OBSERVATIONS ON MOSQUITOES OVIPOSITING IN SMALL CONTAINERS IN ZIKA FOREST, UGANDA

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During 1958–59 a preliminary survey was made of mosquitoes breeding in small containers in Mpanga Forest, Uganda (Corbet 1961). The work centred on a high steel tower (Haddow, Corbet & Gillett 1961), on which test containers were exposed at different levels in and above the forest. This study showed that several species of mosquito exhibited a non-random vertical distribution of larval occurrence at Mpanga. *Aedes apicoargenteus* (Theobald) predominated above the canopy, whereas predatory species of *Toxorhynchites* and *Eretmapodites* were commonest below it, particularly near ground level. Despite the complementary vertical distributions of predators and prey, it was shown that in this instance the observed distribution of *Aedes apicoargenteus* resulted mainly from site preference and not from predation. It became clear, however, that allowance would have to be made for the effects of predation in future studies of site preference, particularly when predator and prey showed markedly different spatial distributions.

In 1960 the tower was moved to Zika Forest, a site about 17 miles (27 km) south-east of the one at Mpanga (Haddow, Gillett & Corbet 1961). At the new site, during 1961–62, work on the mosquitoes breeding in small containers was extended with the view of obtaining information on the horizontal and vertical distribution of oviposition activity inside forest and at its margins, and on the effects of predation on the commoner species.

THE SITE

Zika Forest (32° 30′ E, 0° 7′ N) is part of a narrow sinuous strip of lakeside forest skirting the extensive grass and papyrus swamps of Waiya Bay, a sheltered inlet of Lake Victoria lying to the north and east of Entebbe. The vegetation and geology of this patch of forest have been described by Buxton (1952). At the spot where the tower stands (almost exactly midway between Buxton's observation-posts V and VII) the ground slopes appreciably and the forest is only about 150 yd (130 m) wide, being bounded on one side by permanent reed and papyrus swamp and on the other by open pasture grassland. From swamp to grassland, Buxton recognized three zones in the forest, each distinguished by the height of the water table and by characteristic vegetation. In permanent swamp forest the water table is always at or above ground level; in raised wet forest it is below ground level, but close to the surface, and is perennially accessible to tree roots; and in raised seasonal forest water is not permanently available to tree roots. For purposes of the present work a transect was established at ground level, the lower end being at the boundary between permanent swamp forest and raised wet forest, and the upper end lying more than 100 yd (90 m) outside the forest in the open grassland. Along this transect five main zones were recognized. Their characteristics and abbreviated titles are given below. The distribution of these zones, and the position of the tower in relation to the transect, are shown in Fig. 1.

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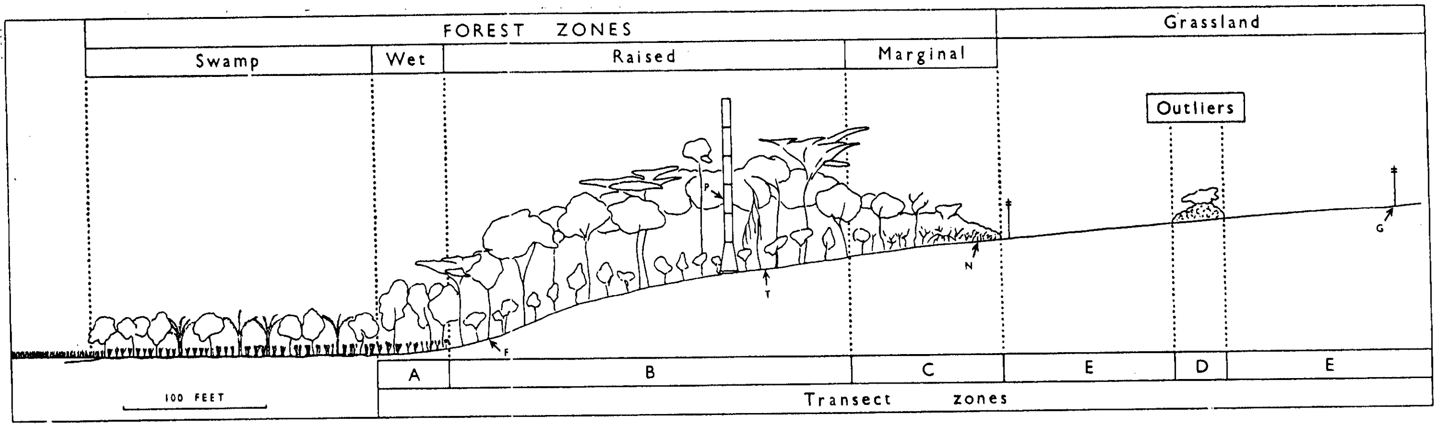

FIG. 1. The disposition of the transect zones, A–E, and the tower in relation to vegetation types at Zika Forest. Horizontal and vertical scales are the same; west is to the left and east to the right. Preferred oviposition sites in the transects for the five commonest mosquitoes are shown by arrows: *Aedes africanus* (F), *A. apicoargenteus* (P, at a height of 50 ft (15 m) on the tower), *Toxorhynchites brevipalpis* (T), *Culex nebulosus* (N) and *Aedes aegypti* (G). The full extent of zone E is not shown. The preferred oviposition site of *A. aegypti* in the whole transect is 95 yd (85 m) east of the one shown in the figure.

