Observations on Mosquitoes in Iraq

by

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(With plates 5–8)

Aedes caspius (Pallas).

Aedes caspius was observed in the field in September and October, 1955, at the experimental farm, Abu Ghraib (44° 5' E 33° 15' N), which is 20 km west of Baghdad on the road to Fellujah and Ramadi.

Surrounding the farm buildings are gardens, date palm groves, and orchards, with a network of very wide roads paralleling irrigation ditches and shaded by tall *Eucalyptus* trees and *Oleander* bushes (pl. 5, fig. a). Along the western border of the central building area there runs the road from the chaikhan (tea house) on the Fellujah road northwards toward the village of Khairnabad; this road consists of three lanes 30 m wide, separated by ditches and trees. There are a few houses west of the road at this point while the dairy is to the south and a *Eucalyptus* grove and nursery are to the north; beyond and between these and extending absolutely flat as far as the eye can see is the sparsely vegetated and dusty plain, more or less cultivated only close to the farm.

The first few days we made observations on small swarms out on the plain, but nearly all the observations reported below were made just west of the west lane of the Khairnabad road and south of the *Eucalyptus* wood, in a field separated from the wood by a westward running lateral ditch and from the road by an irrigation canal (map, fig. 1). Most of this field was covered with *Sesbania* (pl. 5, fig. b), a legume two to three meters high which is often used as windbreak in the vicinity of Baghdad and for which seed is grown on several fields of the farm. In the northeastern corner of this field was an open, grassy area with scattered Shoch (*Prosopis*), Shoch-es-Shams (*Acacia*), a sort of large bur, and isolated *Sesbanias.*

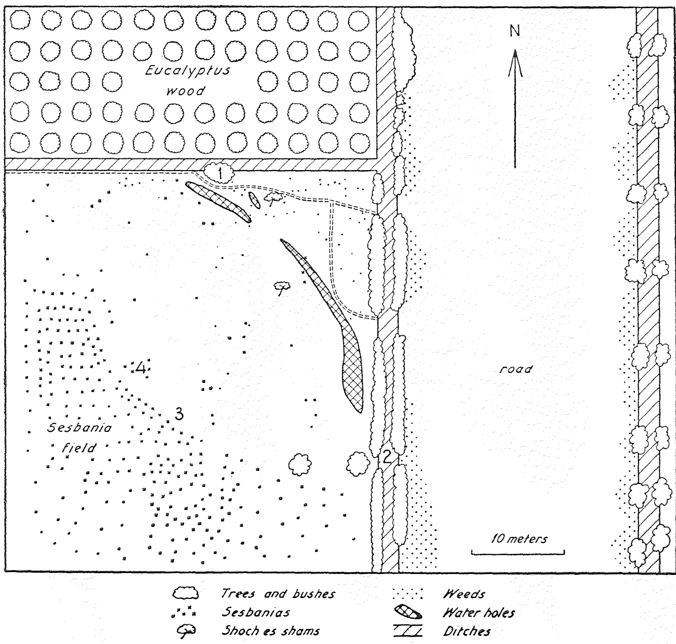

Fig. 1. Sketch Map of observation area in Abu Ghraib.

In the above corner were some curved, oblong holes, apparently plow furrows left unharrowed on the turn. The corner was flooded through an opening in the bank of the main ditch. When flooding stopped, the water receded to the afore-mentioned plow furrows resulting in pools wherein the mosquitoes hatched by the flooding could finish their development. The irrigation hole in the ditch bank was never carefully closed, so there was considerable seepage into the area whenever the main ditch carried water for irrigation to the south. This seepage kept water in the plow furrows. New irrigation or winter rains would again flood the area, scattering the old larvae and hatching the next brood.

From September to February this area was continuously producing *Aedes caspius* (pl. 5, fig. c), with two interruptions: October 21—25 and November 7—11. This breeding was attributable mainly to carelessness in stopping the irrigation inlet. A little better care would probably have reduced the mosquito annoyance in Abu Ghraib to practically nil since it was mild only, despite the complaints of residents, and since we failed to locate any other mosquito breeding area on the farm.

1. Ecological Factors.

As the opportunity to observe mosquitoes swarming under the conditions prevailing at Abu Ghraib was not likely to reappear for us in the foreseeable future, we did our best to measure the physical factors during the swarming. We were, however, hampered by our rather limited equipment. Furthermore it was rather difficult for two persons to make simultaneous observations on two or three different mosquito swarms and also read the instruments.

(a) Time.

Before leaving our house for the afternoon observations we corrected our watches by the time signal from the British Broadcasting Corporation on short-wave radio. Sunset was determined every evening at the moment when half of the sun's disc had apparently disappeared below the horizon. Such observations were made on 28 evenings between September 17 and October 27; the sunset was easily observed on everyone of these evenings, albeit a thin cloud cover occurred on two evenings.

Astronomical tables consider sunset as the moment when the topmost part of the sun appears to coincide with the horizon. We must then compute the duration of 16' of angular movement, the radius of the sun being 16'. At the apparent sunset, the center of the sun is actually 50' below the horizon, so the duration of twilight corresponds to an actual angular movement of $5^0 10'$. If twilight lasts 25 minutes our indication of sunset and end of twilight is thus $16 \times \frac{25}{5^0 10'}$ or 1 minute 17 seconds too early.

Earlier investigations of swarming (Nielsen & Greve, 1950; Nielsen & Nielsen, 1953) demonstrated a definite correlation between swarming and the duration of twilight. Civil twilight is described in European calendars as the period during which the sun is less than $6^0 24'$ below the horizon; the Meteorological Tables of the Smithsonian Institution consider twilight as the period between sunset and the time when the sun is 6^0 below the horizon. We have herein used the latter American concept of twilight. During the period of our observations in Abu Ghraib the twilight lasted 25 minutes except for the last two evenings when it lasted 26 minutes.

(b) Light.

Light measurements were taken with a barrier layer photocell with attached milliamperemeter manufactured by Sight Light Corporation, with scales 0—100 and 0—1000 foot candles (1 f. c. = 10.76 lux). The instrument was placed horizontally during the reading and exposed to the diffused light from the sky. When readings were taken early enough in the afternoon for the sun's rays to hit the cell directly, it was shaded by hand. A similar position of the hand after the sun had disappeared had no influence on the reading.

In Fig. 5 are given all our light measurements (expressed as log lux) around sunset on the days we observed swarms in Abu Ghraib. The decrease in intensity had its maximum shortly after sunset. Unfortunately our lightmeter was not sensitive enough to show the retardation in the decrease which normally sets in at the end of twilight.

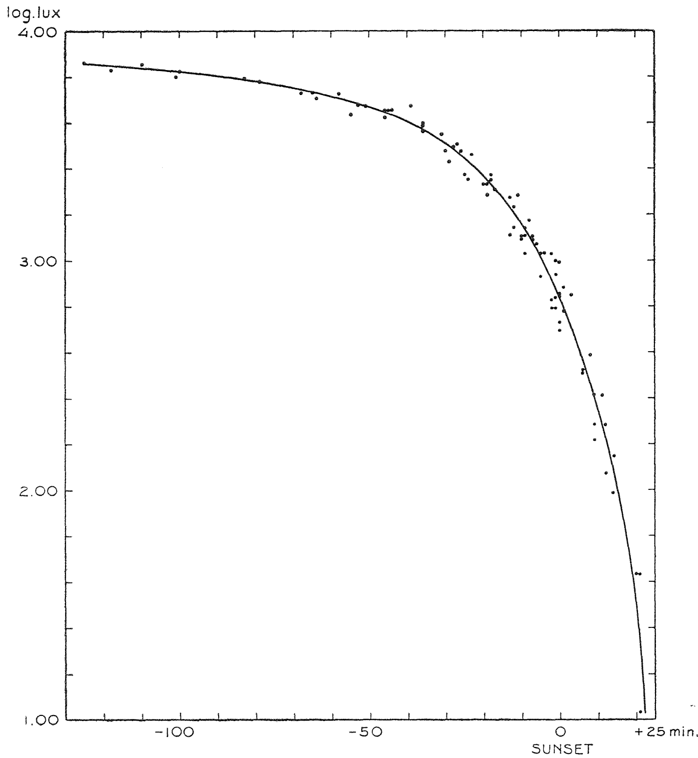

Fig. 2. Change of light in Abu Ghraib about sunset, Sept. 23 to Oct. 26, 1955.

The light intensity varied very little from day to day. At the moment of sunset all observations were within a range of 2.69 to 3.00 log lux; converted, this meant a variation of ± 3 minutes.

The thin cirrus sky cover of the last few evenings had no influence on the intensity of the zenith light.

(c) Temperature.

