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STUDIES ON WEST AFRICAN FOREST MOSQUITOS.
PART II.—THE LESS COMMONLY OCCURRING SPECIES.

BY

P. F. MATTINGLY.

(From the *Yellow Fever Research Institute, Yaba, Lagos, Nigeria.*)

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STUDIES ON WEST AFRICAN FOREST MOSQUITOS.
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The details of the area studied and of the techniques employed have already been given elsewhere (Mattingly, 1949) and will be repeated here only in outline. The Field Station, consisting of a single tree fitted with four platforms, at ground level, 22 ft., 40 ft. and 52 ft., respectively, was situated on the left bank of the Ogun River about three miles from the point at which it flows into Lagos Lagoon, S. Nigeria. Each platform was designed to hold two Africans whose duty it was to catch mosquitos on themselves and on one another. Each individual catch was continued for 24 hours without a break, during which time the boys were kept under constant supervision. Every two hours the boys were changed from one platform to another in order so far as possible to eliminate artificial periodicities due to variations in individual attractiveness to mosquitos or other causes. The mosquitos were collected punctually at the end of each hour and at the same time hourly psychrometer readings were taken. The biting cycle of each species, as defined later, was determined by summing the total numbers of that species biting during each hour over a series of 22 catches. The figures were broken down by platforms to obtain vertical distribution data and, to secure a picture of the seasonal variation in numbers, the monthly totals were divided by the number of catches made in each particular month.

The Mosquito Population.

The four species *Taeniorhynchus africanus*, Theo., *Anopheles hargreavesi*, Theo., *Anopheles gambiae*, Giles, and *Aedes africanus*, Theo., have already been discussed in detail (Mattingly, 1949) and will be referred to in the present paper only incidentally. Of the remaining species, which are listed below, only the first ten were sufficiently abundant to afford a reliable indication of their biting cycles and vertical distribution. The full list of species taken was as follows:—

- | | |
|--|---|
| <i>Anopheles (A.) paludis</i> , Theo. | <i>Aedes (Finlaya) ingrami</i> , Edw. |
| <i>Anopheles (Myzomyia) moucheti</i> var. <i>nigeriensis</i> , Ev. | <i>Aedes (Stegomyia) apicoargenteus</i> , Theo. |
| <i>Aedomyia africana</i> , N.-L. | <i>Aedes (Aedimorphus) punctothoracis</i> , Theo. |
| <i>Aedes (Mucidus) grahami</i> , Theo. | <i>Aedes (Aedimorphus) domesticus</i> , Theo. |
| <i>Aedes (Aedimorphus) nigricephalus</i> , Theo. | <i>Aedes (Aedimorphus) albocephalus</i> , Theo. |
| <i>Aedes (Aedimorphus) irritans</i> , Theo. | <i>Aedes (Banksinella) punctocostalis</i> , Theo. |
| <i>Aedes (Banksinella) circumluteolus</i> , Theo. | <i>Culex (Neoculex) andreanus</i> , Edw. |
| <i>Aedes (Diceromyia) flavicollis</i> , Edw. | <i>Culex (Neoculex) rima</i> , Theo. |
| <i>Aedes (Diceromyia) taylora</i> , Edw. | <i>Culex (Neoculex) subrima</i> , Edw. |
| <i>Culex (Culex) thalassius</i> , Theo. | <i>Culex (Neoculex) insignis</i> , Cart. |
| <i>Anopheles (A.) coustani</i> var. <i>ziemanni</i> , Grünb. | <i>Culex (Neoculex) sunyaniensis</i> , Edw. |
| <i>Anopheles (A.) obscurus</i> , Grünb. | <i>Culex (Neoculex) wigglesworthi</i> , Edw. |
| <i>Anopheles (Myzomyia) nili</i> , Theo. | <i>Culex (Mochthogenes) inconspicuus</i> , Theo. |
| <i>Anopheles (Myzomyia) pharoensis</i> , Theo. | <i>Culex (C.) poicilipes</i> , Theo. |
| <i>Uranotaenia pallidocephala</i> , Theo. | <i>Culex (C.) decens</i> , Theo. |
| <i>Uranotaenia philonuzia</i> , Edw. | <i>Culex (C.) perfuscus</i> , Edw. |
| <i>Uranotaenia annulata</i> , Theo. | <i>Culex (C.) perfidiosus</i> , Edw. |
| <i>Uranotaenia ornata</i> , Theo. | <i>Culex (C.) guiarai</i> , Bl. |
| <i>Ficalbia (Mimomyia) hispida</i> , Theo. | <i>Culex (C.) ingrami</i> , Edw. |
| <i>Ficalbia (Mimomyia) mimomyiaformis</i> , Newst. | <i>Culex (C.) philipi</i> , Edw. |
| <i>Ficalbia (F.) uniformis</i> var. <i>malfeysi</i> , Newst. | <i>Taeniorhynchus (Coquillettidia) metallicus</i> , Theo. (males only). |
| <i>Taeniorhynchus (Coquillettidia) annetti</i> , Theo. | <i>Ficalbia (Mimomyia) pallida</i> , Edw. (male only). |
| <i>Taeniorhynchus (Coquillettidia) aurites</i> , Theo. | <i>Aedes (Aedimorphus) tarsalis</i> , Newst. (male only). |
| <i>Taeniorhynchus (Mansonioides) uniformis</i> , Theo. | |
| <i>Aedes (Finlaya) longipalpis</i> , Grünb. | |

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A number of specimens of *Anopheles obscurus* was of the form described as "var. *nowlini*" by Evans (1932) but stated by De Meillon (1947) to vary in the characters originally regarded as diagnostic. The specimens of *Aedes grahami* corresponded in general with the pale form described by Edwards (1941) but had many pale scales on the costa and a variable number of pale scales in the dark area on the front tibia.

