and 12. On July 13, to find out about swarms of *A. caspius* over cows, an "artificial cow" was made by piling up some of our gear and covering it with coats etc., using a black lumber-jacket as surface. *A. caspius* was not interested in the crude attrape but after some thirty minutes a nice little swarm of *Culex* was formed. Contrary to *A. caspius* they did not scatter when a white net was placed under them but they did not concentrate as *A. dorsalis* or *A. annulipes* would have done; the swarm loosened up a little and could then be moved around but only for a short distance. This observation lends support to the idea that the marker swarm in this species is formed over any contrast between light and dark background.

The swarms over the head of the observer, especially in the first part of the evening, was mixed with chironomids and the same was also true in swarms formed over a couple of freely exposed fence-posts (there were never swarms over the posts in the fence running along the high vegetation of the ditch).

In the wettest part of the meadows there are often places where the cows have trod down the soil between the grass plants which remain on small knolls. The holes between the knolls often retain water and thus become the most prolific breeding places for *A. caspius, A. dorsalis,* and *C. pipiens.* Thanks to the frequent visits of cows to such places the water is rich in nutrients. We used to call this type of meadow a "kotrin" ('cowstep'). On of the few cases of free swarming we have seen in *C. pipiens* was early (—0.86 crep) on September 9 when there was a mixed swarm of this species and chironomids over the "kotrin" NW of the alder.

At Molslaboratoriet in Jutland (see *Theobaldia annulata*) we happened to see a few *Culex* forming a swarm over the borderline between two fields (July 22, at about +0.4 crep). Although it appeared to be a free swarm there might well have been contrasting spots on the borderline.

A little west of Skave on the road to Holstebro in the northern part of Jutland a few single swarmers of *C. pipiens* were seen at a partly inundated meadow close to the road. Also these swarms might have been performed over slightly contrasting spots.

We do not have any actual observation of individuals from the marker swarms flying to the alder and participating in the swarming there. Until some time before the end of the swarming period, swarmers arrived from everywhere, usually flying 2-3 meters above the ground. As swarms of all types stopped at the time the arrival of newcomers ended, there is some reason to believe that all these swarms were part of the ascent. This is supported by the erratic appearance of these swarms contrary to the swarm at the alder which day after day appeared in the same way. It has to be noted, however, that as long as these (probably preliminary) swarms lasted and when they occurred, they appeared as normal markerswarms, etc. and not as the ascent swarms of *A. cantans* or *A. annulipes.*

The number of *C. pipiens* changed somewhat during the period they were observed. Especially many were seen the last days of observations, on September 18 and 19 with somewhat fewer on September 20 and 21. The first of these days it was cloudy (10/10 nimbus and cumulus) and slightly misty with a temperature dropping from 15.5° to 14.7° and the relative humidity rising from 79 % to 92 %. The sunset illumination had already occurred at —0.4 crep and the east wind came in from the water at 3 meter/sec measured one and a half meters above ground. Wherever there was shelter for the wind there were swarming *Culex*. One swarm was found sheltered by an unusually large horse-dropping. The swarm was estimated to consist of between 50 and 75 individuals (one sweep with the net caught 29 mosquitoes).

Matings frequently occurred both during the ascent and the swarming. During the increase in numbers, and especially on September 19, females flew in from all directions toward the alder to rest for the night (the weather was like the preceding day except that is was calm). Many copulated before they arrived at the tree but still more copulations occurred in the swarms. Right after the swarming commenced, at —0.14 crep, 48 matings were counted per minute in one of the several swarms. At sunset the number had decreased to 32 and at +0.22 crep it fell to 15 matings per minute. In another swarm 26 matings were observed at +0.19 crep. The decrease continued and during the last part of the swarming the females were already resting. The swarm ended at +1.08 crep.

13. **Aedes (Finlaya) geniculatus** Olivier.

The habits of the imagines of this mosquito have never been described. Wesenberg-Lund (1921) who for some time kept a number of tree holes containing larvae of this species under observation never saw an adult in nature and thought that it would be very unlikely to find one.

On June 20 when crossing through Næbskoven we happened to come into an area (map, fig. 2 (2)) with a ditch running about N—S between high beechwood and a small piece of spruce wood. There was no open water in the ditch but the place was dark and humid and there were many mosquitoes of several species. The time was about —1.0 crep. Of *A. geniculatus* one male was found with extended fibrillae, and another one was swarming at the edge of the spruce wood and finally one was caught among a number of other mosquitoes in the grass.

The next day in the afternoon between —4.5 and —3.0 crep males were swarming irregularly 1 to 1½ meters above the ground at several places in the beechwood but they often stopped and went to rest under leaves. The illumination measured as zenith light decreased to sunset value at about —3.6 crep. The swarming still went on in shafts of sunlight between —1.7 and about —0.6 crep. On June 22 there was no swarming in the afternoon but later until —1.1 crep several swarms were seen and the same was the case on June 23. The following day there were only few, and when after some days' absence we returned on June 27 no more could be found.

Several tree holes were examined but only in one old tree stump a couple of pupal skins (possibly of *Finlaya*) were found. We saw very little of the females although a few were caught by sweepnet. Of the rather many females biting us none were *A. geniculatus* (they were mostly *A. cataphylla* and *A. rusticus*).

The swarming always took place in sunrays falling between the tree trunks (plate 5, fig. 1). At first it was thought that we found swarming in the sunrays only because it was easier to see the males flying there but such was not the case. It was possible for the observer to split a swarm in two by means of his own shadow. When the sun disappeared a few individuals might continue the swarming but only for a very short period of time after which they flew away. After the swarming single individuals were seen and caught, presumably on their way to the night resting places which we never found. Tipulids swarmed at the same places and on June 23 there was a swarm of flies above the *A. geniculatus* swarm. There were most swarmers in the fairly narrow beams: in one, 1 to 1½ meters wide, there was a swarm of about 30 *A. geniculatus* but fewer (about 20) in one 4-5 meters wide, and none in one still larger.

The swarming flight consisted of back and forth movements across the light beam. When a group of individuals were performing together in one part of a sunray there was fairly little movement along the beam. A single individual swarming by itself also made zig-zag movements but with a slight wind blowing from west to east these movements brought the swarmer forward against the wind for a distance of a couple of meters. The animal would then turn and with no zig zag movements let itself drift back with the wind for a couple of meters and the performance would be repeated (fig. 9).

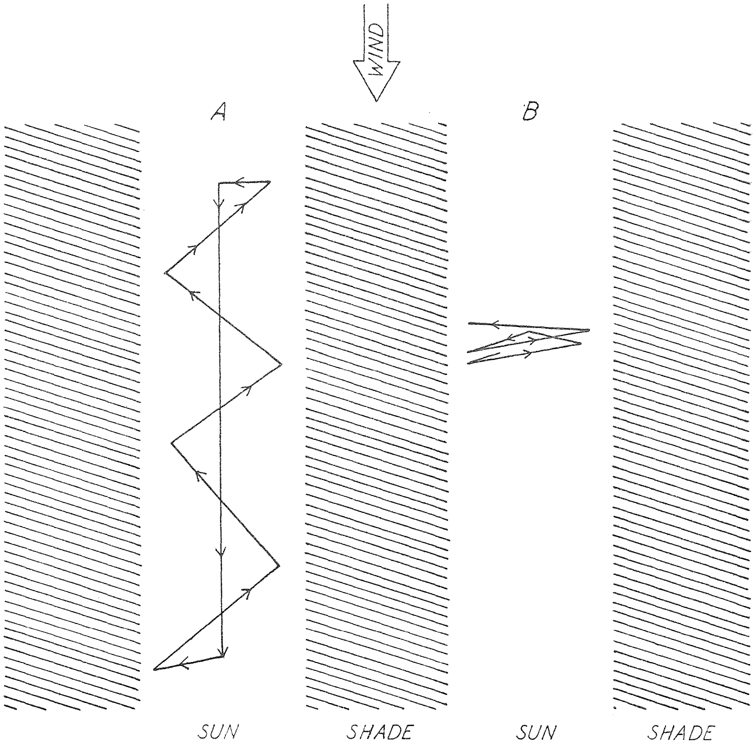

Fig. 9. Swarming of *A. geniculatus* in rays of sun. A: flight pattern of single individuals; B: flight pattern of a group of individuals.