A. *Wet forest.* Equivalent to Buxton's raised wet forest, and recognized by the absence of permanent ground-pools and by the presence of *Marantochloa leucantha* (K. Schum.). This zone is well shaded because the higher trees (*c.* 18–24 m) of the raised seasonal forest lean out over the shorter ones (*c.* 9–12 m) of the wet and swamp forests. Ground-pools and leaf-pools are common, and tree-holes are scarce.

B. *Raised forest.* That part of Buxton's raised seasonal forest which has a canopy at least 18 m high. *Leptaspis cochleata* Thwaites replaces *Marantochloa leucantha* as the dominant constituent of the ground-herb layer. The canopy is discontinuous and has numerous gaps through which sunlight can penetrate without interruption to the forest floor. Ground-pools and leaf-pools are scarce, because the ground is sloping, and tree-holes are common.

C. *Marginal forest.* The transition zone (sometimes termed 'colonizing forest') between the raised seasonal forest and the open grassland. This is not shaded by the canopy of the seasonal forest and has very few trees more than 9 m high. Towards the grassland margin it consists mainly of thick low bushes among which an introduced shrub (*Lantana* sp.) predominates. More sunlight penetrates to ground level than in zones A or B. As in B, pools are scarce but tree-holes common.

D. *Outliers.* Discrete patches of bushes scattered over the open grassland. Each typically comprises one or two small trees growing on a disused termite-mound (*Macrotermes natalensis* Sjöstedt) and encircled by a dense stand of *Lantana* bushes. These outliers closely resemble zone C in facies, save for the fact that they lack continuity with the forest. The three chosen for study (diameters 10–12 yd, 9–11 m) were situated 26, 40 and 100 yd (23, 36 and 90 m), respectively, from the nearest forest edge. The second of these contained *Sanseveria* and the third *Dracaena* plants, both of which can provide breeding places for mosquitoes.

E. *Grassland.* The unshaded pasture grassland with areas of bare laterite. Sampling sites in this zone were three upright poles standing in line 2, 92 and 187 yd (1·8, 82 and 168 m), respectively, from the forest edge. The last pole stood just inside a native garden and about 50 yd (45 m) from the nearest occupied hut.

METHODS

Thirty-four bamboo sections ('bamboos') were exposed as test-containers along the transect at ground level, and another fifty-two on the tower. The bamboos (height 12–15 in. (30–38 cm), internal diameter 2–4 in. (5–10 cm)) were freshly cut for this purpose and each remained permanently at the spot where it was first exposed. Each had a small overflow-hole about 3 in. below the top and was banded with wire below this to counteract cracking by the sun. When the bamboos were first exposed, a duplicate series, also containing tap-water but covered, was set aside to provide replacements for those which became unserviceable through use. Thus damaged bamboos were always replaced by ones of comparable age. Only 3% of bamboos were replaced, most of these being in zone E where they cracked under exposure to the sun. In zones B and C damage was caused mainly by workers of the termite, *Macrotermes* aff. *natalensis* Sjöstedt.

All bamboos were placed within 3 ft (1 m) of the ground and those in zones A–D were arranged in pairs, one member of each pair being more exposed to sunlight than the other. The exposed bamboo was placed so as to receive uninterrupted sunlight at some time near noon, whereas the other was put in a heavily shaded spot which probably never received direct sunlight. In zone D, where a pair of bamboos was placed in each

Table 1. *Incident light directly above shaded and exposed bamboos in Zika Forest*

Zone	Suntime (noon being 1200) (hours)	Incident light (ft candles)	
		Shaded	Exposed
A	1032–1039	6–30	1000–1500
B	1008–1030	7–30	1600–5000
C	1050–1104	28–50	3000–5000
D	1421–1439	25–85	>5000

of the three outliers, the exposed bamboo was at the outer margin of the *Lantana* and the shaded one in the centre of the outlier. In zone E all of the six bamboos were exposed to direct sunlight, although they were attached to the southern, slightly more sheltered, sides of the poles. During the work the changes in seasonal aspect of the sun and the growth of vegetation did not significantly change the category of any bamboo at ground level with regard to its exposure to illumination. The relative illumination of exposed and shaded bamboos must obviously have varied continuously according to weather and time of day, but an indication of the order of the differences involved can be gauged from