Aedes taylori, as recorded by Lewis (1945) from the Sudan, had numerous scattered pale scales on the dorsal surface of the abdomen and their identity was established by examining the terminalia of the males by which they were accompanied. The members of the *Culex rima* group (*Culex rima*, *subrima*, *insignis*, *sunyaniensis* and *wigglesworthi*) were also separated by the characters of the male terminalia and it was not found possible to identify the females with confidence. The same was true of *Culex perfuscus* and *C. perfidiosus*. All the available data regarding the less abundant species are summarised in Table I which shows the numbers taken and the date, time and platform on which or at which they occurred. All times given throughout the present paper are Local Mean Time and represent the times at which the mosquitos were collected from the platforms, i.e., the ends of the one-hourly periods during which they were taken into the collecting tubes by the boys. The platforms are numbered in ascending order from the ground upwards, i.e., the ground platform is numbered I, the 22 ft. platform II, the 40 ft. platform III and the top platform at 52 ft. IV.

Males.

Except where otherwise stated, all remarks made and figures given in the present paper refer to female mosquitos only. Males of a number of species were, however, taken and in three species, *Taeniorhynchus africanus*, *Aedes flavicollis* and *A. taylori*, they were abundant. Table II shows the vertical distribution of males of these three species and the proportions of the total catch occurring during each hour. It will be noted that in each case the proportion of the total catch of males taken during the hour after sunset (hour ending 19.15) is very much greater than in the case of the females. The vertical distribution of the two sexes is also somewhat different. Thus, the majority of the females of *Taeniorhynchus africanus* occur on the ground whilst the males occur in greatest abundance on the two middle platforms. As against this, however, the proportion of females occurring on the middle platforms is very much greater during the two hours following sunset than at other times during the night (Mattingly, 1949). The great concentration of both males and females on the middle platforms during this period strongly suggests a swarming activity associated with mating. In the case of *Aedes flavicollis* and *A. taylori*, which are predominantly tree-top biters, the vertical distribution of the females is not very markedly different during the early hours of darkness from the remainder of the night. All that can be said is that, in general, it agrees fairly closely with that of the males and so is not at variance with a hypothesis which postulates the occurrence of mating or other activities associated with swarming during the early part of the night (Table VI).

Other species of which males were taken are given in Table III.

Rainfall and seasonal Distribution.

The seasonal distribution curves shown in fig. 1 are based on average monthly catches, i.e. on the monthly totals divided, in each case, by the number of catches made during the month in question. The figures on which the curves are based are given in Table IV. The rainfall curve superimposed for purposes of comparison on the distribution curves is based on figures given in Mattingly (1949). No catches were made during December 1945 and January 1946. The dates given in Table IV refer to the days on which the catches were begun. Since each catch was begun at

TABLE II.
Distribution of male mosquitos at Itowolo.

Species	Platform	Time (L.M.T.)												07.15			
		16.15	17.15	18.15	19.15	20.15	21.15	22.15	23.15	00.15	01.15	02.15	03.15		04.15	05.15	06.15
<i>T. africanus</i>	IV	—	—	—	4	3	1	0	4	2	2	1	5	4	2	1	29
	III	—	—	—	23	19	10	8	17	8	10	12	10	3	3	2	125
	II	—	—	—	45	30	14	13	19	13	10	12	18	8	13	1	198
	I	—	—	—	5	14	14	3	8	8	9	1	10	9	8	2	97
	Total	1	1	5	77	66	39	24	48	31	31	26	43	24	26	6	449*
% of Total Catch	0.2	0.4	1.1	17.1	14.7	8.7	5.3	10.7	6.9	6.9	5.8	9.6	5.3	5.8	1.3	99.8%	
<i>Aë. flavicollis</i>	IV	—	—	2	73	23	4	4	5	5	5	6	7	6	3	—	146
	III	—	—	6	75	15	5	5	5	3	4	4	3	2	1	—	126
	II	—	—	1	10	10	2	—	1	1	1	2	—	1	—	—	28
	I	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1
	Total	0	0	9	159	48	11	9	11	10	9	12	10	9	4	0	301
% of Total Catch	0.0	0.0	3.0	52.8	15.9	3.7	3.0	3.7	3.3	3.0	4.0	3.3	3.0	1.3	0.0	100.0%	
<i>Aë. taylori</i>	IV	—	—	3	41	15	4	4	7	4	1	—	1	1	—	—	79
	III	—	—	2	40	13	2	3	2	2	1	—	—	2	1	—	67
	II	—	—	—	12	7	—	—	1	—	—	—	—	1	—	—	24
	I	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
	Total	0	0	5	93	35	6	7	8	6	6	2	0	1	4	2	0
% of Total Catch	0.0	0.0	2.9	54.7	20.6	3.5	4.1	4.7	3.5	3.5	1.2	0.6	2.4	1.2	0.0	0.6	100.0%

* 1 male of *T. africanus* was taken on platform I during the hour ending 15.15. No males of *A. flavicollis* or *A. taylori* were taken after 07.15.