14. **Aedes (Ochlerotatus) caspius** Pallas.

This is essentially a salt-marsh mosquito distributed over larger parts of the Eurasian continent and North Africa. In Denmark it breeds continuously after the seaside meadows have become inundated during the summer. Also in some years there is a brood in the spring according to Wesenberg-Lund (1921) who gave information on several habits of this mosquito which under the name of "valbymyggen" used to be unpleasantly well known in Copenhagen. He did not distinguish it from *A. dorsalis*. Stachelberg (Natvig 1948) indicates grass and bullrush as daytime resting places. Bro Larsen (1948) found that during the daytime these mosquitoes feed in large numbers on flowers, especially *Tanacetum*. E. T. & H. T. Nielsen (1958) observed the habits of *A. caspius* in Iraq: the newly emerged mosquitoes departed from the breeding places after an ascent, and while an increasing percentage of the males extended the fibrillae both sexes performed the climbing phase of the ascent but no ground swarms were seen. The swarms were high and without any marker on the ground. There were only few matings in or during the swarming. Both males and females fed on extrafloral nectaries of *Sesbania* after the swarming.

After the middle of June easterly winds prevailed for some time, raising the water level in Præstø Fjord so much that a number of ditches and the ”kotrin” on Næbengen became flooded, and here we found larvae of *A. caspius* on June 24. From June 27 we tried to make account for the development of the brood by counting samples from 13 different places several times a day. The first day the percentage of pupae was about 15, the next two days about 25, and the following two days about 50. It was found however that there were irregular changes in the water level and the water constantly running in and out of the ditches swept considerable parts of the populatlon with it. The temperature of the water was found to vary between about 12° and 20° during the daily change and the movement of the water did not influence this as much as was feared.

On June 30, when the pupa percentage increased to 49 $^0/_0$ the first imagines appeared, but not until July 2 did they emerge in numbers. They were nearly all males, with recumbent fibrillae, resting close to the water seemingly unable to fly more than a meter or so down wind. The next day the number had increased considerably and there also appeared some females; the males still had closed fibrillae. In the following days the number increased fast and by July 4, 16 $^0/_0$ of the males had the fibrillae extended and more than half had completed the rotation of the terminalia.

On July 5 there were many new animals and many had extended fibrillae. On July 6 it rained most of the day, and the mosquitoes rested at places so well hidden that we hardly saw any during the daytime inspections. The weather cleared towards evening, becoming calm and rather cool (13.5° to 11,1°) with high humidity and formation of evening mists. From about —0.4 crep an increasing number of *A. caspius* were on the wing. Most of them flew from the grass where they had rested, towards the woods surrounding the meadow with a slow steady and straight flight usually above the head of the observer. Lower flights might have been more abundant than observed as they were less conspicuous against a background of vegetation than against the sky.

Besides this flight, which undoubtedly was an exodus, several males were seen flying in curves with large amplitude and frequent turns, now and then performing a real swarming flight for a moment. To the observer it appeared as a premature, not yet fully developed, swarming. At +0.04 crep a swarm was formed over the head of the observer (who wore black headgear) lasting about five minutes. Shortly after the swarm was found at the alder which has been mentioned above (*Culex pipiens*, p. 135). The swarming here began in the lower niches between the branches on the lee side of the tree. When there were most swarmers they filled not only the niches but overflooded from one niche to another until the whole lee side of the tree was covered by the swarming mosquitoes as by a cloak. The topswarm on the alder was probably normally a *Culex pipiens* swarm but on August 7 in Kongelunden it was possible to catch samples from a topswarm continuing a cloak swarm over the top of the tree and it was found to consists of *A. caspius*.

While the cloak swarm at the alder undoubtedly was the final and definitive swarm of *A. caspius* a rich variety of other swarm types and swarm-like flights were seen. Most of these lasted shorter periods, changed in position from one evening to another or occurred only on certain evenings. At sunrise the cloak swarm was rather normally developed but most of the other swarms usually were missing, except the swarms over the cows.

There were probably swarms every evening over the breeding places at the "kotrin". On July 11 the swarms kept in the windside of the "kotrin" area regardless of the presence of markers. On July 14 swarms were located over dark holes with water and over a dense cover of water plants and stiff, tall *Carex*. Sometimes there were very large swarms here, e. g. July 15. It was a pleasant calm evening with temperatures dropping from 18.7° to 15.1°, and relative humidity ranging from 83 % to 95 %, the sky half covered by cirrus veil, slightly obscuring the sun. Illumination was normal and it was nearly completely calm all night. At —1.25 crep the whole "kotrin" area — about 20 × 30 meters — was teeming with ascending and swarming mosquitoes and tipulids. Of the males yet resting in the grass 80 % had extended fibrillae. At —1.04 crep only 3 of 40 resting males had the fibrillae closed and at —0.42 crep the swarmers concentrated in definite swarms. This evening there were two very large swarms. One of them was 5-6 meters long in south-north direction the flight movements went from one end to the other. The other swarm was in east-west direction and had a main part 7-8 meters long, 2 meters high and 1½ meters thick with the lower part ½ to 1 meter above the vegetation (*Carex*). From the west end of the swarm there was a long thin swarm continuing another 7-8 meters to the border of the ”kotrin”. There were many attempts to mate in these swarms but few of them seemed to be successful. At —0.06 crep the females started biting. A little whiff of wind reduced the amplitude of the flights in the first mentioned swarm. Later in the evening this swarm concentrated in the southernmost part and the flights generally became of shorter amplitude. From about sunset two large swarms were formed over the head of the observer the upper one of *A. dorsalis,* the lower one of *Culix pipiens*. The latter eventually came down so low that they swarmed around the head of the observer which was rather pleasant because *A. caspius* females approaching to obtain a bloodmeal were chased by the *Culex*-males. The swarms began to reduce at +0.49 crep but lasted the same lenght of time as those at the alder.

The cows and calves on Næbengen were sometimes in our vicinity in the evening and *A. caspius* frequently swarmed over them especially over the darker ones but there was not much regularity in the distribution. On the flower meadow were tethered a cow, a calf (plate 8, fig. 1), and a horse. No swarm was ever seen over the horse which was light colored. The first evening these swarms were noticed the swarm over the cow was much larger than over the calf; the next evening the reverse was the case. Among the freely roaming cattle on Næbengen we noticed one evening that a big black cow had a swarm and a small black one did not; when they met and for at litte while stayed close by one another the swarm moved over to the small cow but when they parted the swarm first rose high in the air and then descended again over the big cow. Later, however, the little one acquired a swarm of its own. During the evening, besides the male swarms, the cattle became surrounded by an increasing cloud of blood-seeking females which made it difficult to be sure when the male swarms stopped; but it appeared to be a good deal earlier than the end of the cloak swarm at the alder.

During the first part of the swarming at the alder mosquitoes from everywhere were seen flying towards the tree. *A. caspius* were flying over the entire meadow apparently trying to find a place to swarm; whereever they found a possibility they would form a temporary swarm: over the observer, a cow, etc. The many which rested in the dense brim of reeds growing along the edge of the bay and along the ditch in which the alder was standing, often made small short-lasting swarms over the reeds, now here, now there. On July 14, a pleasant calm evening with a very faint wind from the south, the participants in these swarms remained flying at the same spot with their heads against the wind, now and then they would make a dart forward and at the same time either up or down to the side, or a combination of these directions. The darts were usually only a few centimeters. As these darts always had a forward component a number of them would bring the swarmer to the south edge of the swarm where it suddenly turned and flew back out of the swarm, a big turn around before it joined the swarm. Sometimes the darts were interrupted by circling, sometimes a flight in the shape of figure 8. The following day, with nearly the same weather except a slightly higher temperature (at sunset 16.5° instead of 15.2°) there were similar swarms but the movements were quite different: mostly pendel movements across the wind direction with the head against the wind, but during the flight turned slightly towards the flight direction. The pendel movements were occasionally interrupted by wider flights around, crosses, circles, or figure 8.