Incidental temperature measurements were made during the whole observation period, but systematic determinations were made only on the last ten days. Tem-

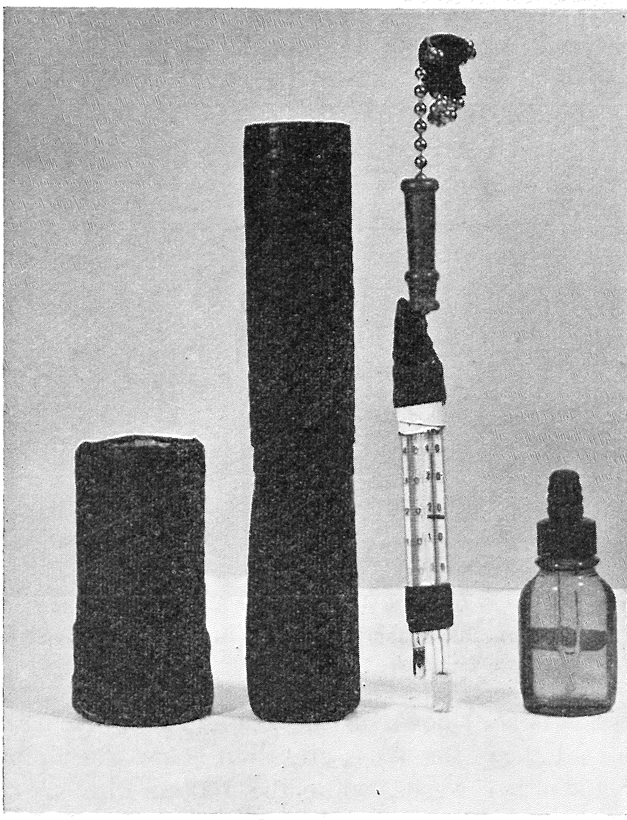

Fig. 3. The improvised sling psychrometer with bottle with distilled water, and case.

perature and humidity were measured with an improvised sling-psychrometer (fig. 3) made of two short thermometers, 0^0—60^0, $^1/_1{}^0$ divisions, taped together and provided with a short chain and a handle. The psychrometer was swung horizontally to permit readings at different elevations above ground. All measurements were taken at the same place, just outside the dense vegetation ("3", fig. 1), the operator's feet being similarly placed every time, as far as possible from the place of measurement. Once or twice a straw had to be trimmed away to give room enough for the lowest determination, 30 cm,

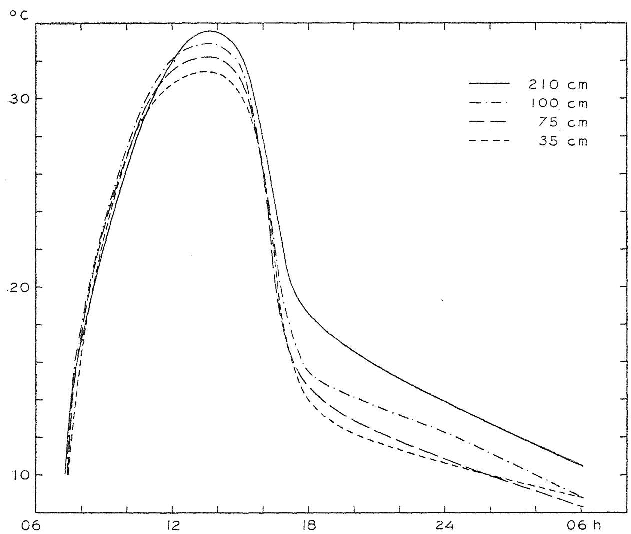

Fig. 4. Variation in temperature in four different nights above ground through 24 hours.

which was well down in the grass. The 75 cm reading was well above the dense grass but below the top of the bur and other weeds, while the 100 cm was above all dense vegetation. The highest measurement, 210 cm, was at least 5 m from any *Sesbanias* reaching higher.

Temperature, as well as other factors, varied little from one day to another with the exception of October 20 (see below). Round-the-clock measurements were made once only (Oct. 23—24), but the pattern is considered quite representative (figs. 4, 5a, 5b), as verified by several measurements on October 17.

Fig. a. Road in Abu Ghraib

Fig. b. *Sesbania*

Fig. c. *Aedes caspius,* female

Fig. a. Ascent of *Aedes caspius* from the grass

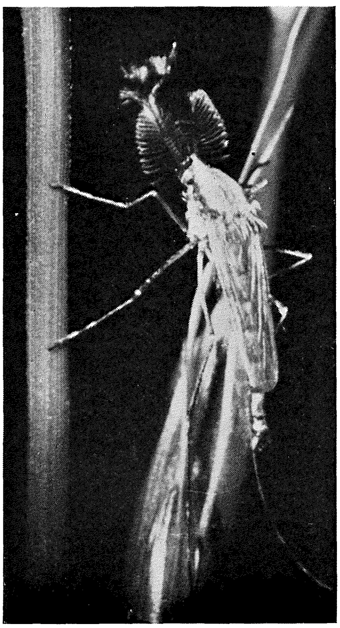

Fig. b. Male *Aedes caspius* with extended fibrillae photographed in the field

Fig. c. Extrafloral nectar drop on a leaflet of *Sesbania*

The most characteristic feature of the daily temperature cycle is the closeness of the readings at the four

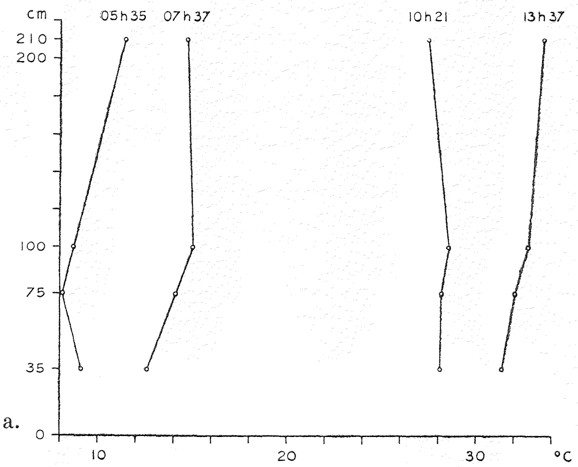

Fig. 5 a.

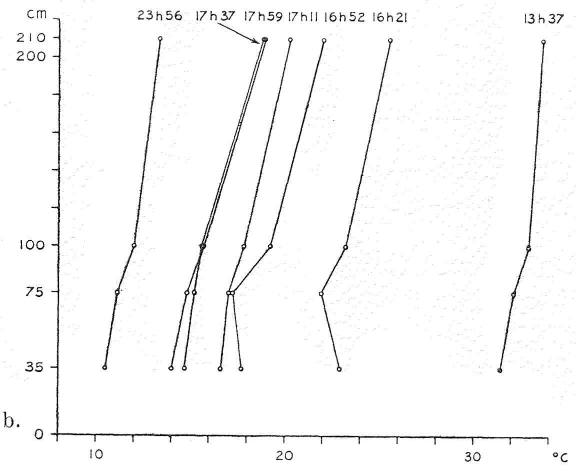

Fig. 5 b.

Fig. 5. Temperature tautochrones; (a) from before sunrise to early afternoon, (b) afternoon and evening observations.

elevations. Although the temperature during the daytime rose from 8^0—10^0 to well above 30^0 and back to well below 20^0 at sunset, the range for the four elevations never much exceeded two degrees. Another interesting feature is the total absence of the typical insolation distribution. The tautochrones for $07^{h}37'$ and $10^{h}21'$ (fig. 5a) show maxima at 100 cm, which is rather close to the top of the weeds. This could mean that the top of the lower vegetation is the virtual surface (Geiger, 1950), but the differences between 100 cm and 210 cm

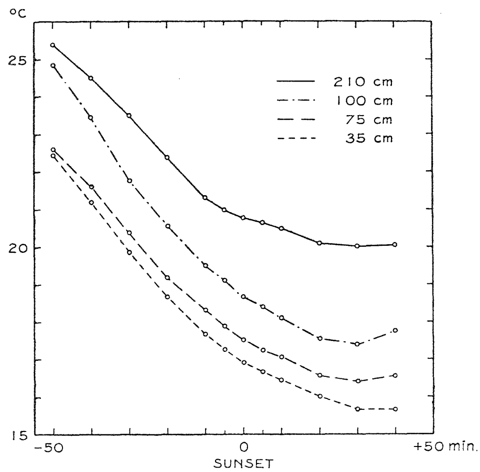

Fig. 6. Temperature around sunset at four different heights above ground: average of ten evenings.

are only 0.5° and 1.0° respectively; and furthermore at $13^{h}37'$ when we would expect the most extreme insolation-type distribution there is already a distinct inversion. About an hour before sunset, two readings gave the lowest temperature at 75 cm (fig. 5b). This could be significant since, first, there is a gradual return to the night inversion during the following hour, and, secondly, a similar crossing occurred every afternoon except October 20 and 24. After sunset the night inversion was firmly established and lasted until sunrise. Finally, the night inversion is rather light, seldom exceeding four degrees. High wind would have explained the peculiar temperature distribution, but calms prevailed; only in the middle of the day did wind velocities ever rise above 2 m/sec.