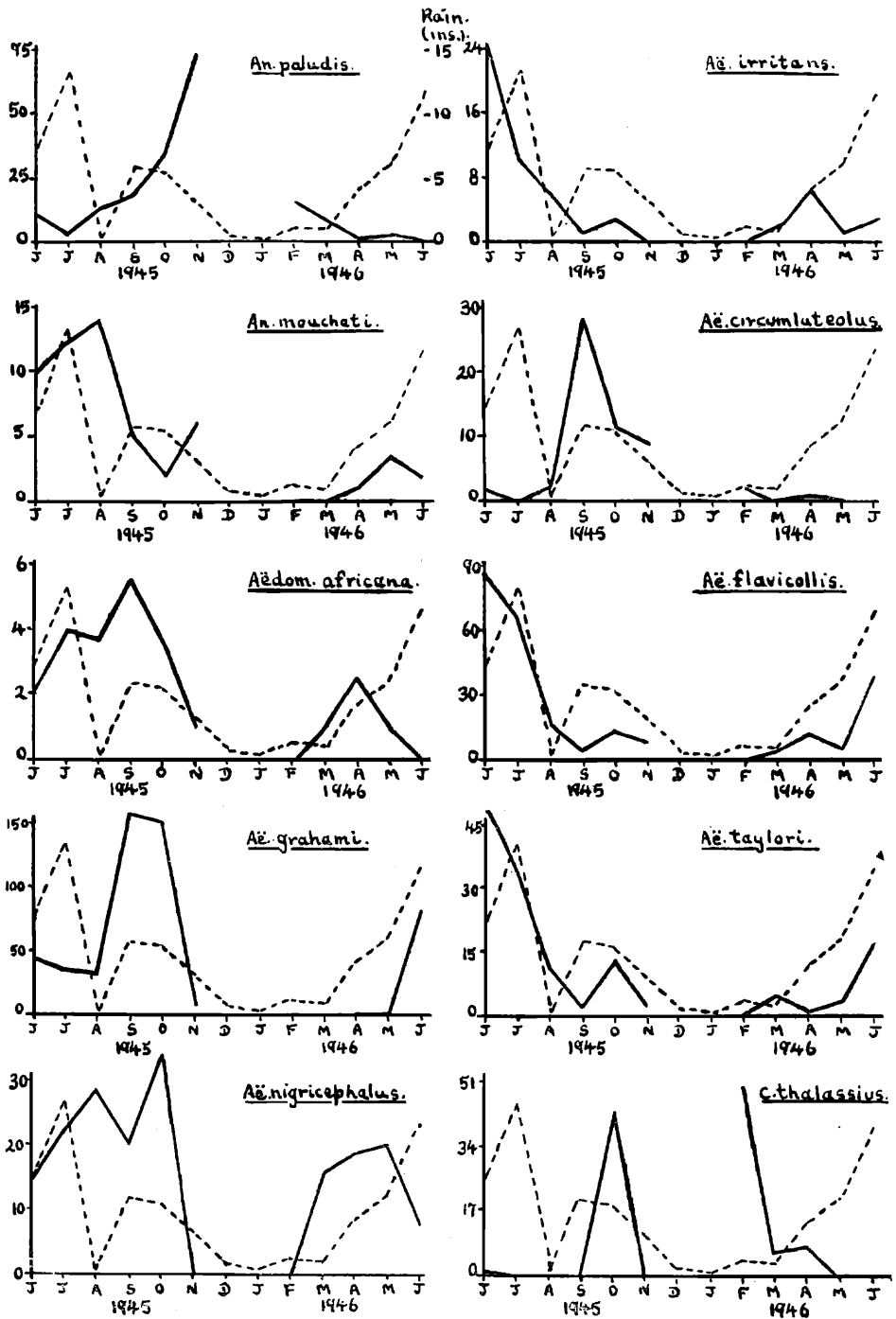


Fig. 1.—Seasonal distribution at Itowolo. (Rainfall indicated by broken line.)