In order to see whether the freely roaming males could be induced to form another cloak swarm we erected an artificial tree freely on the meadow about 50 meters west of the alder. It was a cut-off top of a spruce which we found in the wood to which we tied a couple of beech branches. On all the three evenings we used it, July 8, 9, and 10, there were swarms around it, but only on the second night the weather was calm and a cloak swarm formed all around the tree. The slightest wind would concentrate the swarmers on the lee side. The last evening the swarms were small, 10-12 individuals which gave an opportunity to test the turn-over of swarmers. Once 9 of 12 swarmers were caught and once all ten. In both cases the swarm was formed again, in the first case very suddenly after 0.05 crep (3 minutes), in the other more gradually over a period of 0.16 crep (9 minutes). Further experiments were given up because it was troublesome to put up the tree every day after the cattle had turned it over. They had also eaten so much of it that it looked rather shabby.

A. caspius, of all the mosquitoes we have observed, is the one which feeds most openly. Bro Larsen (1948) found that it has peaks of feeding in the morning and afternoon and Nielsen & Greve found the same in *A. cantans* (1950). We did not make inspections often enough to establish such a rhythm but at least they were busy feeding on flowers in the afternoon. Counts made July 12 and 13 seemed to indicate that most of those feeding on flowers on which the sun was shining were females, while most of the flowers in the shade were visited by males.

Copulations were seen rather frequently both in the different swarms and during the ascent but not during the last part of the swarming. Compared to the large number of individuals most of the matings probably took place outside the period of swarming; matings never occurred in numbers as they did in *A. annulipes* and *Culex pipiens.*

On September 9 a few individuals of a small fly *(Phryne punctata)* swarmed in the niches between the branches of the alder. The simultaneously swarming males of *A. caspius* made desperate attempts to copulate with the flies; but as the flies flew up and down the same way as many tipulids do, the male mosquitoes did not seem to be able to follow these unexpected movements and they never got a real hold on the flies. The incident was highly amusing. It shows that the flight pattern of the female is not a stimulus for copulatory activity of the male *A. caspius.*

It was mentioned above how the newly emerged *A. caspius* in large numbers performed a rather straight-lined flight from the breeding places toward the nearest point of the surrounding woods. Here they disappeared from view but the flight was somewhat similar to the departure observed in Iraq where the newly emerged mosquitoes gathered in a tree before the take-off for the migration even if the flight in Iraq was only a few meters whereas in Denmark it was more than a hundred. Similar flights were noticed on several other nights, most spectacularly in September. Counts of streams 3-4 meters wide showed a passage of up to 80 mosquitoes per minute, to which has to be added at least as many chironomids of different sizes, tipulids and even small moths. Most of the culicides were *A. caspius* but also *A. dorsalis, A. detritus, Culex pipiens* and occasionally other culicides took part in these flights. Besides the flight toward the trees there were also other flights in a complicated pattern which we decided to try to analyse by means of stationary nets. When we had the first one ready for use the weather deteriorated and an easterly wind swept over the meadow with velocities which more or less inhibited the flight activity; where shelter could be found there were small swarms lasting a much shorter time than normally was the case but no migration was seen. The last few days when the weather had again improved there were so few *A. caspius* that the observations were suspended and we did not get another opportunity to investigate these flights.

15. **Theobaldia annulata** Schrank.

During a visit to Molslaboratoriet in Jutland on July 22 we happened to admire the sunset from a heather-clad hill just south of the laboratory when one single mosquito started to swarm over the head of the tallest of the observers. We were unprepared for work, and while one observer hurried to the laboratory to get a net and a killing-jar the other one managed to keep the swarmer over the head. It was *T. annulata.* Dr. Alan Stone who was kind enough to look at the single, very rubbed specimen agreed with this determination although it did not have the mid and posterior cross veins on the wings in line with one another which is one of the characters used in the keys (Marshall 1938, Natvig 1948) to separate it from the other species of *Theobaldia.* A few others were observed later over the highest point of this hill and another close by. All swarmers emitted a very loud humming. They first swarmed over a *Sarothamnus* bush which was lower than the observer, then moved over the observer's head. The swarm remained there even when the observer walked about. By returning to the bush and bending down below the top of the bush the swarmers could be returned to their natural swarming site.

16. **Anopheles (Anopheles) claviger** Meigen.

Syn.: **An. bifurcatus** L.

Twice in September we had a chance to observe this species. On September 8 at Bøndernes Egehoved a climbing ascent was seen at —0.65 crep and consisted mostly of this species as did the majority of the swarms later that evening. The first swarm, apparently a markerswarm, was found in a "room" at —0.59 crep. It was formed over black horse droppings strikingly contrasting (at least to the human eye) to the surrounding pale green weeds. A free swarm began at —0.51 crep over an open meadow. Further inland several free swarms were found on the big meadow down to the waterhole at +0.30 crep, and at +0.43 crep a markerswarm over one of the cows was noticed.

On September 12 and 13 observations were made in the garden of Svend Gjønges Kro. Two swarms of *An. claviger* were seen on both these evenings, both swarms were free columnar swarms, one close to a garage, the other one in the garden closer to the water in Tubæk Å; the latter swarm was the larger one. Shortly before the cessation on September 13 at +0.62 crep it was repeatedly observed that two swarmers collided in the swarm. A copulation occurred a little east of the swarm.

17. **Aedes (Aedimorphus) vexans** Meigen.

A male of this species was collected on Bøndernes Egehoved September 17, and two days later a female was caught between migrants on Næbengen.

18. **Mansonia (Coquilletidia) richiardii** Ficalbi.

A female of this species was caught on the dry, sandy hills, Tibirke Bakker, in North-Zealand. During investigations made several years ago the senior author had occasionally been bitten by mosquitoes at this locality in the middle of the day. The mosquitoes probably were breeding in the marsh with peat ditches at the foot of the hills, a few hundred meters away.

C. DISCUSSION.

1. **The Ecology of Swarming.**

If we try to combine the observations we have made of the swarms of mosquitoes, reported here and in previous papers, and from them obtain lines guiding us to a better understanding of this habit, there are two ways to go. One is to discuss the different types of swarms and their occurrence in relation to species and conditions; this comparative-ethological viewpoint shall be discussed below. The other way of analysis is an examination of the stimulatory and regulating effect of external factors on the habit of swarming appearing as a correlation between the variation in such factors and variation in the manifestation of the habit, especially in time.

There is ample evidence for the assumption that the causative stimulus for swarming is the light conditions at sunset and sunrise. Mosquitoes kept at uniform conditions and exposed only to a daily change in illumination will swarm daily at the same phase of the light cycle. As already mentioned the causative change in illumination is mainly dependent on the altitude of the sun rather than on the hour angle. There is here reason to consider the possibility of swarming activity being a circadian, endogenous rhythm which, as shown by Aschoff (1960), is corrected daily by the actual stimulus of the change in illumination. For some years actograph studies of culicids have been carried out at the Entomological Research Center in Vero Beach, Florida; they have so far not lent any support to the concept of the activity of these animals being an endogenous rhythm: in the absence of a change in illumination the activity becomes arhythmically distributed over the diel. In the laboratory it is possible to produce swarming in certain species by changing the illumination. The animals will not form swarms without such a change, and they respond to light changes occurring with irregular intervals several times during a 24-hour period. There has, however, to be an interval of a few hours between the changes. (H. T. & E. T. Nielsen 1962). Whether this period of latency should be considered a sign of an endogenous component in the activity is perhaps doubtful and for the present investigation irrelevant. Whether the light change is correcting an internal clock or directly causing the activity, there cannot be any doubt about it being the relevant stimulus for swarming. If, therefore, there is a variation from day to day in the creps at which the swarming occurs, it must be an effect of variation in the regulatory stimulus.