On all evenings except that involved in the above 24-hour study, temperatures were read five to nine times from 1 to 2 hours before sunset until ½ to 1 hour after.

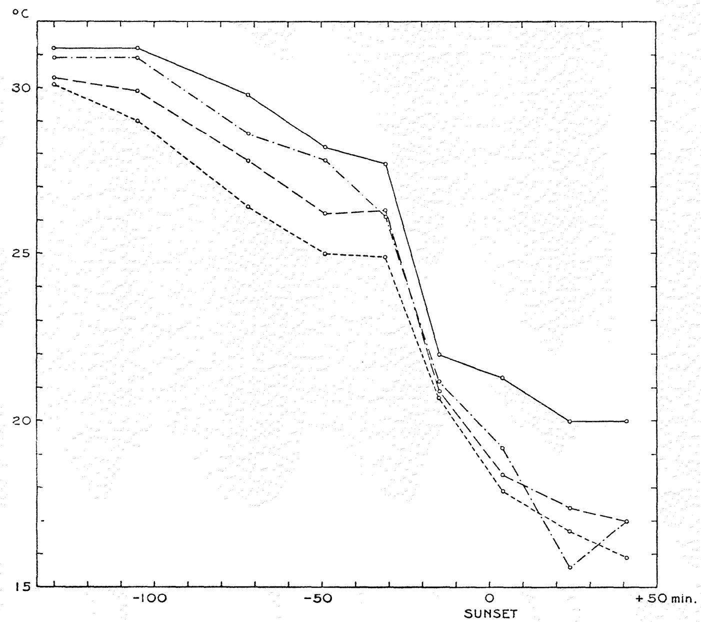

Fig. 7. Temperature around sunset for Oct. 20, 1955.

The temperature at sunset 150—200 cm above ground reflected the seasonal change. It was still around 30° Sept. 18—22. The first days of October it was 28°. During the Oct. 16—26 period of systematic temperature measurement the day-to-day variation was small: 22.2°—21.2° Oct. 16—20 and 21.0°—18.0° Oct. 21—26, the corresponding temperatures at 30 cm being 18.8°—18.0° and 17.2°—15.6°.

Fig. 6 shows the average temperature change during the period of importance to swarming. The only essentially different day was October 20 (fig. 7). On that day the temperature drop in late afternoon was unusually small and half an hour before sunset the temperatures at the four elevations were still 25°—28°. Fifteen minutes later they suddenly dropped to 21°—22° and kept on dropping until a normal value of 16°—20° was reached at the end of twilight.

(d) Humidity.

The technique for measurement was described above. The 24-hour distribution of relative humidities is given in fig. 8. During the middle of the day, the humidity closest to the ground remains highest (minimum 40 %) while at 75 cm and 210 cm it drops to 30 % and at 100 cm even to 25 %. Corresponding to the drop in temperature towards sunset there is a rapid rise in the relative humidity, the curves for different elevations crossing one another while that for 210 cm remains definitely lower. This was the case on most other evenings as well, although the average of ten evenings for the sunset period (fig. 9) clearly shows the increase in re-

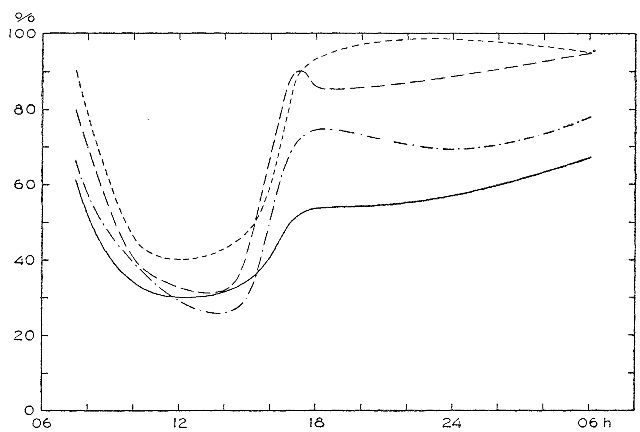

Fig. 8. Variation in relative humidity at four different heights above ground through 24 hours.

lative humidity as the ground is approached. The maximum humidity at 210 cm was at ten minutes before sunset, at 100 and 75 cm there were similar but weaker maxima at 15—20 minutes after sunset, whereas at the lowest elevation (35 cm) the maximum humidity was not attained until a few minutes after the end of twilight. The final attainment of saturation in the vegeta-

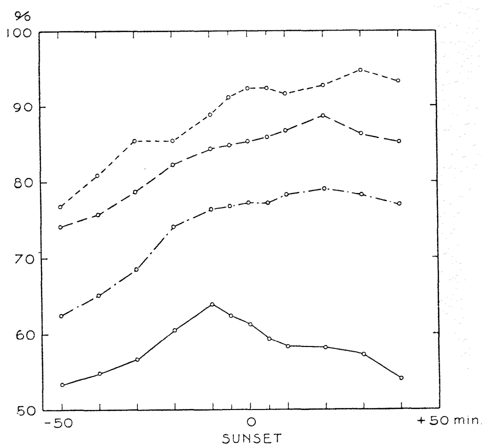

Fig. 9. Relative humidity around sunset at four different heights above ground; average of 10 evenings.

tion usually was delayed until in the morning before sunrise. October 21 was the first evening of saturation at twilight, and the notebook has the following entry: "It is cold on the feet tonight, and so humid that my cigarette goes out," — a noteworthy observation after five months without dewfall and nearly without a cloud. On October 20, when the temperature remained high until shortly before sunset, the relative humidity showed a corresponding increase, the average for all four elevations rising within 15 minutes from 39 $^0/_0$ to 67 $^0/_0$.

The saturation deficit presented essentially the same picture as the relative humidity, the highest value being 28 mm (fig. 10). The average of measurements around sunset (fig. 11) indicates that the decrease in saturation deficit 210 cm above the ground ends as early as 20 minutes before sunset while at the three lower elevations it ended only at the end of twilight.

Absolute humidity (mm partial pressure) was rather uniform during the 24-hour period, with a maximum of

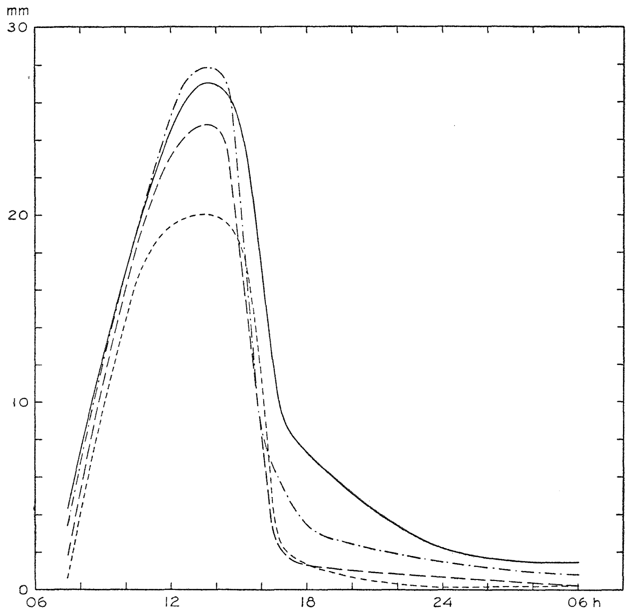

Fig. 10. Variation in the saturation deficit at four different heights above ground through 24 hours.

12—15 mm around 15^h and a minimum of 6—8 mm shortly before sunrise (fig. 12). The situation around sunset on an average evening is presented in fig. 13. The sudden drop in temperature on October 20, so well reflected in relative humidity and saturation deficit, had no clear effect on the absolute humidity. The curves for that date (fig. 14), however, indicate an unusual situation. Instead of the normal decrease, the absolute humidity remained constant until the sudden drop in temperature when it rose slowly before assuming the normal slight decrease.