15.15 hours on one day and continued until 15.15 hours on the next, each catch covered two successive days. The curves for *Aedes flavicollis* and *A. taylori*, the only two tree-hole breeders shown, should be compared with that for *A. africanus* (Mattingly, 1949), also a tree-hole breeder. The resemblance is very close. It will be noted that the species in question are most abundant before the occurrence of maximum rainfall in July, although in all the other species the period of abundance follows the period of maximum rainfall. As against this a small secondary peak occurs at the end of October and follows the "small rains". It appears likely from this that the optimum rainfall for these species is well below the maximum which actually occurs and that, whereas sufficient rain to fill the tree-holes is required, too much will wash them out. Alternatively if a long breeding cycle is envisaged it may be that the peak rainfall in July coincides with a period of exhaustion of the breeding-places following on the initial stimulus provided by the onset of the rains in April. *Aedes irritans*, a crab-hole breeder, shows a similar curve and here the same arguments would apply. *Anopheles paludis* shows a very marked dry season peak and resembles in this respect *A. hargreavesi* and *Taeniorhynchus africanus* (Mattingly, 1949), a fact which probably indicates a similarity in breeding-places, but *Aedomyia africana*, which also breeds in *Pistia*, has quite a different type of curve. The accumulation of large masses of *Pistia* in the creeks around Itowolo is bound up with their closure and isolation from the river during the dry season. Heavy flood water tends to sluice them out. *Aedes grahami*, a ground-pool breeder with a cannibalistic larva, reaches its peak well after *Anopheles gambiae*, and the reduction in numbers of the latter species after the middle of August may be accounted for in part by the presence of larvae of *A. grahami* in its breeding-places.

Other meteorological and microclimatic data are given in Mattingly (1949).

Biting Cycles.

A discussion of the precise implications of the term "biting cycle" will be found at the end of the present paper. For practical purposes it may be taken to imply the hour to hour changes in the numbers of any particular species taken during the course of a standard twenty-four hour catch. Where, as in the present instance, a number of such catches are made, the series of biting cycles can be combined to give a single mean biting cycle by adding the twenty-four separate sets of figures corresponding to the twenty-four hours. The figures for all four platforms may be combined in the same way or kept separate as desired. The figures given in Table V represent the mean biting cycles of the species concerned and are based on all four platforms combined. To facilitate comparison, the hourly totals have been reduced to percentages of the grand total. Fig. 2 shows the curves based on these figures. In order to smooth and simplify them they have been based on two-hourly aggregates. This has necessitated choosing between curves based on the assumption that the mosquitos were collected at the end of the odd hours (17.15, 19.15, 21.15, etc.), or at the end of the even hours (16.15, 18.15, etc.). In each case the choice made has been such as to give the most faithful picture of the biting cycle as revealed by the hourly figures but the method of grouping inevitably leads to some loss of significant detail and the curves should be regarded only as diagrams.

Aedes grahami.

This was easily the most abundant tree-top biter at Itowolo. Its mean biting curve (fig. 2) resembled to some extent that of *Anopheles gambiae* (Mattingly, 1949) but the peak biting time occurred an hour earlier. At this time marked peaks were recorded from both the upper platforms but the peak on platform II occurred an hour earlier still. The peak hour was not constant from catch to catch. Haddow (1945 & 1947) gives small figures from Uganda which appear to indicate a peak occurring during the 4-hour period 22.00-02.00 hours.

TABLE V.
Hourly and 2-hourly biting cycles at Itwolo.

Time (L.M. T.)	<i>A. paludis</i> . %	<i>A. moucheti</i> %	<i>Aedom. africana</i> %	<i>Aë. grahami</i> %	<i>Aë. nigri- cephalus</i> %	<i>Aë. irritans</i> %	<i>Aë. circum- luteolus</i> %	<i>Aë. flavicollis</i> %	<i>Aë. taylori</i> %	<i>Cu. thalassius</i> %
16:15	0.3	0.0	0.0	0.0	2.4	3.7	3.9	0.1	0.3	1.2
17:15	1.0	0.0	0.0	0.3	4.9	9.9	9.7	0.0	0.0	0.0
18:15	1.0	0.0	0.0	0.4	6.8	14.9	15.5	0.1	0.0	1.2
19:15	6.6	0.0	8.3	1.2	7.5	8.0	3.9	14.1	11.5	18.0
20:15	2.7	2.0	38.3	3.0	9.0	1.2	1.0	13.2	11.5	23.0
21:15	8.0	3.3	15.0	3.0	5.9	1.9	6.8	9.4	9.4	10.6
22:15	7.6	4.0	8.3	6.9	5.2	1.9	8.7	7.5	9.6	8.1
23:15	9.3	3.3	3.3	11.6	8.0	0.6	3.9	8.9	10.2	6.8
00:15	12.3	2.6	13.3	10.0	5.9	3.1	7.8	6.3	6.0	12.4
01:15	9.6	4.6	3.3	16.6	6.6	1.2	1.9	7.3	8.9	5.0
02:15	8.6	8.6	3.3	12.7	3.5	0.6	1.9	7.3	7.8	5.0
03:15	6.6	11.9	1.7	12.9	6.1	1.2	0.0	9.4	7.6	4.3
04:15	6.6	12.6	3.3	17.2	5.0	3.1	3.9	10.6	9.4	7.5
05:15	5.3	29.1	1.7	8.0	5.4	1.9	1.9	4.5	6.8	4.3
06:15	8.6	10.6	0.0	0.6	2.8	6.2	2.9	1.2	1.3	1.2
07:15	0.7	11.3	0.0	0.4	4.0	14.9	2.9	0.0	0.0	2.5
08:15	1.7	1.3	0.0	0.2	3.3	9.3	6.8	0.0	0.0	0.6
09:15	1.0	0.7	0.0	0.3	2.6	5.6	3.9	0.0	0.0	0.6
10:15	0.7	0.0	0.0	0.3	0.7	2.5	2.9	0.0	0.0	0.6
11:15	0.7	0.0	0.0	0.0	0.9	3.1	2.9	0.0	0.0	0.0
12:15	0.7	0.7	0.0	0.3	0.2	0.0	2.9	0.0	0.0	0.0
13:15	0.0	0.7	0.0	0.2	0.9	0.6	0.0	0.0	0.0	0.6
14:15	0.3	2.0	0.0	0.1	1.9	2.5	1.9	0.0	0.0	1.2
15:15	0.7	1.3	0.0	0.2	0.5	1.9	1.9	0.0	0.0	0.0
Total	99.9	100.0	99.8	100.1	100.0	99.8	99.8	99.9	100.3	99.8