There are a couple of complications which should be kept in mind during this discussion. In many swarms, each single individual takes part in the flight for only a fraction (5—10 %) of the total duration of the swarm. The total duration of the swarm, therefore, is the sum of the duration of the time the individual mosquitoes participate in it. It is well known that a mosquito swarm may be composed of any number of individuals down to a single one. Through studies of the time relationship in swarming it is necessary to disregard swarms made up of one or very few individuals because these swarms last a shorter time than normal swarms. This has been directly shown in *Aedes taeniorhynchus* (E. T. & A. T. Nielsen 1953).

In discussing the time aspect of swarming we are dealing with several parameters:

(a) The commencement of swarming is the moment when the first continuous flight begins. The commencement is sometimes preceded by single mosquitoes swarming for a very short period followed by an interval without swarming.

(b) Even though the swarming often begins with a single individual, the number usually increases quickly to a maximum level which lasts most of the swarming period. In most cases, a decrease is noted after $^2/_3$ or $^3/_4$ of the flight is over, after which the number of swarmers gradually decreases and the swarm usually ends by a single individual swarming solo. The end of his flight is the cessation of the swarming.

(c) The duration is, of course, the difference between the commencement and the cessation, most conveniently expressed in crep.

(d) Duration in log lux (dlx) is the difference between the illumination at the commencement and that of the cessation expressed in log lux.

To facilitate an analysis of the factors influencing the commencement of swarming fig. 10 has been drawn. The abscissa is the temperature of the air and the ordinate is the average crep at which each of the species we have observed began the swarming in the corresponding temperature. It will be noted first that three species seem to differ from all the others. They are the two Danish species which appeared first, *Aedes rusticus* and *Aedes cataphylla,* both of which formed low swarms with large flight amplitude more like the ascent swarms of other species. The third one is *Psorophora ferox* which differs from all other mosquitoes in swarming habits (H. T. Nielsen, 1963). Apart from these three species the others seem to fall into two groups which we may conveniently call A and B, in which case the three first mentioned species might be called group C. The A-species include all Danish species appearing later in the year than *A. rusticus* and *A. cataphylla.* Most of the observations have been made at temperatures between 12° and 17° and there is much variation within each species even if there is still more difference between the species. This is confirmed by the simultaneous

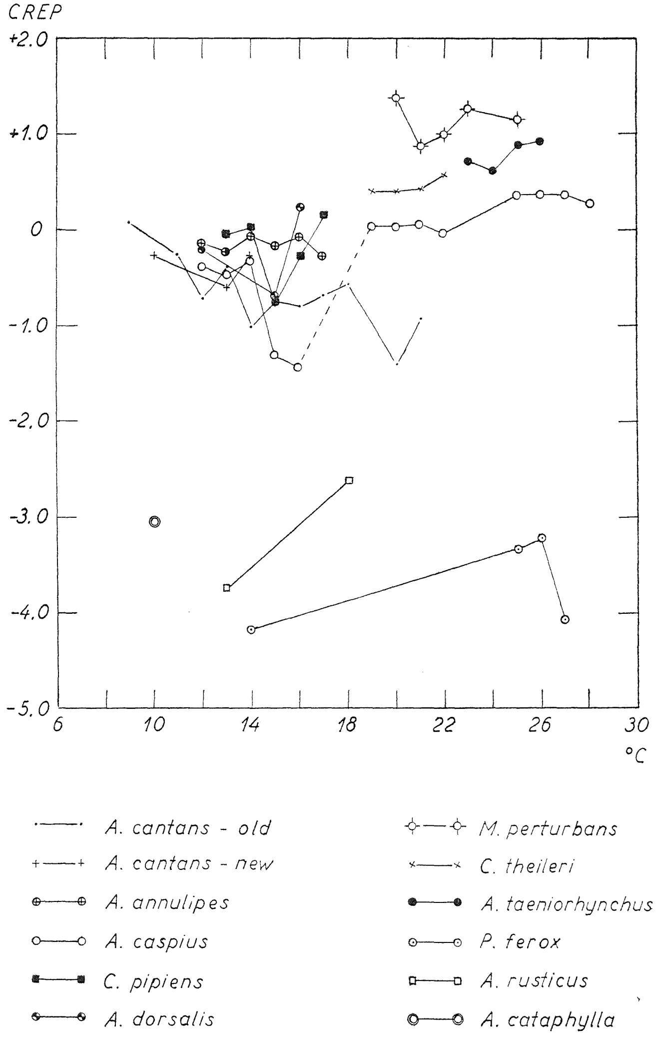

Fig. 10. Commencement of swarming.

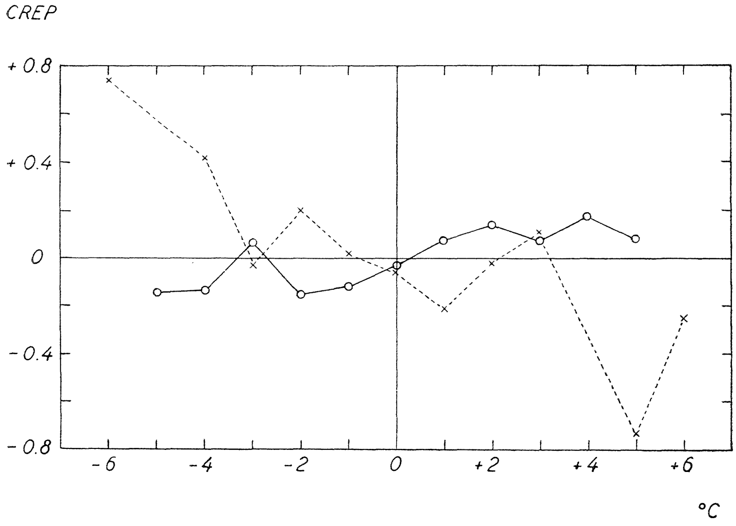

Fig. 11. Deviation of commencement from mean against deviation from mean temperature.
x --- x A species.
o——o B species.

observation of *A. caspius* and *Culex pipiens* which clearly showed the swarming of *Culex* to be later than that of *A. caspius*. The B-group is the four species studied under subtropical conditions. The intraspecific variation is smaller than in the A-group and the interspecific differences are therefore more conspicuous. Also in this group we have simultaneous observations of two species to confirm the species-specific differences: in Iraq *Culex theileri* swarmed simultaneously with *A. caspius*, and in Florida some observations of *A. taeniorhynchus* were made at the same time as *Mansonia perturbans* were flying.

In this connection it is important to recall the observations of Shute (Marshall 1938) who found that *Mansonia richiardii* in England started swarming after *Culex pipiens* had stopped in the evening (and vice versa in the morning). The presented data is insufficient to permit transforming it into crep values but there is no reason to doubt that *Culex* (the latest of the Danish species we observed) swarmed at about the same crep in England as in Denmark, and *Mansonia* at the same crep as the Florida species.

It is regrettable that the observations we have of the two groups happened to have been made at such different temperatures that we cannot compare them directly.

It is true that *A. caspius* belongs to both groups but we have insufficient evidence that the Iraqi and Danish individuals are identical and, therefore, we cannot establish a comparison as to temperature on *A. caspius* alone. This will be discussed below, but fig. 10 indicates plainly that it is not justifiable to consider the species ethologically homogenous. Altogether, there seems to be a definite difference between the A and B species; the former, which begins swarming earlier the warmer the air is, and the latter which shows a slight tendency in the opposite direction. This is more clearly seen from fig. 11 in which the deviations from the mean commencement is plotted against the corresponding deviation from the mean temperature of the observational material. The possibility that the difference between the groups is a simple effect of temperature may be examined by fig. 12 in which the deviations from the mean commencement are plotted against the actual temperature. It shows that the difference between the two types of species, A and B, could well be explained as species-specific variation.