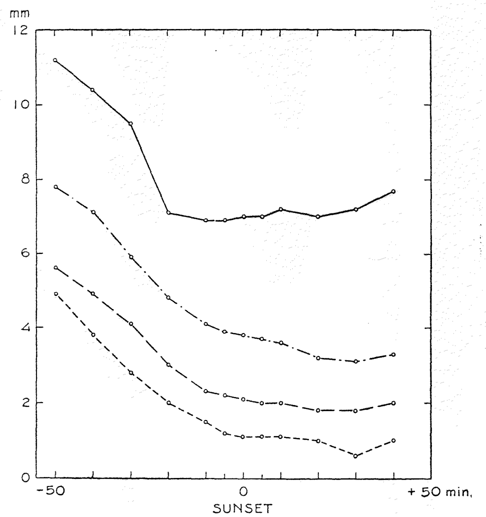

Fig. 11. Saturation deficit around sunset at four different heights above ground; average of 10 evenings.

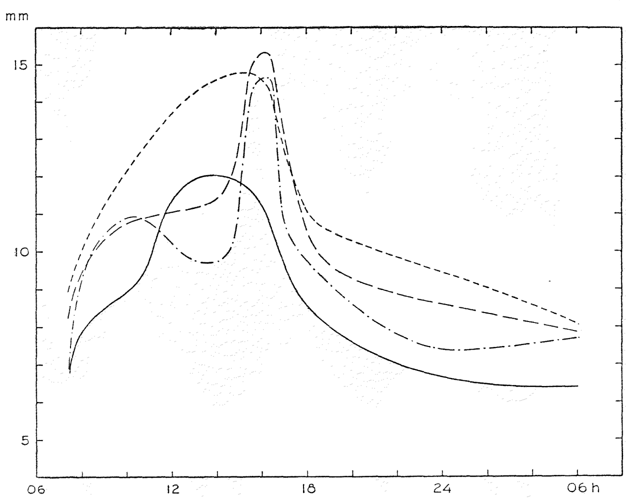

Fig. 12. Variation in the absolute humidity at four different heights above ground through 24 hours.

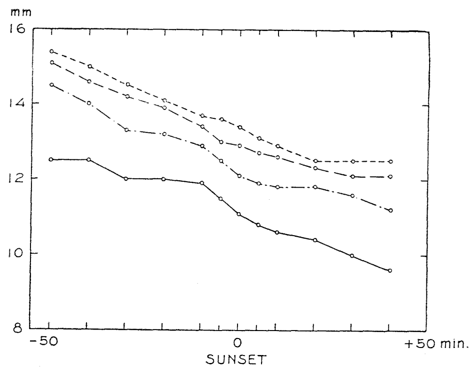

Fig. 13. Absolute humidity around sunset at four different heights above ground; average of 10 evenings.

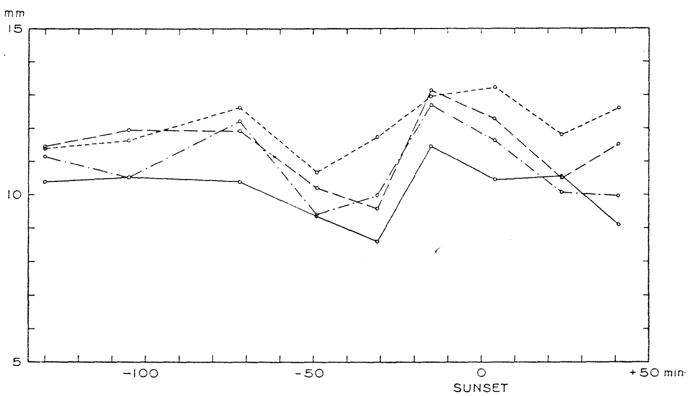

Fig. 14. Absolute humidity around sunset for Oct. 20, 1955.

(e) Wind.

In the middle of the day the wind was usually less than 2—2½ m/sec and it would always diminish towards sunset. During the swarming interval it never exceeded ½ m/sec and on at least 20 of the 28 evenings it was calm or dead calm. There were periods of over 24 hours without enough wind to move a *Eucalyptus* leaf. None of the unpleasant sandstorms occurred during the period of observation.

(f) Photography.

The photographic equipment was simple. The camera was an Exa with a Steinheil 50 mm, f: 2.9 Cassar to which could be attached a simple lens for close-ups. A Metz' Mecablitz rendered excellent service and we found that exposing with this flash disturbed neither resting nor swarming mosquitoes, an observation later used in developing a cinematographic actograph method (Nielsen, 1957). *A. caspius* often swarm so high and so late that it is impossible to see them by natural light; we found the flash useful in making them visible then. We also used, of course, the well known method of calling the swarms down (Nielsen & Greve, 1950).

2. Development.

(a) In the field.

Eggs hatched on September 25 by the first flooding produced the only brood in the field for which duration of development could be determined. The first pupae were seen on October 1, five days later, and the next day $^1/_3$ to $^1/_2$ were pupae in the various pools. The adults emerged Oct. 3—5, or seven to nine days after egg-hatching. We did not take water temperatures regularly during this period, but air temperatures averaged between 25^0 and 30^0. When this brood emerged males of a preceding brood were still swarming; an increase in size of swarms on the nights of October 6 and 7 probably meant males of the new brood were beginning to take part in the swarming. The first day biting females constituted an annoyance was October 7. Subsequent broods overlapped to a degree making it impossible to follow the development.

(b) Duration of pupal stage.

The duration of the pupal stage at different temperatures (Nielsen & Haeger, 1954) is a useful indicator of the influence of temperature on development. The larval stages, egg to pupa, usually last 3½ times as long as the pupal stage.

Fourth-instar larvae were caught in the field and newly-transformed pupae placed in individual vials at the desired temperature. We had some trouble maintaining constant temperatures until we found that room

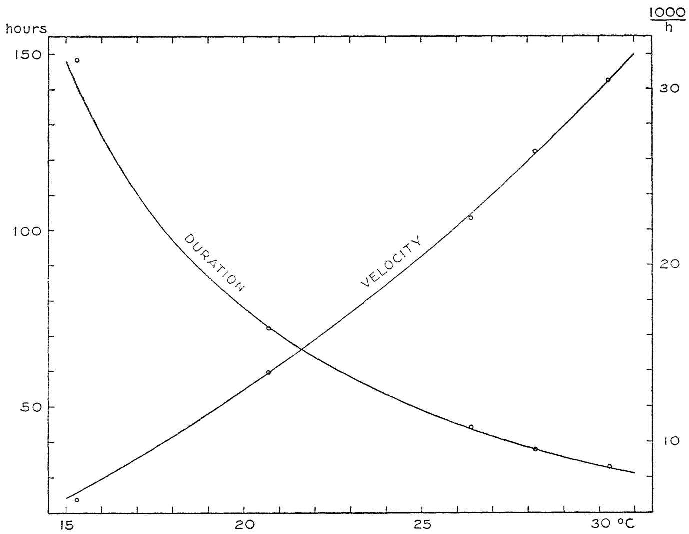

Fig. 15. Duration and velocity of the pupal stage in *Aedes caspius* in relation to temperature.

temperature in our house could be fairly well regulated by opening and closing the windows; the half-meter thick clay walls provided excellent insulation. Temperatures were measured by means of a thermometer with the bulb in a vial simulating those containing pupae, with the same amount of water, and similarly capped with a cotton plug.

For the higher temperatures we used an ordinary wardrobe with baffles and a fan for air circulation, lamp bulbs for heating, and a thermostat fashioned from a piece of bimetal and some odds and ends from Ukaidy's Radio

Shop in Baghdad. Corrugated cardboard from old boxes and thin sheets of cotton provided the insulation. This cabinet worked well for the three months of experiments, keeping temperatures from 26° to 30° within a few tenths of a degree throughout any one experiment.

Lower temperatures in the rooms were, of course, much less constant, and we had to compute the average temperature for each pupa. It was found that even very small variations in the average temperature could be recognized in the duration of the pupal stage. In future studies it must be remembered that temperature control is extremely critical in such experiments.

The results of our determinations of temperature effect on pupal duration are presented in table 1 and figure 15.

Table 1.

Duration of the pupal stage in *Aedes caspius* at different temperatures.

Number of Animals	Temperature (°C.)	Duration (hrs.)	Velocity (1000/hrs.)
16	15.3	148.4	6.7
135	20.7	72.0	13.9
34	26.4	44.1	22.7
111	28.2	37.8	26.5
73	30.3	32.8	30.5

3. Swarming Habits.

(a) Ascent and extension of antennal fibrillae.

Nielsen & Greve (1950) described several types of swarming which generally succeed one another: between the first "ground swarms" to the final top-swarms and ceiling-swarms there is an intermediate stage during which all mosquitoes (females included) take part in an upward movement, the females to come to rest in the foliage of trees while the males pass through the ceremonial swarming before they end up in the foliage, joining the females. To this upward movement was applied the term "ascent", covering several types of flight: from grass or ground swarms directly to the tree tops or high swarms or, more often, to the foliage of a tree or bush slowly and interruptedly, moving from leaf to leaf in shorter or longer flights each ending a little higher than the preceding resting place.