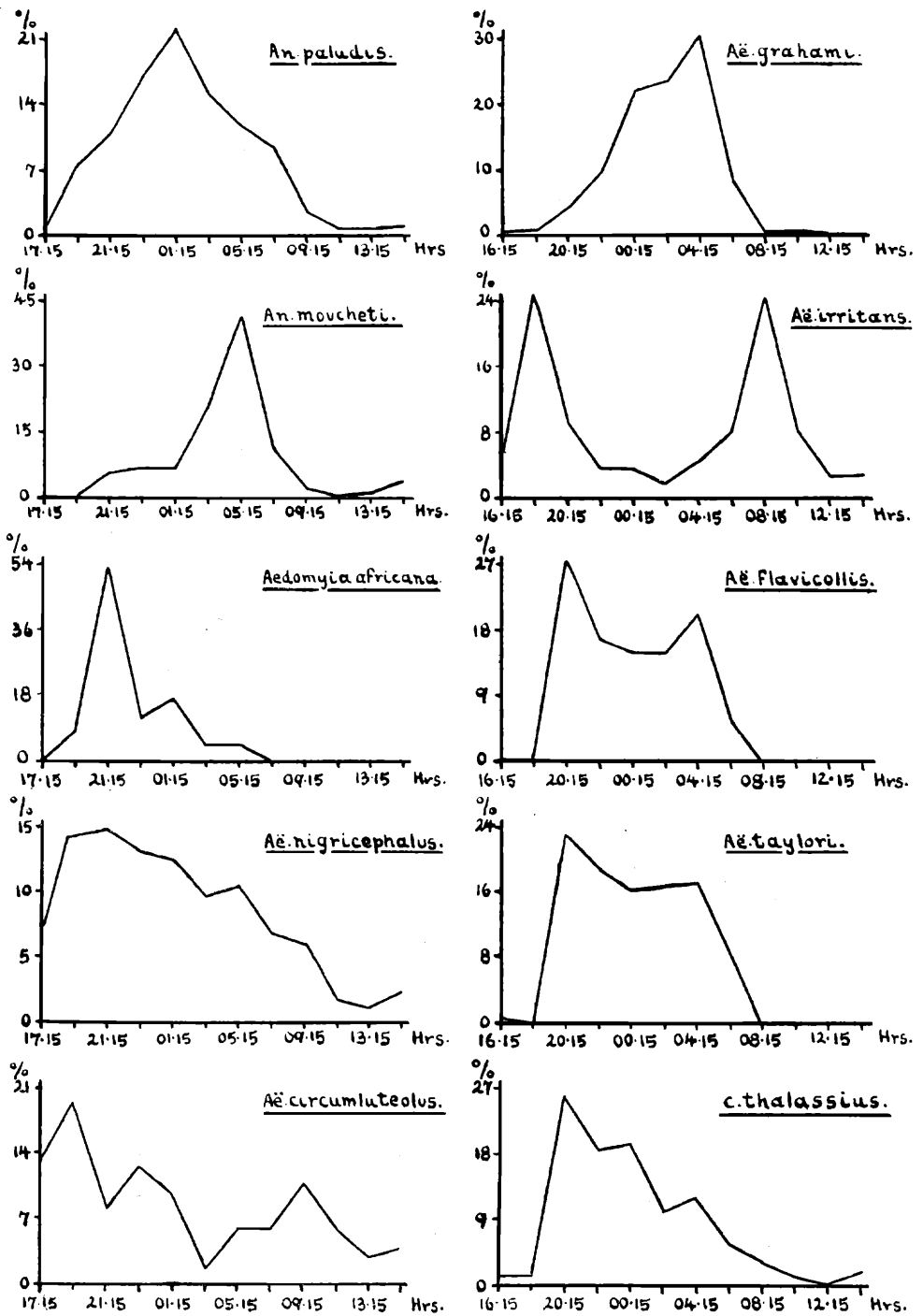


Fig. 2.—Biting cycles at Itowolo. The curves on the left are based on the odd hours, those on the right on the even hours.

Aedes flavicollis.

The mean biting curve is similar in general type to that of *Aedes africanus*, another tree-hole breeder (Mattingly, 1949). It shows, however, less concentration of biting into the peak hour and a relatively higher biting activity during the hour following and during the remainder of the night. There is a small morning peak but depression of activity begins early. The comparison with *A. africanus*, at both ends of the cycle suggests a greater sensitivity to light. Only one mosquito of this species was taken between 05.15 and 17.15.

Aedes taylori.