The cessation of the swarming shows much less interspecific variation than the beginning (fig. 13); *Mansonia* ends later, and the three C-species earlier than the rest of the mosquitoes. They all seem to fall within a random variation around a slightly rising line, indicating a tendency to end the swarming later at higher temperatures except, perhaps, at the highest ones above

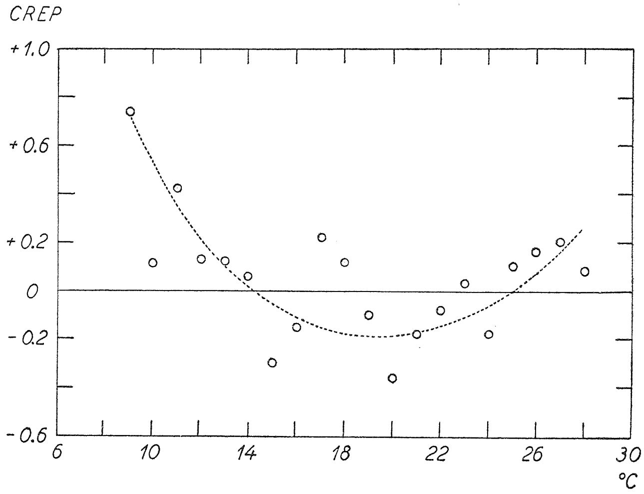

Fig. 12. Deviation from mean commencement by actual temperature.

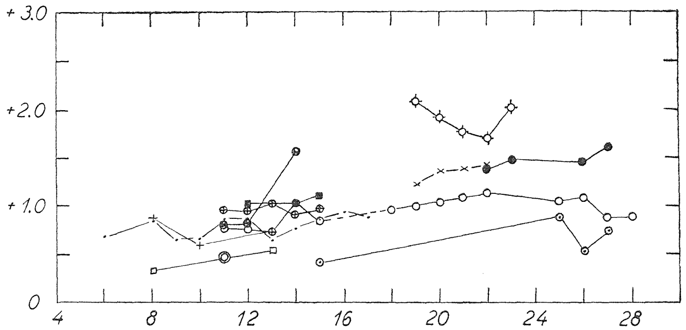

Fig. 13. End of swarming.

26°. Closer examination discloses that there are rather definite differences between the species, and those which were the latest to appear are also the latest to disappear. Compared to the variation in the commencement the differences in crep are small. As could be expected, the duration of the swarming in the different species plotted against the temperature reflects essentially the variation in commencement. The intraspecies variation is considerable but with *Psorophora ferox* as the only exception the

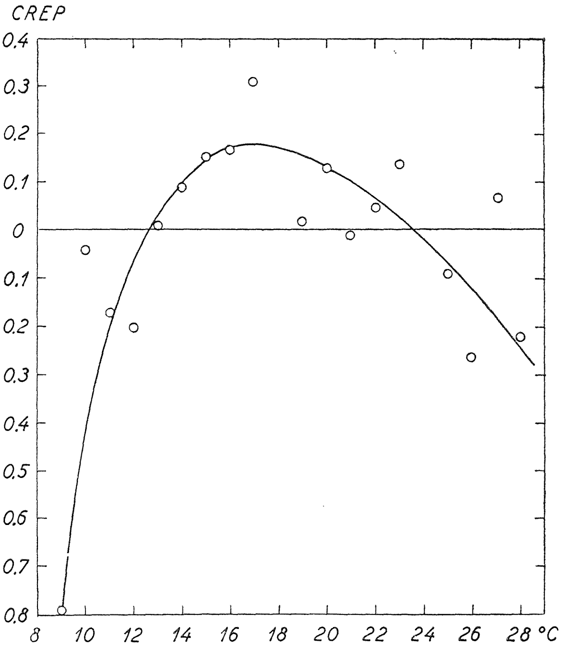

Fig. 14. Deviation from mean duration against temperature.

interspecific differences are quite unimportant. Fig. 14 shows the duration in crep against the temperature.

The idea that the swarming ceases at a certain threshold of illumination may be the explanation for the variation of the cessation being smaller than that of the commencement, because the slope of the crep-log lux function increases during the evening until the end of twilight; in other words until this moment a certain difference in crep corresponds to an increasing difference in illumination. For each of the 166 complete observations we have, the difference in log lux (dlx) corresponding to the crep at the beginning and the end of the swarming was calculated by means of the standard table. This method contains the error that the illumination on cloudy days is less than that given in the standard table; but in the numerous observations this summer, the error is less than 5 %.

If the log lux differences are plotted against the temperature (table 2, fig. 15) the relationship already indicated by the tempe-

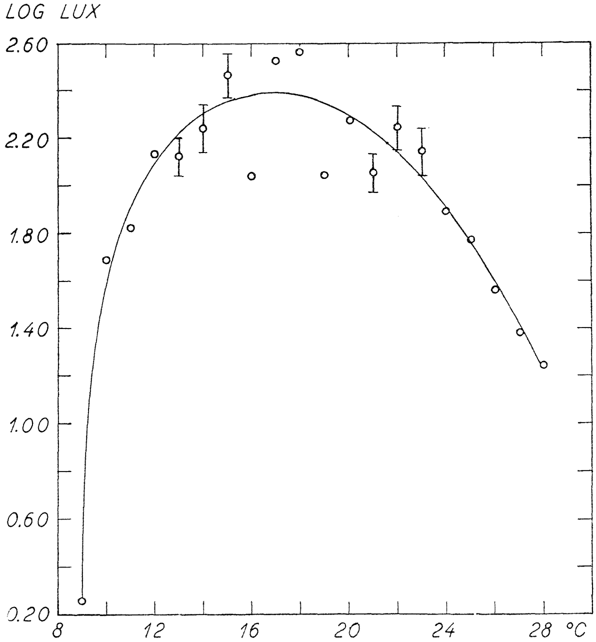

Fig. 15. Duration in terms of the difference in illumination between that at the beginning and that at the end of swarming. All species observed. For the temperatures at which we have 10 or more observations the standard deviation is indicated by a vertical bar.

Table 2.

Temperature	Number of observations	dlx	Standard deviation	Standard curve	Temperature correction
(9)	(1)	(0.26)	- - -	0.26	+1.83
10	6	1.69	- - -	1.61	+0.48
11	5	1.82	- - -	1.89	+0.20
12	9	2.13	- - -	2.09	0
13	10	2.12	0.082	2.20	—0.11
14	17	2.24	0.103	2.29	—0.20
15	19	2.46	0.092	2.34	—0.25
16	7	2.04	- - -	2.37	—0.28
17	9	2.52	- - -	2.39	—0.30
18	4	2.56	- - -	2.37	—0.28
19	8	2.04	- - -	2.33	—0.24
20	6	2.27	- - -	2.28	—0.19
21	12	2.05	0.082	2.21	—0.12
22	12	2.24	0.089	2.13	—0.04
23	16	2.14	0.102	2.03	+0.06
24	3	1.89	- - -	1.91	+0.18
25	7	1.77	- - -	1.76	+0.33
26	4	1.56	- - -	1.58	+0.51
27	7	1.38	- - -	1.39	+0.70
28	4	1.25	- - -	1.24	+0.85

rature function of the duration becomes still more evident. The average of all the differences is 2.09 log lux (table 2, column 3). We may calculate a correction for temperature (col. 6) as the difference between the observed dlx and a smoothed curve based on 3-point sliding, weighted average (col. 5).

If all observations for each species are corrected for temperature in this way, the 82 observations of A-species have an average dlx of 2.10 log lux, the B-species (77 observations) of 2.03 log lux, and the 7 observations of C-species have a dlx of 2.29 log lux. In other words the illumination at the cessation of swarming is very nearly one percent of the illumination at which it starts. This difference in illumination is about the same as that which takes place during the twilight from 2.60 log lux at sunset to 0.55 log lux at the end of twilight. This moment was originally determined by Lambert in 1760 (Kimball 1916) as the time when man has to suspend his labor because it gets too dark. Some natural phenomena coincide with the end of twilight: stars of first magnitude become visible, the anticrepuscular arch reaches zenith, etc. Lambert found that this moment occurred when the sun was 6° 23½' below the horizon; others have proposed other altitudes until now it has become customary to consider twilight to last until the sun's altitude is —6° 00'. The moment may, however, also be given a more rational definition (Nielsen 1961, 1963): From the culmination of the sun at noon the illumination in log lux is reduced at an increasing rate until about +0.7 crep when the maximum rate of reduction is reached and lasts until about +1.2 crep; after that it becomes darker at a slower rate. The maximum rate is at about +0.9 crep corresponding to an altitude of the sun of about 5° 30'.