In *Aedes taeniorhynchus* Wied. in Florida (Nielsen & Nielsen, 1953) no ascent associated with swarming was ever seen, the males seemed suddenly to appear in the swarm and just as suddenly to vanish. Their whereabouts outside the swarm is still unknown. However, gradually rising flights very similar to the ascent have been observed in the newly-emerged, before they leave the rearing site (Nielsen, 1958).

On September 12 when we first visited the Abu Ghraib site, described above, we noticed a very marked ascent of *A. caspius* from the grass to the big *Eucalyptus* tree (see sketch, fig. 1, "1", and pl. 6, fig. a). The grass was seemingly dry, and when we arrived four minutes before sunset one wave after another was rising from the grass and flying to the lower branches of the big *Eucalyptus,* whose canopy partly reclined towards the grass. The mosquitoes then moved by short flights higher and higher up, many of them coming to rest 3 to 4 m above the grass. At nine minutes after sunset they began to depart, some leaving 3—4 m up, but most of them from higher leaves where the increasing darkness made observations difficult. This ascent greatly resembled the ascent to swarm in *A. cantans,* but the fact that both sexes left the foliage and that the hypopygial rotation in males was not completed indicated that these were newly emerged. No svarms were seen but there was a faint humming during the latter part of the ascent.

There were no ascents on subsequent evenings until the October 3 emergence of the next brood. Observations of ascent from Oct. 3 to Oct. 8 are summarized in table 2.

Table 2.

Time for the commencement and cessation of the ascent before the departure of *Aedes caspius.*

Date	Sunset	End of Twilight	Ascent Commencement	Ascent Cessation
October 3, 1955	17h42	18h07	17h43	18h12
„ 4, „	17h41	18h06	17h12	18h07
„ 5, „	17h41	18h06	17h20	18h03
„ 6, „	17h39	18h04	17h19	18h08
„ 7, „	17h38	18h03	17h17	18h10
„ 8, „	17h37	18h02	17h15	17h38

After these first days our attention was increasingly drawn to the larger numbers of males swarming. At the same time the ascent had undergone a change: although both sexes participated in the upward movement only males left the foliage. Furthermore, the ascent ended earlier, mostly before the start of swarming which coincided closely with sunset. There was, indeed, plenty of activity on the part of the females, but most of it was the normal appetential behavior associated with the bloodmeal. As during observations in Denmark and Florida, we had the impression that biting activity was more intense before than during the males' swarming interval; but this could be psychological on our part rather than behavioral on the part of the mosquitoes, — we were too occupied at swarming time to notice the biting annoyance.

In ascending before swarming, the males displayed a characteristic which made it easy for us to give the ascent a numerical expression. It was the habit of the ascending males to extend the fibrillae thereby giving the antennae a "bushy" appearence (pl. 6, fig. b). Our procedure was to count, at short intervals, the number out of ten mosquitoes which had the fibrillae extended. Beginning at one to one and a half hours before sunset there was found a gradually increasing proportion of extended fibrillae (Ef) until all males had them extended a few minutes before sunset and before the first humming from swarms. It was sometimes observed that a male would extend the fibrillae for a few minutes and then retract them again for a little while. The actual procedure of extension was frequently observed. When the males returned from swarming the fibrillae were still extended but as soon as the animals came to rest, usually on the upper leaves of *Sesbania,* they were retracted.

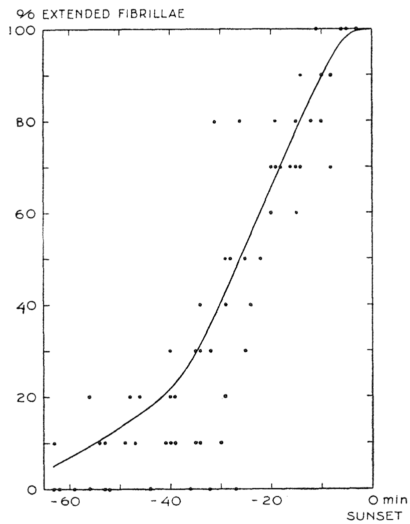

Fig. 16. The average of all observations of extended fibrillae in relation to sunset.

At any hour of the day or night individual males could be found with extended fibrillae; we have counted 30—40 $^0/_0$ at 07^h and 10^h. However, on most days the Ef was zero one to one and a half hours before sunset. At 50 minutes before sunset the average Ef was 5 $^0/_0$. The average of all observations then rose fast, Ef being 25 $^0/_0$ at 40 minutes before sunset, 50 $^0/_0$ at 25 minutes before sunset and 100 $^0/_0$ at 3 minutes before sunset (fig. 16). This is just the period when light intensity decreases fast. It seems reasonable to believe that the Ef is dependent either on a certain threshold or a certain rate of decrease in light intensity. If we consider the phenomenon part of the ascent, as it apparently is, there is reason to compare it with the ascent of *Aedes cantans* Meig. (Nielsen

& Greve, 1950). It is not known if the fibrillae are extended during ascent in that species, but the concurrent formation of low free swarms is easily observed. It was found highly probable that the most important factor for the initiation of ascent in *cantans* was the rate of change in light intensity combined with a delaying influence of low temperatures.

Table 3.

Extension of antennal fibrillae in male *A. caspius,* Oct. 20, 1955.

Minutes before sunset	Number of ten males with extended fibrillae
57	0
53	0
44	0
40	1
36	0
34	1
32	0
30	1
27	0
19	8
15	8
14	9
11	10

If we consider the different evenings it is easy to see that there is a considerable variation from day to day. The observations of October 20 (table 3) are of special interest. Up until 20 minutes before sunset only a few scattered males had bushy antennae. Then suddenly at 19 minutes before sunset 8 of 10 males had bushy antennae, and as early as 11 minutes before sunset all males had their fibrillae extended. An explanation is probably to be found in the unusual weather situation. The temperature remained high and the humidity low abnormally late and returned to normalcy quite suddenly between 30 and 15 minutes before sunset. There can hardly be any doubt that one or more of the climatic factors had inhibited the fibrillar extension. In analyzing this problem we attempted for all evenings of observation to find which of these factors was correlated in time with the appearance of bushy antennae. For criterion we used the moment at which Ef is 50 %, this being determined by drawing a free-hand curve through the observational points and finding the hour corresponding to the crossing of the line with the 50 % ordinate. The hour for Ef = 50 % on each of the seven evenings for which we had sufficient data was then plotted against the various physical factors. The only obvious correlation was with temperature, most pronouncedly with temperature 100 cm above ground.

At this point it might be worthwhile to summarize the concept of ascent derived from these and previous observations. It is a preamble to flight, either migratory (both sexes) or swarming, and includes at least three different phenomena: (1) gradual rising to the top of vegetation, (2) formation of low swarms over the ground, and (3) extension of the antennal fibrillae in males.

In *A. cantans* it was observed that after the emergence ended an increasing number of females remained at ground level. Since this species is usually not considered migratory, it is possible that the young females undertake an ascent without actually departing on a migratory flight, — they just remain in the tree tops. In both *A. caspius* and *A. taeniorhynchus*, however, the first ascent after emergence is followed by a departure. It is not likely that the males of *A. taeniorhynchus* have an ascent for swarming comparable to that before the migratory departure; *A. caspius* does have the ascent but not the low free swarms characteristic of the activity before actual swarming in *A. cantans*. Whether these different types of behavior are species characters or whether the different patterns are latent in all species but patent

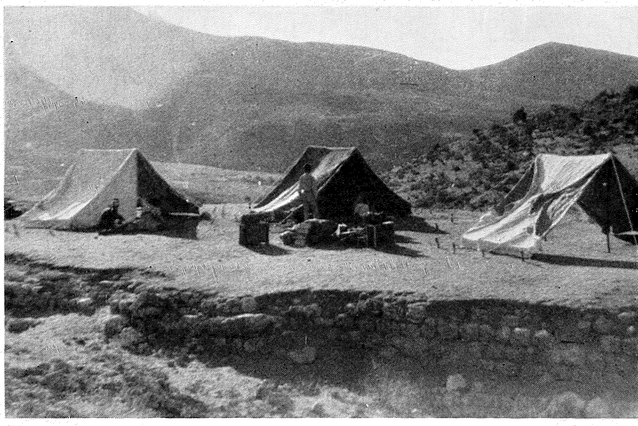

Fig. a. Camp at Shaikh'Adi on the roof of the old building. Seen towards SE

Fig. b. The old building on the roof of which we had the camp. Seen towards NNE. In the foreground the upper part of the path down the slope to the creek where the swarming was observed