The mean biting cycle very closely resembled that of *A. flavicollis* to which this species is nearly related.

Aedes nigricephalus.

This species, like all the others so far considered, showed its maximum biting activity between sunset and sunrise but it had a much higher level of daytime activity and almost 30 per cent. of the total catch was taken during the hours of daylight (06.15-18.15). It was thus surpassed as a daytime biter only by *A. irritans* and *A. circumluteolus*. Kerr (1933), working on the ground and during the hours of darkness only, recorded peak activity during the hour ending 19.15 but his figures are very small.

Anopheles paludis.

This resembled *Taeniorhynchus africanus* (Mattingly, 1949) in having a rather indeterminate biting peak during the middle part of the night. Haddow (1945) gives 4-hourly figures indicating a rather earlier peak in Uganda and Kerr (1933), whose figures include a small proportion of *A. coustani* var. *ziemanni*, recorded peak activity during the hour ending 19.15.

Aedes irritans.

This species, with its remarkably symmetrical bimodal biting curve, showed maximum activity just before sunset and about an hour after sunrise. With the possible exception of *A. circumluteolus*, it was the most active daytime biter taken at Itowolo. Kerr (1933) gives figures for night-time catches made on the ground only. He did not start his catches until 19.00 hours, Nigerian Standard Time (18.15 hours L.M.T.), i.e. an hour after the peak biting time at Itowolo, and he obtained his peak during the first hour of his catches. He finished his catches before the time of the morning peak at Itowolo of which his figures give no indication.

Anopheles moucheti var. *nigeriensis*.

The mean biting curve belongs to the same general type as that of *Anopheles gambiae* and, on the ground only, *A. hargreavesi* (Mattingly, 1949) and this type may prove to be characteristic of the subgenus *Myzomyia*. In *A. moucheti*, however, activity is much lower over most of the night and, in consequence, there is a very pronounced biting peak during the hour or so before sunrise. The figures given by Kerr (1933) for *A. hargreavesi* included a small number of *moucheti* but it is not possible to separate them out. At Itowolo the peak was well marked on the three lower platforms. The numbers taken from the top platform were too small to be significant.

Aedomyia africana.

This species appears to be very sensitive to light since the well-marked evening peak did not occur until an hour later than that shown by other species with a similar type of curve. No specimens were taken before sunrise or after sunset. The mean biting curve most closely resembled those of *A. (Diceromyia) flavicollis* and *A. taylori*,

differing at the evening end mainly in the low level of activity during the hour ending 19.15 and the corresponding high concentration of activity in the following hour. The distribution of the two *Diceromyia* species over the 2-hour period 18.15–20.15, however, suggests that most activity probably took place during the latter part of the first hour, so that the difference may not have been so great as it appears.

Aedes circumluteolus.

Haddow and others (1947) give moderately large four-hourly figures for this species from Uganda. In general, the agreement with those obtained at Itowolo is good, the principal difference being a rather higher level of daytime activity in Uganda. Nevertheless this species was second only to *A. irritans* as a day biter at Itowolo and was even slightly more active than that species during the most severe part of the day. Kerr (1933) gives figures for *A. lineatopennis* which probably refer to this species but they are based on night-time catches only and are very small and of no value for comparison.

Culex thalassius.

Figures given by Kerr (1933) indicate a morning peak for this species. They were taken from the ground only. At Itowolo the figures from the ground platform only also indicate a morning peak but on the upper platforms, where most of the biting occurred, there was a well-marked evening peak and this characterises the curve as a whole. The figures are too small for detailed analysis.

Vertical Distribution.

Table VI shows the percentage of the total catch of each species at each platform.

Anopheles paludis.

The detailed figures for this species most closely resemble those for *Taeniorhynchus africanus* (Mattingly, 1949), from which it differed mainly in being rather more abundant on the ground.

TABLE VI.
Vertical distribution at Itowolo.

Platform	<i>An. paludis</i>	<i>An. moucheti</i>	<i>Aëdom. africana</i>	<i>Aë. grahami</i>	<i>Aë. nigricephalus</i>	<i>Aë. irritans</i>	<i>Aë. circumluteolus</i>	<i>Aë. flavicollis</i>	<i>Aë. taylori</i>	<i>C. thalassius</i>
	%	%	%	%	%	%	%	%	%	%
IV	4.3	2.0	56.7	46.8	5.7	1.2	0.0	48.6	36.5	25.5
III	7.0	14.6	30.0	35.4	1.9	1.9	1.0	37.3	40.6	27.3
II	24.3	49.0	13.3	16.4	5.9	8.1	8.7	13.2	20.1	14.9
I	64.5	34.4	0.0	1.4	86.6	88.8	90.3	0.8	2.9	32.3
Total	100.1	100.0	100.0	100.0	100.1	100.0	100.0	99.9	100.1	100.0

Anopheles moucheti.

The small figures available for this species, and their subdivision in order to obtain vertical distribution data, render the occurrence of maximum numbers on platform II of doubtful significance.

Aëdomyia africana.

Although only small numbers of this species were taken, the greatest numbers occurred regularly on the two upper platforms. It appears to be a typical tree-top biter. It is interesting to note that its vertical distribution resembles that of *Aëdes flavicollis*; its biting cycle also appears to resemble that of *flavicollis* more than others with the possible exception of *Aëdes taylori*.