It may of course be incidental that the change of illumination during twilight is 2.06 log lux, and the average duration of the swarming of all observed mosquitoes expressed as the change of illumination is 2.07 log lux but it could alse be significant, especially because the differences between the three groups nearly vanishes: By a twilight of 30 minutes the average A mosquito will swarm 30 minutes and 38 seconds, the B- and C-mosquito 29' 46", and 32' 51", resp.

It does not seem unreasonable to assume that swarming is typically stimulated by the conditions of illumination prevailing from sunset until the rate of change in intensity slows down. The duration is longer at temperatures of 18—20° and shorter at both extremes. Besides this correlation between temperature and the duration of swarming it seems that species living at temperatures differing from the optimal have acquired a genetically fixed adaptation so that in a hot climate they have a species-specific habit of swarming late when it has become cooler, and species with a polar distribution perform the swarming earlier before the temperature drops too low in the evening. Finally, besides the species-specific adaptation, the beginning of swarming for each species is in a similar way correlated with the temperature.

This general concept of the influence of temperature on swarming needs more observational support before it can be accepted, especially of swarming at optimal temperatures and at different temperatures for the same species. Also needed is an explanation of the early swarming of the subtropical *Psorophora ferox* and the late swarming of the temperate *Mansonia richiardii.*

Besides illumination and temperature only one other factor has been found to influence the swarming, namely wind. During the first year of the investigation of *Aedes cantans* (Nielsen &

Greve 1950) a delay was observed in the commencement of the swarming on evenings with strong winds, but later observations did not confirm this. These observations were carried out in a locality with tall dense vegetation which offered good protection against high winds. During the present work swarming on the wind-exposed meadows was delayed several times or even suspended on evenings with high winds as described for *A. dorsalis* and *A. caspius* above (p. 126 and 146).

Even if the wind is not strong enough to affect the time of swarming, it always has some modifying effect on the manifestation of swarming, examples of which may be found in the description of the observations.

2. Types of Swarming.

Aedes cantans was the first mosquito known to make swarms of more than one type (Nielsen & Greve 1950). This species (see also p. 118) formed low swarms, provoked, or during the ascent, spontaneously; and three definite or final types of swarms; the free swarm, the topswarm, and the rarely occurring ceiling swarm. In 1940 Cambournac and Hill showed that the swarming of *Anopheles maculipennis* var. *atroparvus* was performed over an area on the ground of contrasting brightness. Downes, who found similar behavior in culicoides, introduced the term ”swarm-marker” for such areas (1955). During the work reported here we found several new types of swarms; hedgeswarms, tipswarms at the tips of branches, interstitial swarms between branches, and the special development of the last mentioned, the cloak swarm; furthermore, we found more than one swarm type in at least four species besides *A. cantans*. With the knowledge we now have, the most essential difference between the types is between the preliminary and the definitive swarms. The two terms refer, of course, to cases of the same species swarming in different ways in the early part of the evening and later. Preliminary swarms are part of the activity which takes place before swarming. Above, in the discussion of the differences between *A. cantans* and *A. annulipes*, it has already been mentioned that the ascent may be either a climbing up in the vegetation or preliminary swarming or both. The daytime swarming of *Psorophora ferox* is the only example known to us of preliminary swarming in mosquitoes from warm climates, but climbing occours in *A. taeniorhynchus* before departure for migration, and ascent precedes swarming and migration in *A. caspius* in Iraq.

The definitive swarms are typically orientated towards a swarmmarker, either a brightness contrast area or a prominent object. They occur every evening at the same place. The preliminary swarms are usually formed low over the ground without reference points noticeable by man; they often change place and occur erratically. The flight has big amplitudes and few turns and often covers a considerable area. *Culex pipiens* (and perhaps other species) have preliminary swarms of a type which normally is definitive, formed over a swarmmarker but later the definitive swarm appears to be around the tips of branches. The swarms formed by species with only one type of swarm are usually of the definitive type.

Exceptions are the swarms of *A. rusticus* and *A. cataphylla*; they are of the same character as the preliminary swarms; although a few individuals at least sometimes take part in definitive swarms, it seems that these two species to a large extent have replaced the definitive swarming by the preparatory. They are the first to swarm in the year and the low temperature prevailing after sunset at that season might have had something to do with shifting the emphasis to the early form of swarming.

3. Extension of the Antennal Fibrillae.

In Iraq it was observed how the males of *A. caspius* extended the fibrillae, and the importance of this habit was discussed in the paper by E. T. and H. T. Nielsen (1958). It was concluded that it is an indication of readiness for general flight activity rather than for sexual activity as found by Roth (1948). It seems obvious that the factors releasing the crepuscular activity may stimulate this preliminary reaction some time prior to the climax of activity — the swarming.

The observation of this phenomenon is hampered in many mosquitoes by the habit of the males to rest in places of dense vegetation defying the inspection of the animals without disturbing them. *A. caspius* in Iraq was the easiest to observe: the vegetation was not very dense, and the males rested fairly often freely exposed so that it was easy to inspect them all day long. During the forenoon and early afternoon a few extended fibrillae, but later in the afternoon all fibrillae were usually recumbent. From —2 crep (which was about one hour before sunset) an increasing number of males extended the fibrillae at the same time they started to move up to the taller plants *(Sesbania)* — the "climbing". Within a few minutes around sunset all had arrived at the top part of the vegetation and all males had the antennae "bushy"; this was usually the moment when the swarming commenced.

The Danish *A. caspius* behaved quite differently. The males resting in the low vegetation were never seen to have the fibrillae extended during the daytime, and instead of climbing the reeds as a part of the ascent they flew with closed fibrillae to the flowers in the open to feed during the afternoon. They generally remained here until just before beginning of the swarming activity when they extended the fibrillae. As soon as the fibrillae were extended the male became very sensitvie to disturbances and often flew away at the approach of the observer. This, of course, made counting individuals with extended fibrillae unreliable. In the early evening inadequate results were obtained by counting males caught in a sweep net because the males closed the fibrillae when they got into the net; later in the evening the antennae of the males remained bushy when caught in this way.

A special observation may be worth quoting in detail for enlightment of the problem of the extension of the fibrillae: On July 11 heavy thunder clouds covered the sky over Næbengen. The swarming of *A. caspius* had already started at —2.30 crep, and many of the resting individuals had the fibrillae extended. At —1.58 crep, about 1½ hour before sunset the illumination was 2.84 log lux, a light intensity which normally occurs at —0.2 crep, 11 minutes before sunset. The number of swarmers increased and swarming also took place in higher niches than normally, but after a thunderclap some of them left the swarms and dissipated over the meadow. The rain started with a few drops at —1.87 crep and as it intensified at —1.5 crep the swarm first moved in towards the trunk of the alder and finally stopped when the storm hit at —1.4 crep. The rain lasted about 40 minutes (to —0.65 crep) during which time 17½ mm of rain fell. The few mosquitoes which could be seen in the grass had recumbent fibrillae and none was seen flying until —0.27 crep. A couple of minutes later the swarming started again (—0.24 crep) and at −0.15 crep the swarming was normal and the animals in the vegetation had the fibrillae out. The swarming ended at about the normal time.

The males of *A. cantans* and *A. flavescens* also extended the fibrillae shortly before the start of swarming, and, like *A. caspius* they flew away singly so soon after the extension that it was impossible to obtain a numerical expression for the process.