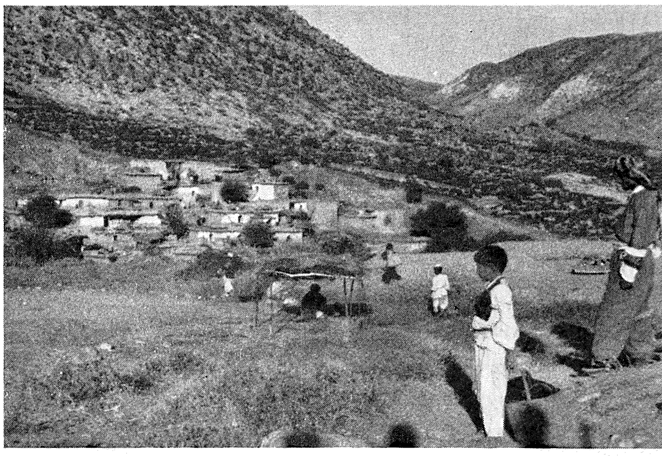

Fig. a. Ahmed's village, seen towards ESE

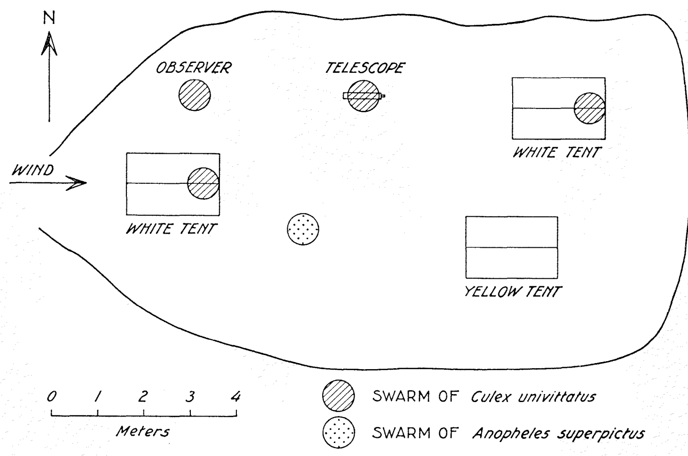

Fig. b. Sketch map of our camp at Shaikh'Adi only under certain conditions remains unknown until we know more of the behavior in widely varied ecological situations.

A few more remarks on the extension of antennal fibrillae are in order. This phenomenon has been described and interpreted, especially by Roth (1948), as a necessity in the preparation for mating. In *A. aegypti* and *Culex pipiens* (as to our observations on *Culex*, see below) the fibrillar extension is gradual during the first few days of adult life, then remains permanent. In *Anopheles quadrimaculatus* the extension takes place during the period of heightened activity at twilight. By removing parts or all of the flagellar segments of the antennae, Roth showed that the larger the extent of amputation the less became the ability to copulate, and after complete amputation the animals scarcely attempted to fly even when provoked. Since mating is initiated only in flight, both Roth's experiments and our observations demonstrate that extended fibrillae in the male mosquito indicates readiness for flight. Roth showed clearly that fibrillar extension is necessary for a male to become attracted to the flight tone of the female, but the ability to hear may also be important for other flight activities, especially swarming.

(b) Swarming.

By "swarm" is here understood a special type of flight performed by male mosquitoes (or other insects), usually in numbers, normally confined to a certain period of the twenty-four hour day, and performed within certain spatial coordinates, as if each individual were flying within an imaginary box. This "enclosure" may move somewhat in accordance with wind movements, etc., but its position is very often fixed by reference to a swarm-marker, an area of contrasting light and dark, or a vertical object protruding above the surroundings. In the latter case the swarm is called a "topswarm"; it is often formed above the tops of trees or larger bushes, or in the lee of these if the wind is strong. In other cases the aggregations of swarming mosquitoes constitute high "free swarms", seemingly independent of swarm-markers although found in the same places year after year. A special case of the free swarm is the "ceiling swarm", a vast cloud-like aggregation of swarming males high up in the air, sometimes with columnar, stalactitic protuberances. Flight action is faster during swarming and with many more short turns or circlings than in any other kind of flight; true swarming may thus be distinguished from the ground swarms during the ascent, or from the movements in a cloud of females about a blood source.

The term "swarming" has two connotations rendering it unfortunate. First of all, it gives the impression of some kind of mass behavior, implying that there is a certain amount of rapport between the individuals, a certain degree of gregariousness. This may be the case but there is no supporting evidence whatsoever, and it seems to us correct never to accept an explanation involving activities of higher complexity than absolutely necessary to cover the known facts. The only relevant evidence we have in this matter is that single mosquitoes have been frequently seen performing the well known swarming flight pattern by themselves. This has been noted by other observers as well (Frohne & Frohne, 1952).

The other unfortunate implication of the word swarming is that of epigamic behavior, in the minds of some authors (Bates, 1949). Nielsen & Greve, 1950, found that in *A. cantans* most matings occur elsewhere than in swarms. Although copulations were seen rather often during the ascent and early part of the swarming when males and females are both active, sexual activity was practically never seen in the most typical form of swarming such as the topswarms which occurred to some extent after the females had gone to rest in the evening and before they resumed activity in the morning. From this it was concluded that male swarming cannot be considered a part of sexual behavior, which viewpoint has been corroborated by observations of other species. However, some observers (Frohne & Frohne, 1952; Senior-White, 1953) have expressed doubt about this conception, and a paper is being prepared by the senior author, in collaboration with Mr. J. S. Haeger, which will analyze the problem further on the basis of more recent observations.

Mating was observed six times in *A. caspius*. It was seen twice during swarming, 18 minutes after sunset on Oct. 10 and 16 minutes after sunset on Oct. 14. It was observed during the ascent, 7 minutes before sunset on Oct. 14, and 10 minutes before sunset on Oct. 15, — in both cases well before swarming had begun. The two other matings were also during the ascent, Oct. 11, but 2 and 4 minutes after sunset, swarming having started at 3 minutes after sunset. These six matings were the only ones seen and they all occurred within four evenings; neither during the three weeks observations before October 10 nor during the 12 days after October 15 were other copulations seen, in spite of considerable effort, especially during the latter period, to observe the phenomenon.

Although we frequently saw males taking off shortly after sunset, the first sign of swarming was usually the humming and the swarms were normally free swarms so high that they were barely visible to the naked eye. This was the case on all calm evenings; when there was a little wind the swarms were usually a little lower. Many observations were made with field glasses, and to collect samples it was necessary to call the swarms down (Nielsen & Greve, 1950, p. 228). This was very easy as the males of *A. caspius* are extremely sensitive to a large variety of sounds besides the human baritone. Honking cars on the highway (only in some cases), crows, cows, but not donkeys, the barking of larger dogs, but not the yapping of smaller ones, voices of men — all changed the pitch of the humming. In some cases the change in pitch caught our attention before we noticed the noise. One evening (Oct. 7) the humming was continuously interrupted by grace notes, quick alterations to a lower pitch (mordents, ꟿ); they came with irregular intervals, about 30 per minute, and lasted quite some time. We were unable to find the cause but it was probably some noise we did not hear.

Swarming usually began shortly after sunset, the average of 25 evenings being $3^1/_2$ minutes after sunset. The earliest swarm beginning was two minutes before sunset (Oct. 26) and the latest, 12 minutes after sunset (Oct. 8) (See also table 4, below). The cessations of swarms was very close to the end of twilight 25 minutes after sunset; it averaged $26^1/_2$ minutes after sunset and varied from 18 to 32 minutes after sunset. The swarm duration then averaged 23 minutes. The very small swarms of Oct. 2—3, before the new brood appeared, were the shortest, lasting 15 and 10 minutes; the maximum of swarms was 33 minutes, on October 26. The midpoint of the swarming varied less, averaging 15 minutes after sunset and varying from 11 to 20 minutes after sunset.

Earlier swarming studies had impressed upon us the fact that many other biological phenomena are synchronized at sunset. In Denmark the swarming of *A. cantans* coincided with the activity of swallows, green frogs, bats, and goatsuckers; in Florida, fireflies appeared five minutes before the end of *A. taeniorhynchus* swarming. In Abu Ghraib, the magpies, after a very noisy spell, often came to rest in the middle of *A. caspius* swarming. The jackals began their evening song when swarming ended; in 28 nights swarming ended $26^1/_2$ minutes after sunset

Table 4.

Swarming in relation to sunset (+ minutes after, — minutes before sunset); observations in Iraq. The uncorrected figures for Shaikh'Adi are in parentheses.