Aëdes grahami.

This also appears to be a typical tree-top biter. It was more abundant on the top platform than on the third in every catch except the 4th, in which there were 39 from platform III and 29 from platform IV, and the 22nd which yielded only one *grahami* and that from platform III.

Aëdes nigricephalus, irritans and circumluteolus.

The very large proportions of these species occurring on the ground reflect their high degree of daytime activity. All species taken at Itowolo, whatever their vertical distribution during the night, were very largely confined to the ground during the daytime. The small numbers of *A. nigricephalus* taken on the upper platforms render the apparent inversion between platforms III and IV of very doubtful significance. Haddow & others (1947) give good figures for *A. circumluteolus* from two localities in Uganda. They obtained 96 per cent. on the ground at Mongiro and 89 per cent. on the ground at Mamirimiri.

Aëdes flavicollis and A. taylori.

The well-marked difference in vertical distribution between these species is interesting in view of their close relationship and the similarity of their biting cycle. *A. flavicollis* was more abundant on the top platform than on the third in all the larger catches except the 2nd in which 32 were taken from platform III as compared with 23 from platform IV. In the larger catches of *A. taylori* the numbers taken on platforms III and IV respectively were 11 and 11 in the 2nd, 15 and 26 in the 3rd, 21 and 30 in the 4th, 14 and 13 in the 5th, 12 and 7 in the 6th, 19 and 12 in the 7th and 26 and 9 in the 8th.

Culex thalassius.

The occurrence of maxima on the ground and the 3rd platform may indicate two different types of behaviour within this species and this is also suggested by the biting cycle (see above). The figures, when subdivided, are, however, very small and the species occurred in significant numbers in only two catches. It is therefore by no means improbable that neither the biting cycle nor the vertical distribution is of a very sharply defined type and that larger figures would be required to give a satisfactory picture of either.

General Discussion.

The expression "biting cycle", as a term in general use, has been employed throughout the present paper. That the phenomena so named represent merely a variation in the urge to bite is, however, very doubtful. The cycle is in fact a record of the frequency with which the mosquitos come into contact with the bait and, as such, may be accounted for either by the urge to bite or by changes in the general level of activity of the mosquito and, in particular, of its speed and duration of flight. The distinction is important since biting *per se* may well be affected by the difference between the skin temperature and humidity of the bait (Parker, 1948) and the temperature and humidity of the surrounding atmosphere. Light, on the other hand, seems unlikely to affect biting except in so far as it affects the general level of activity of the mosquito. Finally, there is the possibility that intrinsic rhythms, affecting the mosquito independently of changes in its physical environment, may be to a greater

or lesser extent involved. The possibility that all three factors are involved and that their degree of interdependence may vary with the species and with varying conditions cannot be excluded. As an initial simplification it is not, however, unreasonable to picture the biting cycle as representing the frequency with which a population of mosquitos in random flight comes within the range of attraction of the bait. If this is so then the form which it takes will be governed by the effective velocity of the mosquitos, a rate compounded of their actual velocity of flight and the relative lengths of the periods during which they are at rest and on the wing, and the range of attraction of the bait which may vary independently. If the general level of activity of the mosquito possesses the importance which such a picture would imply, then it might be expected that the biting cycle would be related to changes in vertical distribution, since both would be affected by the same factors. Attempts have been made to relate these two aspects of mosquito behaviour as revealed by the data obtained at Itowolo and some interesting results have been obtained, but it is clear that it would be unwise to put forward even a tentative hypothesis in the absence of more detailed studies.

There is evidence that changes in the vertical distribution of certain species are associated with swarming and if this is so then it would introduce a further complication. Unfortunately, the phenomenon of swarming has been very little studied in African mosquitos but extensive researches on the subject have been carried out by Nielsen and Greve in Denmark. A preliminary account of this work was presented to the International Entomological Congress at Stockholm by the first-named author from which it is clear that the cyclical activities involved bear a striking resemblance to those under discussion in the present paper. There is every reason to hope that light will be shed on the problems arising from the work at Itowolo by the full account of Nielsen and Greve's work which is at present in preparation.

With regard to the biting cycle, the inhibitory effect of light, even of quite low intensities, seems to be clearly indicated by the sudden cessation of activity at daybreak when changes in temperature and humidity are negligible. It might be inferred that the sharp rise in activity which most species exhibit at nightfall is due to the removal of this inhibitory influence but such an inference cannot at present be supported by direct evidence since changes in temperature and humidity are quite pronounced during the critical period. That light of a certain preferred intensity (or even wave length) may have a stimulatory effect is not proven, but it appears to afford the simplest explanation of the behaviour of such species as *Anopheles moucheti*, which has a strongly marked peak associated with the period of morning twilight. Variations on this type of cycle, such as those shown by *A. gambiae* and *A. hargreavesi*, might be accounted for by different effects of temperature and humidity during the night when these are still undergoing fairly marked changes.