The only Danish species which behaved so that it was possible to make counts similar to those made of *A. caspius* in Iraq was *A. dorsalis*. This species was mostly observed at Kongelundsengen where strong winds made observations difficult as it caused the animals to seek shelter deep in the grass. Only on one evening, June 15, a complete record was made; and this showed a similar increase in the extension of the fibrillae as that found in *A. caspius* in Iraq.

A. rusticus and *A. cataphylla* have both been seen with extended fibrillae throughout the day especially at the darkest hiding places in the "rooms" at Bøndernes Egehoved. Illuminations at such places is often 1.0 log lux lower than the outside and the difference may even amount to more than 1.6 log lux which means that even in the middle of the day there will be places where the illumination never gets higher than in the open at sunset.

On September 8 a small swarm of *Anopheles claviger* was found in one of the "rooms" at an illumination of 2.27 log lux. Four of the swarmers were caught and placed in vials; when they were brought out in the open where the illumination was 2.96 log lux they retracted the antennal fibrillae. At the same time, however, a small, probably preliminary swarm of the same species was formed over the head of the observer.

In the extension of the fibrillae there are differences which can only be explained as species-specific. Among *A. annulipes* males, most of which were resting in the open among the nettles and thistles or on the outer branches of thistles or on the outer branches of the bushes, nearly all individuals observed had the fibrillae extended very early in the afternoon.

The rest of the Danish species we have observed were never found in such numbers at the resting places that any information could be obtained about the extension of the fibrillae.

The extension of the antennal fibrillae being an indication of readiness to perform prolonged flights might at least partly give an explanation to the problem of why some species have swarms in the morning and others do not.

Let us presume that the pattern for crepuscular activity is begun at a certain level of light intensity by the extension of the fibrillae, and at a higher light intensity the swarming habit is activated, and at a still higher intensity the light becomes so bright as to inhibit the swarming.

Species which always have extended fibrillae may always be ready to swarm and will do so in the morning, while in those species which do not swarm at sunrise the activation may take so long time that the release may first take place when the illumination has reached a higher level than the upper limit for swarming.

Of the mosquitoes which have permanently extended fibrillae e. g. most *Culex* species — all have morning swarms except *Culex univittatus* in Iraq. *Culex theileri* (also observed in Iraq) extended and closed the fibrillae but did so while hiding deep in the grass and not as *A. caspius* while ascending. *Culex fatigans* made equally good morning and evening swarms in cages under laboratory conditions with artificial "sunrise" and "sunset".

Mosquitoes with movable fibrillae making morning swarms present a more confused picture: *Psorophora ferox* and *Aedes taeniorhynchus* in Florida both made morning swarms but the latter species did so with only a few individuals compared with the evening swarms. *Mansonia pertubans* did not swarm at sunrise. In Iraq neither *A. caspius, Culex univittatus,* nor *An. superpictus* made swarms in the morning. In Denmark *A. caspius* made morning swarms as did *Culex pipiens* and *A. cantans* (Nielsen & Greve 1950) while *A. dorsalis, A. flavescens* and *A. annulipes* did not.

4. Comparison of the Swarming Habits of *A. caspius* in Denmark and Iraq.

In Iraq we observed *A. caspius* during two periods, the first from September 22 to October 3 (1955), the second from October 13 to 27. The most essential difference between the periods is that of the temperature: the six observations of the first period were made at an average temperature of 25.9° while the fourteen evenings of the second period were made at temperatures varying between 17.7° and 22.4° with an average very close to

20⁰. All other factors were the same during the two periods: the twilight lasted 25 minutes except for the last two evenings when it was closer to 26 minutes; it was completely calm and only on the last two evenings was there a light cover of cirrus clouds which did not affect the illumination.

The observations in Denmark of the same species were also made in two periods: the first series was nine observations in July made at an average temperature of 15,0⁰ and a duration of the twilight of 55 minutes, the second series was nine observations in September at 13.9⁰ and 37 minutes twilight.

Morphologically the two populations are different in coloration (see appendix) but in the opinion of Dr. Alan Stone, who was so kind as to examine our collections, the differences are insufficient to consider the populations distinct races. In their habits there are characteristic differences, and if we try to find whether these differences are caused by the differences in external conditions we meet the difficulty that all relevant factors are different during the observations of the two populations. However, it is helpful that in both cases the observations include periods with differences in only one of the factors.

Comparing the two populations, it has to be said that our knowledge of the developmental stages is insufficient to permit finding any differences; but in the habits of the imagines there are many:

In Iraq *A. caspius* was rarely seen feeding on nectar, and when it did so, it fed mostly during the night, after the swarming. In Denmark Bro Larsen (1949) found the species feeding in large numbers on flowers, especially in the morning and the afternoon. This was corroborated by the present investigation although we did not make counts frequently enough to show it in figures. The feeding in the afternoon was especially spectacular.

The daytime feeding of the Danish populations may be understood as an adaptation to the low night temperatures which frequently may be inhibitory.

The Iraqi *A. caspius* was also in general more active at night than the Danish *A. caspius* which usually escaped notice at the nocturnal resting places.

The swarming activity is very much different. During the ascent the population in Iraq showed a progressive extension of the fibrillae (see above) during a movement to the higher vegetation here called "climbing". The population in Præstø did no climbing, but the individuals left the resting places, when the fibrillae were extended to take part in the preliminary flights which never were seen in Iraq. The swarming also differed in relation to sunset, a point we shall return to below. The swarm type was different in the two populations. In Iraq *A. caspius* made high, free swarms for which we were not able to distinguish any swarmmarker although they usually occurred at certain places. In Denmark the swarms were always related to an object, often dark in color or brightness; most characteristic was the swarm at the alder on Næbengen as described above.

Matings were rarely seen in Iraq and must have taken place at the resting places; in Denmark they were rather frequently observed especially during the ascent and the early part of the swarming although most of the matings probably occurred elsewhere.

Some of the differences might be caused by the difference in climate but that is unlikely to be the main explanation because the closely related *A. dorsalis* in many of its habits is very similar to *A. caspius* in Iraq. In practically all points mentioned above *A. dorsalis* behaves as *A. caspius* in Iraq except perhaps in the type of swarm; it was usually easy to identify a light colored area as a marker for the *A. dorsalis* swarms.

Some interesting points in the comparison between the two populations are found in the relationship of swarming to sunset and twilight. We have already pointed to the difficulty of making such a comparison with the variation in the several conditions, but we are able to make corrections for some of them thus rendering the Danish material more uniform.

Most of the nights in Denmark were fairly calm and we have no evidence of any effect of the wind on the swarming of *A. caspius* except on two evenings in September (15 and 16). Strong winds on these days delayed the beginning of the swarming as we directly observed it: At the usual time for swarming, single individuals tried time and time again to begin but went back to rest after a few moments' flight. As usual, we indicated the first continuous swarming as the commencement. In table 3 we have therefore kept these two evenings separate from the others and called them September II.

Another factor for which it is possible to make some correction is the illumination. In Iraq all evenings were clear; in Den-

Table 3.

Time Parameters for Swarms of *A. caspius* and *A. dorsalis* (September II are the two evenings with strong wind).