	Number of Observations	Commencement Average	Commencement Earliest	Commencement Latest	Cessation Average	Cessation Earliest	Cessation Latest	Duration Average	Midpoint Average
Aedes caspius	28	+ $3^{1}/_{2}$	+ 2	+12	+$26^{1}/_{2}$	+18	+32	23	+15
Culex univittatus 1)	3	+ 2	0	+ 3	+20	+15	+25	18	+11
Culex univittatus 2)	4	+18 (+55)	+13	+25	+25 (+62)	+20	+31	8	+22 (59)
Culex univittatus 3)	4	+ 3 (+40)	+ 1	+ 5	+29 (+66)	+20	+39	26	+16 (53)
Culex theileri	10	+12	+10	+17	+33	+29	+38	21	+23
Anopheles superpictus 4)	6	— 3 (+34)	—10	+ 3	+29 (+66)	+26	+38	26	+16 (50)
Anopheles superpictus 5)	3	+ 3 (+40)	— 1	+ 6	+21 (+58)	+14	+30	18	+12 (49)

1) Swarm over ditch, Abu Ghraib.
2) Over tent, Shaikh'Adi.
3) At creek, Shaikh'Adi.
4) At creek, Shaikh'Adi.
5) Between tents, Shaikh'Adi.

sunset as an average, while the average for first jackal singing was 27 minutes after sunset. On one evening (Oct. 18) the jackals were all of 10 minutes early, while on October 21 they were the extreme of 24 minutes late.

4. Activity Patterns.

After swarming the males came to a relative rest and most of them retracted their antennal fibrillae. The repose was far from complete, however, and they frequently moved or flew about, mostly in the upper parts of the *Sesbanias*. The females did likewise. Around midnight there were still a few flying about. We have only six morning observations (Sept. 19, 24; Oct. 8, 11, 13, 24). Before dawn the mosquitoes were resting low in the grass and were difficult to stir up, but as sunrise neared there was a tendency toward increased activity. On Oct. 11 there was a slight ascent until 10 minutes before sunrise, followed by a slight descent. On Oct. 13, with the temperature about 10^0, none of the mosquitoes were seen higher than 100 cm from the ground, while on Oct. 24, with a slightly lower temperature of 8.6^0—9.7^0 hardly any *A. caspius* were seen except low in the grass, — while *Culex* made its usual topswarm (see below).

The absence of morning swarms in *A. caspius* nevertheless was not the result simply of low temperature, because we had not found any swarming on the morning of Sept. 19 when the temperature was 19^0—20^0. We had also looked in vain for morning swarms at Shaikh'Adi in Kurdistan (see below). As we have no reason to believe that either temperature or humidity should reach more critical levels in the morning than in the evening, we are left with no easy explanation for the absence of morning swarms in all Iraqi mosquitoes but *Culex*. In this respect as well as in many others an investigation of the habits of *A. caspius* in the northern part of its distribution would be extremely desirable.

5. Food Habits.

We spent considerable time searching for the food source of the adults. The possibilities during the season were, indeed, few. The flowers of *Sesbania* were the most conspicuous nectar source, but the papilionaceous flowers seemed inaccessible to the mosquitoes and none were ever found feeding on them although many flew about the flowering buds in a manner suggestive of the feeding drive. It was not until Oct. 19 that we first discovered a nectary on the underside of the first pair of leaflets: the basal fourth of the midrib becomes dark green, swollen, and glasslike, and a drop is formed at the distal end of this swelling (pl. 6, fig. c). These *Sesbania* nectaries are found only during the period when the axillary flower clusters are in bloom.

The drops from these nectaries were very sweet to the taste and mosquitoes were several times observed feeding on them. Feeding on extrafloral or rather extranuptial nectaries had been reported earlier for *A. taeniorhynchus* by Haeger (1955). During the subsequent days we made many notes on the nectar drops, which varied in both size and numbers. They were most abundant in late afternoon, but it was not possible to decide from our observations whether the scarcity of nectar at other times was the result of a reduced production by the plant or of an increased consumption by mosquitoes and other animals.

Swarming of *Culex univittatus* Theob.

A swarm of this species was observed on October 21 and 22 over the main ditch ("2" in sketch map, fig. 1, p. 283) at the Abu Ghraib study area. The bushes here formed a gap like a window opening towards the west, thus facilitating observation considerably. The swarm was very low, about at eye level to an observer sitting on the ditch bank. On Oct. 21 swarming started 2 minutes after sunset and lasted until the end of twilight. There were never more than 5 or 7 mosquitoes in the swarm.

Swarming and ascent in *Culex theileri* Theob.

On October 14, again at Abu Ghraib, a topswarm was spotted over a *Sesbania* ("4", fig. 1) which looked different from the free *A. caspius* swarms. It proved to be *Culex theileri*. It normally comprised 20—30 individuals, so it is not likely that it should have been previously overlooked. One or two smaller swarms of this species sometimes occurred over other nearby *Sesbanias*.

Swarming of this mosquito was observed ten nights and found to be later than that of *A. caspius*. It started $11^1/_2$ (10—17) minutes after sunset and ended 33 (29—38) minutes after sunset; this meant starting and stopping 8 and 7 minutes later than *A. caspius*. The duration of *Culex theileri* swarms, $21^3/_4$ minutes, was a minute and a half shorter than the duration af *A. caspius* swarms.

The only morning observation was on Oct. 24 when the swarm was observed between 32 and 19 minutes before sunrise.

This species differed from *A. caspius* in the ascent also. Roth (1948) states that after the first few days *Culex pipiens* males have their antennal fibrillae always extended. However, we found *Culex theileri* extending their fibrillae in the evening. Compared to *A. caspius*, who first extended their fibrillae after they had moved up to the upper leaves of the *Sesbanias*, *C. theileri* males extended them while lower down in the vegetation, usually in the grass.

We have no further information on this species from Abu Ghraib. Their breeding places were never found.

Observations at Shaikh'Adi.

During the week of September 6—13, 1955, we camped in the foothills of the Kurdish mountains, 58 km north of Mosul, 11 km north of Ain Sifni, on the road to Atrush (fig. 17 and pl. 7, fig. a). The elevation was 700—800 m. and the coordinates 36° 52' N and 43° 31' E.

We were in the sanctuary of the Yessidis, named Shaikh'Adi after the founder of this religion of devil worshippers, whose tomb was here. From the holy springs

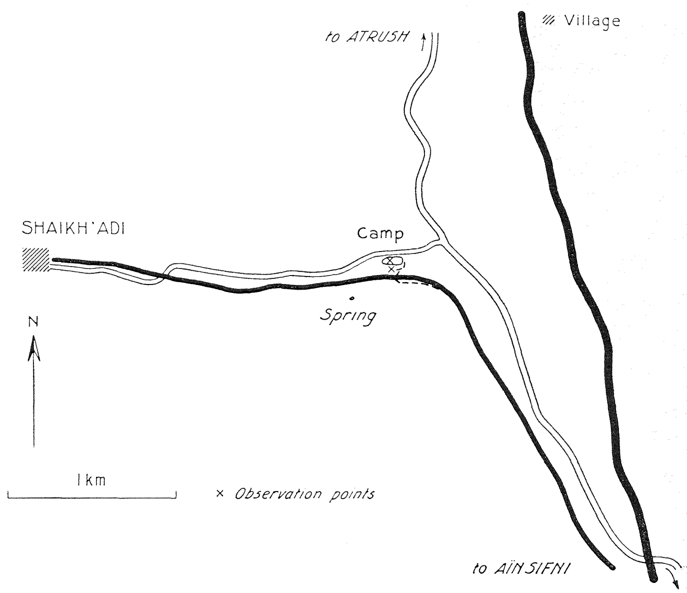

Fig. 17. Sketch Map of Shaikh'Adi.

of Shaikh'Adi a creek ran eastward through a small valley. Another spring arose on the south slope 3 km from the sanctuary. Opposite this latter spring, where the valley was somewhat more open, there was a rather large building half built into the slope so that the roof formed a little plateau close to the sanctuary road. Women from a village some 4 km northwest travelled this road to the spring where they obtained good drinking water. The building was said to have been built for pilgrims to Shaikh'Adi. It was now used only by a local shepherd who rested here during the noon-time heat with his flea-ridden goats, sheep, and cows.

We had our camp on the plateau-like roof of the building (pl. 7, figs. a and b) above mentioned, and our observations were made either there or on the slope between the camp and the creek. While most of this region is rather barren, there is a rich vegetation along the creek, including oaks, figs, and several other trees. In and around the sanctuary there is a wonderful, shady woods, with many kinds of beautiful trees. On the south slope opposite our camp there were rice fields irrigated by the spring.