Finally, it should not be forgotten that environmental factors are not of necessity the only ones which need to be taken into account. Experience in the laboratory (Mattingly, 1946; Seaton & Lumsden, 1941) indicates that mosquitos feed most readily after a certain quite circumscribed period has elapsed since emergence from the pupa. If this is also true in nature then the biting cycle may be related to some extent to the breeding cycle and in particular to the time of emergence from the pupa. The first ten catches at Itowolo were made at intervals of exactly one week and it was observed that the total number of *Aedes africanus* taken in each catch followed closely the proportion occurring on the top platform in the preceding week. The accompanying figure (fig. 3) shows the curves obtained from the last nine of these catches (the first was incomplete). It will be seen that over the first seven catches, which were those in which *A. africanus* was most abundant, the agreement was remarkably close. Catches later than the tenth were made at longer intervals. The agreement between the two curves appears too close to be coincidental. It

appears to be explained in part by the presence of a sibling species, *Aedes* (*S.*) *pseudo-africanus* (Chwatt, 1949) distinguishable from *africanus* only on the male terminalia and possibly on small differences in the scutal markings. Major Chwatt kindly examined my collection at Yaba and found a single undissected male of this species and a search of the British Museum collection revealed several others from Yaba and Lagos placed under *africanus*. Preliminary observations suggest that it is more of a ground-biter than *africanus* and it is possible that it has a rather more diffuse type of biting cycle. This would explain discrepancies in the behaviour of "*africanus*" in Nigeria and Uganda noted in the first part of the present paper. Whether the phenomena under discussion can be wholly explained in this way can only be decided when the biting cycle and vertical distribution of the new species have been fully worked out. It seems not unlikely that some relationship between vertical distribution and the breeding cycle is also involved.

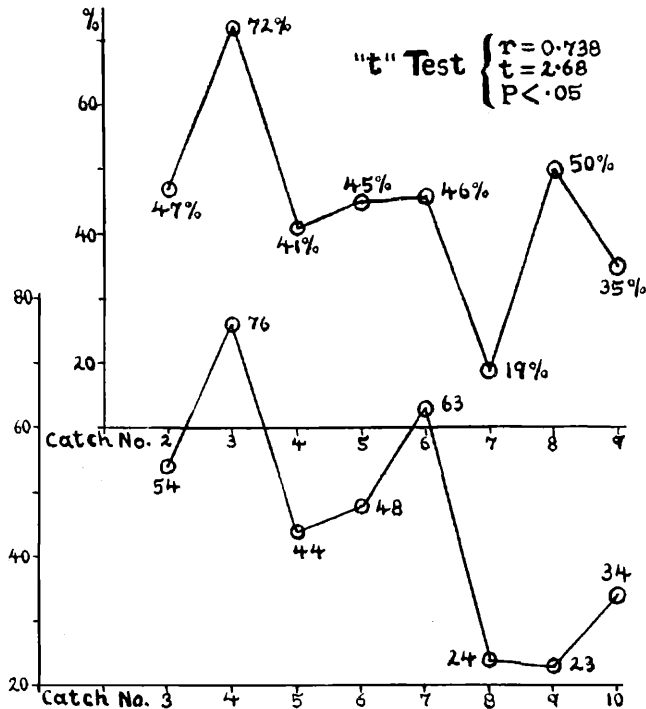


Fig. 3.—Apparent correlation between total catches of *Aedes africanus* and vertical distribution during the previous week. The lower graph shows the numbers taken in each catch, the upper the percentage of the previous catch occurring on Platform IV.

Summary.

The present paper is the second of two dealing with field studies carried out near Lagos, Nigeria. The first paper covered four of the most abundant species encountered and the second is concerned with the remaining forty-eight. These are listed and the data relating to the thirty-eight least abundant, with the exception of two which were taken as males only, are given in tabular form. The other ten are dealt with at greater length. Males of twenty-six species were taken and in the case of three of these species they were so abundant as to create the impression that a swarming activity was involved. In the case of the ten more abundant species seasonal distribution curves are given based on average monthly catches and an attempt is made to relate these to variations in rainfall. The biting curves which

are next discussed show a greater variety of types than those described in the first paper. In general, they are characterised by a fairly sharp peak associated with morning or evening twilight, but some have a more or less pronounced peak at both ends of the cycle and so correspond to the "eo-crepuscular" type of Haddow (1945). *Anopheles paludis*, like *Taeniorhynchus africanus* (described in the first paper) has an ill-defined period of maximum activity during the middle of the night. The necessity of sub-dividing the figures in order to obtain a picture of the vertical distribution of the various species led in one or two cases to anomalous results, but in general a clear and fairly convincing picture was obtained. None of the species dealt with in the present paper was sufficiently abundant to afford reliable data on hourly variations in vertical distribution. In the general discussion, which embodies such inferences as it has seemed permissible to draw from the data, attention is drawn to the fact that the so-called "biting cycle" does not, in all likelihood, depend exclusively on variations in the urge to bite, but is more probably an expression of cyclical changes taking place in the general level of activity of the mosquito. The possible relationship of such changes to changes of a similar kind in the physical environment is discussed, and it is pointed out that intrinsic rhythms in the mosquito, perhaps related to the breeding cycle, may also be involved. Some data are presented which, while partly explained by the presence of a sibling species, may also indicate an interrelationship between the breeding cycle and vertical distribution.

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