	A. caspius					*A. dorsalis*
	Denmark			Iraq		Denmark
	July	Sept. I	Sept. II	Sept.	Oct.	July-Aug.
Number of observations	8	7	2	6	14	3
Duration of twilight	55	37	37	25	25	53
Average temperature	15.0	13.9	14.9	25.9	20.0	13.3
Minutes from sunset						
Commencement	—51	—48	—6	+8	0	—15
Cessation	+52	+30	+32	+23	+28	+52
Duration	103	78	38	15	28	67
Crep						
Commencement	—0.93	—1.30	—0.15	+0.33	+0.02	—0.25
Cessation	+0.94	+0.80	+0.97	+0.93	+1.10	+1.01
Duration	1.87	2.10	1.12	0.60	1.08	1.26
Crep corrected for actual light						
Commencement	—0.76	—0.92	+0.19			—0.25
Cessation	+0.94	+0.80	+0.97			+1.01
Duration	1.70	1.72	0.78			1.26
Crep corrected for temperature and light						
Commencement	—0.98		—0.09	+0.05		—0.50
Cessation	+0.89		+0.98	+1.05		+1.06
Duration	1.87		1.07	1.00		1.56
dlx	2.42		1.98	2.25		2.65

mark in July some of the evenings were so cloudy that the illumination was definitely lower than normal and in September there vere several such evenings. If a certain illumination is an essential stimulus to swarming the swarming will, of course, begin earlier on a dark evening than on a normal one. In the observations corrected for light we have, therefore, substituted the observed commencement in crep with the moment (in crep) when the illumination normally is that which was actually observed at the commencement of swarming. On July 7, e. g. the swarming began 19 minutes before sunset, equal to —0.34 crep. The standard illumination at this moment is 3.00 log lux but the actual light was measured to be 2.72 log lux. According to the standard curve this illumination would normally prevail at —0.09 crep, and this is thus the corrected moment of commencement which corresponds to 5 minutes before sunset. In table 3 both the directly observed commencements and the light corrected values with the different deviated values for the duration etc. are given. It would probably be justifiable to have made a similar correction for the cessation of the swarming but our lightmeter did not permit us to make measurements so late in the evening. The error is probably not serious because the difference between the illumination on a cloudy night and a clear one usually decreased around sunset and most likely was rather small at the end of the swarming, at least in time units. As the change in illumination at this point of the curve is the largest per time unit, the error might be more evident in illumination than in crep, and may be the cause of some of the variation in dlx, the difference in log lux between the beginning and the end of swarming.

As shown above (fig. 10—13) the temperature has a rather definite influence both on the beginning and the end of the swarming, and in spite of the considerable dispersion it might be an advantage to correct the crep values by means of the curves indicated on these figures. To all the moments of commencement and cessation has been added the difference on the ordinate corresponding to the difference between the average temperature for the observations and 18.4 ° which is the average temperature for all the observations on *A. caspius*.

Using the corrected values it is justifiable to pool all observations from Iraq and all from Denmark except the ones for the two windy nights (table 3). It is thus seen that there is a very clear difference between the two populations: in Iraq the swarming begins at sunset and ends at the end of twilight; in Denmark it begins one period of twilight before sunset and ceases well before the end of twilight. The duration of the swarming expressed as crep in Denmark is twice as long as in Iraq, but in terms of difference in illumination (dlx) there is only a small and insignificant difference (2.25 and 2.42 log lux). The midpoint of the swarming in Denmark is shortly before sunset, while in Iraq it appeared after half the twilight was over.

In table 3, a similar summary of the only three observations we have of *A. dorsalis* is also given. While this species in swarm type was much closer to the Iraqi *A. caspius* than to the Danish population of the same species, it is seen from the table that in respect to the time parameters it differs from both populations but is definitely closer to the Danish *A. caspius* than to the Iraqi one.

Finally, if we consider the observations on the two windy nights in Præstø in September, we see that they are in very good agreement with the Iraqi *A. caspius* observations in the points in which the Iraqi population differs from the normal Danish one. In other words: in relation to sunset and twilight there is considerable difference between the two populations but the effect of an external factor as the wind may change the Danish *A. caspius* to react as those from Iraq. This draws attention to the possibility that the difference is simply caused by the different conditions but as we have corrected for all the pertinent factors known to us this is not likely. The only factor we have not considered is the humidity; we have never found that humidity had any influence on the swarming.

Even if it is unlikely that the conditions are directly responsible for the differences, they might be of importance in a more subtle way.

The longhorned grasshopper, *Tettigonia viridissima,* is activated to stridulate by the decrease in illumination at sunset. Some of them live in bushes and small trees, others in the open, in potato and beet fields. Examined in the laboratory there is no difference to be found between them, but in the natural populations those at the low places show an increasing tendency to begin to sing earlier in the evening, up to four to five hours before sunset. Those living in the dense foliage of higher vegetation will remain singing late in the evening — after sunset — until much later in the year. The reason is that the stridulation has a threshold at a minium of 12° and early in the year the temperature in the low places drops below this level during the night while this happens much later or maybe not at all in the trees and bushes. By means of a rhythm the activity period therefore gradually occurs earlier in the day during the life of the animal (the normal lifespan is 6—10 weeks).

We do not know whether it is justifiable to see a parallel to this in swarming; but, apart from obvious exceptions as *Psorophora ferox* and *A. geniculatus,* there is a definite tendency for the inhabitants of hot climates to swarm later than those from the temperate and arctic region even if we apply corrections for twilight and temperature. It does not seem unreasonable that the inhibitory or at least delaying effect of high temperature causes the late swarming we have seen in Florida and Iraq. Similarly, the low temperatures during the night might terminate the swarming so early in the evening in colder climates that the beginning has to be earlier too, especially because, as we think we have shown, the duration of the swarming in terms of the difference in illumination seems to be fairly constant. This means that the commencement in terms of crep occurs much earlier as a result of the function between crep and illumination; and as the early beginning of the swarming thus occurs at latitudes with long durations of twilight, the swarming will start very much before sunset in species under temperate conditions, and they will last much longer than at lower latitudes.

Whether these adaptations are genetically fixed or are individual (as in *Tettigonia*) can only be shown by experiments. Applied to the two populations of *A. caspius,* this means that in the time parameters of the swarming they have different adaptations but their genetic and taxonomic importance is still unknown. In the type of ascent and swarming there are also differences and they are probably species-specific.

For the understanding of swarming as a special habit we approach the following conception:

There are, of course, many more species of mosquitoes than there are types of swarms, but a certain combination of swarm types seems to characterize each species. The movements of the fibrillae on the antennae and the climbing and preliminary flights are elements of the mosaic of single habits which constitute the swarming. It should be especially emphasized that although for each species preliminary and definitive swarming are clearly distinguishable, certain types of swarms in different species may be either part of the ascent or a final swarm type. Perhaps some of these differences are influenced by external conditions but most of them are well anchored in the genetical heritage of the species. The adaptations to the actual conditions may be found in the time parameters of swarming.

D. APPENDIX.

The differences between the Danish and Iraqi *A. caspius* and *A. dorsalis* are subtle, and considerable individual variation makes it difficult to define them. In this table the differences we have found most useful for the identification are presented.

	A. caspius, Iraq	**A. caspius**, Denmark	**A. dorsalis**, Denmark
HEAD:			
Occiput:	White in middle, becoming faint brownish at sides.	White in middle, dark golden spot on each side.	White in middle, black patch on each side.
Proboscis:	Black at tip, the remainder white with scattered dark scales.	Dark scales dominate except near middle.	Dark scaled with a few white scales near middle.
Palpi: (female)	White, sprinkled with dark scales.	Dark, sprinkled with white scales.	Dark with a few white scales.
THORAX:			
Mesonotum:	Pale golden, faintly darker at median third, in some specimens this middle line is marked off by a very thin line of white scales.	Dark golden with two distinct (but thin) lines separating the middle third.	Broad median line of dark brown scales, the rest of scutum covered with white, pale golden or grayish white scales.
Wings:	Light and dark scales evenly mixed or the white scales dominate.	Light and dark scales evenly mixed or the dark scales dominate.	Light and dark scales mixed but basal part of costa and radius$_1$ completely white scaled.
Legs: (front femurae)	White, sprinkled with a few dark scales especially at apical end.	Dark and light scales mixed, nearly all dark scales at apical half.	More or less evenly speckled black and white.
ABDOMEN:	Pattern indistinct: Abdomen chiefly white with dark patches at lateral apical corners. These may be either dark, dark sprinkled with white, or merely be indicated by a few dark scales.	Chiefly dark with more or less distinct center line of white scales. Basal bands broaden laterally but the lateral lines do not reach apical corners. Faint apical bands sometimes present, becoming quite heavy on the last segments.	Blackish brown with white centerline and white lateral lines. The center line broadening either apically, basally, or both, in some specimens thus forming apical and basal bands.

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