1. True and apparent Sunset and Swarms.

Not having a radio with us, we had to rely on our wristwatches for time determination, and we observed sunset on most evenings as we later did in Abu Ghraib (see above). Since the point where we saw the sun disappear was the top of the hills behind the sanctuary of Shaikh'Adi, evidently well above the horizon, the observed sunset was somewhat earlier than the true sunset. This confronted us with two problems of some importance: (1) Was the sky light as we measured it with a horizontally placed photocell influenced by the early apparent sunset? And (2) is the swarming of mosquitoes dependent on the observed or the true sunset?

We tried to measure the angular height of the apparent horizon above the true one by means of an improvised level, a scaled plumb line and a telescope with cross-hairs. The distance to the hill top could only be estimated from a map, so the determination of the apparent horizon could obviously be only a rough estimate. We found the angle to be about 8^0 and the apparent sunset consequently about 40 minutes early. Later calculations (Tide Tables, 1955) showed the observed sunset to have been 36—38 minutes early.

We also measured simultaneously the diffused zenith light at the camp and in the more open valley about one km to the east and found that although the apparent sunset was seven minutes later in the open area, the illumination was practically the same.

A glance at fig. 18 shows clearly that the curve for the change in light intensity will agree perfectly with

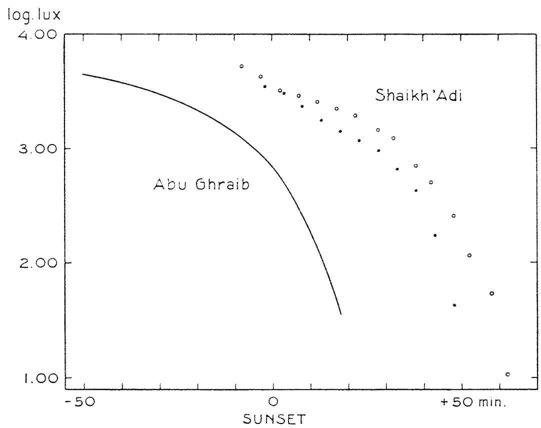

Fig. 18. Change of light at Shaikh'Adi around sunset, compared to Abu Ghraib.

the curve later established for Abu Ghraib if the sunset is corrected about 35 minutes. There is thus no doubt that the diffuse light from the sky as we measure it is independent of the apparent sunset and only dependent on the true sunset.

As to the swarming of mosquitoes, it will be recalled that in Abu Ghraib the midpoints of swarming for the three species were 11, 15, and 23 minutes after sunset. In Shaikh'Adi the range was 49—59 minutes after the apparent sunset, which would be 12—22 minutes after the true sunset if we assume the apparent sunset to be 37 minutes sooner. The different figures will be discussed in more detail below, but the averages just given so clearly indicate the true rather than the apparent sunset to be the important one to swarming that in all that follows time in relation to sunset is given as the observed minus 37 minutes.

It is really noteworthy that both swarming and light intensity are dependent on the true sunset. This increases the probability that illumination or change in illumination is a causative factor in swarming. It also contributes further to the reliability of measuring the diffuse light from the sky as an expression of the relevant illumination.

In the preceding paragraphs we have considered the swarming of different mosquito species in a combined sense as occurring simultaneously, which, of course, is not so. We have already shown that in Abu Ghraib the topswarms of *C. theileri* were consistently a few minutes later than the low swarm of *C. univittatus* and the high, free swarms of *A. caspius.*

2. Culex Swarms.

At Shaikh'Adi *C. univittatus* formed swarms low over the slope down toward the creek. This presented an unusually good opportunity for observation from a convenient point (pl. 7, fig. b). In Abu Ghraib the swarms were over a ditch; at Shaikh'Adi they were unmistakably formed over light-colored swarm-markers: a stone, the net, or the head of the observer. On Sept. 7 and 9 the males of this species swarmed under a large swarm of *Anopheles superpictus.* At times the *Culex* swarm would rise and disappear into the *Anopheles* swarm for a short while, and sometimes only single individuals would mingle with the higher swarm. When through swarming the *Culex* males usually sat down on the ground briefly before flying away.

The low, free swarms of *C. univittatus* over the slope to the creek commenced a few minutes before the (true) sunset just as those in Abu Ghraib but lasted somewhat longer (26 minutes against 18, see table 4). This was probably due to the larger number of participating individuals. As pointed out by Nielsen & Nielsen (1953), the duration of swarms is positively correlated with the number of individuals as a consequence of the greater spread of individual ranges in sensitivity to the causative stimuli. Swarming time for *C. univittatus* is also seen to be very nearly the same as that for the high, free swarms of *A. caspius,* but definitely different from the swarming time of *C. theileri.*

We also found *C. univittatus* swarms over the tents in the camp (pl. 8, fig. b). We had three 2-man tents, two white and one dark yellow. Swarms formed over the white tents only and also over the white telescope on a tripod and over the head of the observer. As was the case on the slope, this species was swarming over swarm-markers. These swarms were late and of short duration, — only 6, 9, 7, and 9 minutes for the four evenings although the number of participants, 20—50, was quite high. In their lateness, these swarms resembled *C. theileri* more than the previously described swarms of the same species. A tentative explanation may be in the different illumination at the sites of swarming. We do not have light measurements on the slope, but the segment of sky visible from the observation point was much smaller than at the camp and the illumination, as a function of the diffused light from the sky, must have been correspondingly lower. If both commencement and cessation of swarming are determined by certain illumination thresholds, so that swarming occurs during a finite period of illumination, this period would definitely be later in the camp than on the slope. It would furthermore be considerably shorter because the rate of change in light intensity, dependent on the sun's angular movement in relation to the horizon, increases in velocity until near the end of twilight.

Although all observers have found a certain relationship between swarming and light conditions it has never been clearly shown whether the relevant factor is a certain threshold or a certain rate of change in light intensity. *Aedes cantans* (Nielsen & Greve, 1950) showed no clear correlation between start of swarming in the evening and light intensity, and since activity could, furthermore, be induced by any change in light intensity irrespective of the initial intensity, the authors concluded that evening swarms were most likely initiated by a certain rate in change of illumination. The cessation of these swarms, however, seemed to take place at a certain light intensity. In the morning, there was some indication of a threshold of illumination for the beginning but not for the cessation of swarming.

The observations of *C. univittatus* swarming described above are most easily understood if we assume a dependence of both commencement and cessation of evening swarms on certain thresholds of light intensity.

3. Anopheles Swarms.

Anopheles superpictus Grassi swarmed in the same places as *Culex univittatus*. However, at camp the single swarm was not over but between tents, and neither here nor on the slope were we able to detect any kind of swarm-marker on the ground except in the case, mentioned above, where *Culex* was svarming under the *Anopheles* swarm, — which was probably accidental.

The several swarms on the slope were formed every evening in the same places. During the last half of the swarming period individuals from swarms higher up the slope would join the swarm under observation. At the same time other individuals would leave the observed swarm and fly down to other swarms closer to the creek.

Not all departures from swarms were of this kind; many individuals were seen leaving the swarm and dropping to the ground and resting there 10—15 seconds. This was particularly the case on windy evenings when in gusts the whole swarm would move down close to the ground.

In addition to the swarming mosquitoes, many individuals were flying hither and thither between and through the swarms. During the six evenings of observation, mating occurred twice in the swarms; the mated pairs dropped out of the swarm to the ground. On September 12 it was noted that the movement of the swarming males slowed down towards the end of the swarming period, gradually assuming a more normal flight.

The males swarmed approximately simultaneously on the slope and at the camp, but the duration of the several swarms on the slope averaging 26 minutes, was considerably longer than that of the single swarm between tents at the camp, averaging 18 minutes. If the difference in swarming time of *C. univittatus* in different places is to be explained as the effect of a dependency on certain light intensity thresholds, it is evident that *A. superpictus* swarming simultaneously at the identical places must depend on the rate of change in light intensity rather than on thresholds. The rate of change in illumination, expressed as log lux, is independent of differences in actual illumination caused by shading objects.

4. Morning observatinos.

Observations were made on three mornings and no swarms whatsoever were seen.

Summary.

Observations are reported on the ethology of *Aedes caspius* and on the swarming habits of this species and of *Culex theileri*, *Culex univittatus* and *Anopheles superpictus*. The observations

were made some west of Baghdad and some in the hills north of Mosul.

The temperature relationship to the duration of the pupal stage was determined for *Aedes caspius*. This species was found to feed on the extrafloral nectaries of *Sesbania.*

It was found that an extension of the fibrillae on male antennae took place during the pre-swarming period.

The influence of light and temperature on the ascent and on swarming upon the various types of swarm was studied.

It was established that mosquito swarming was related in time to the true sunset rather than to an apparent sunset caused by hills on the horizon, and that the mosquitoes respond to the diffused light from the sky.

The climatic and light factor in the twilight picture were studied in some detail.

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