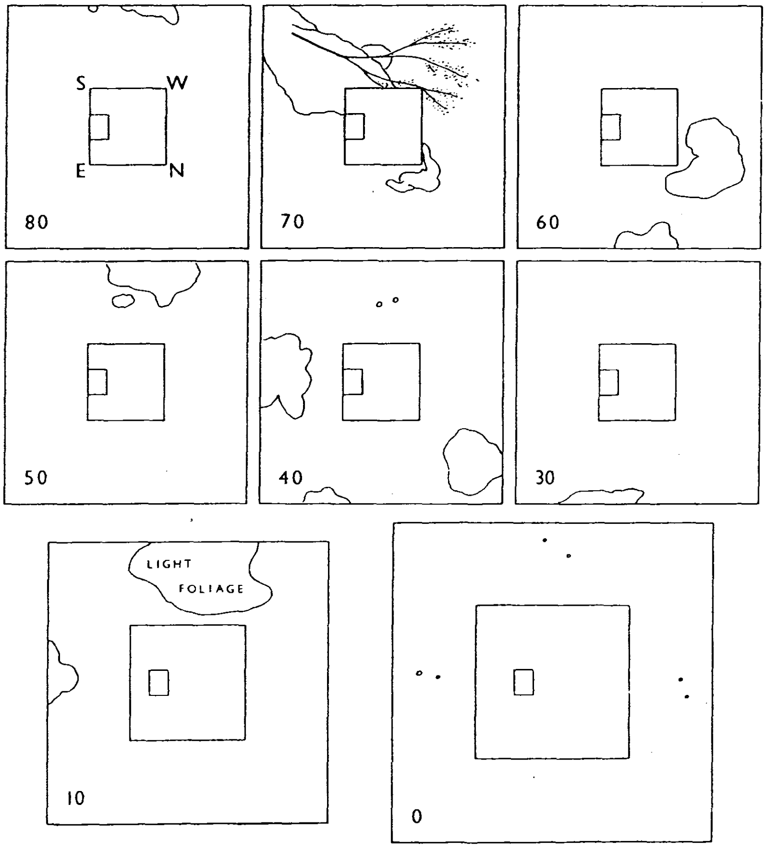

FIG. 2. The distribution of shading vegetation at different levels on the tower. Diagrams are to scale, the tower being 12 ft (3·5 m) square at the base and 6 ft (<2 m) square above 30 ft (9 m). No vegetation stands within 6 ft of the tower at 20 ft or above 80 ft. Along its south-east and north-east sides the tower is heavily shaded by foliage between 60 and 70 ft.

values in Table 1, obtained by exposing a photo-cell (Weston Illumination Meter, Model 756) facing directly upwards above the mouth of each bamboo on a cloudless day (7 March 1961) near noon.

On the tower bamboos were placed in sets of four at vertical intervals of 10 ft (3 m) from ground level to 120 ft (36 m). They were attached to the inside of the corner buttresses and were therefore in the most sheltered sites available. The tower passed through the top of the uneven canopy at a height of 70–80 ft (21–24 m). Owing to the irregular disposition of vegetation (Fig. 2) and to the existence of the opaque platforms at 20 ft (6 m) intervals, light penetration cannot be expected to form a smooth regression on height on the tower. Apparatus was lacking to make simultaneous readings at adjacent levels, as had been done at Mpanga (Dirmhirn 1961), but an indication of the amount of incident light reaching bamboos at different heights is given in Fig. 3. These values

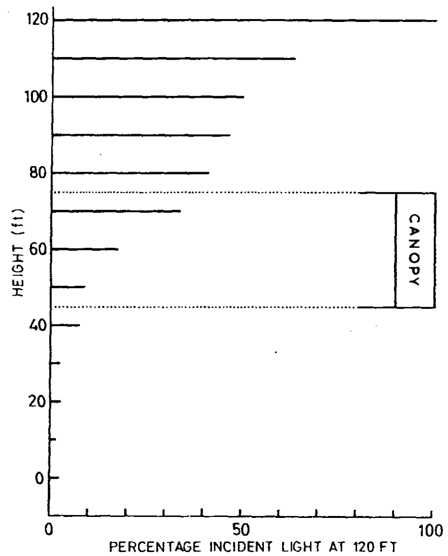

FIG. 3. Light intensity according to level in the positions occupied by bamboos at the southern corner of the tower. The platform at 120 ft (36 m) causes the first abrupt fall in light intensity and the canopy the second.

were obtained on a cloudless day (1 March 1961), 42–67 min before noon, by making readings as quickly as possible from top to bottom. Readings for adjacent levels (never taken more than 3 min apart) were treated as successive pairs for purposes of computing the percentage reduction. The photo-cell of the light meter faced directly upwards immediately above the mouth of the bamboo in the southern corner and was shaded from direct sunlight at all levels by the edges of the corner buttress of the tower. From Fig. 3 it is evident that the incident light at the bamboo declines abruptly immediately below 120 ft (36 m) and again within the canopy. The decline below 120 ft is doubtless occasioned by the top platform of the tower, and thus makes the curve differ in shape from one based on readings taken near but outside the tower (Dirmhirn 1961). At Zika, on account of the east–west slope of the ground, situations at heights of 40–60 ft (12–18 m) are liable to receive direct sunlight during the hour before sunset, namely between about 'crep' 3 and 0 (Nielsen 1961).

The bamboos were first exposed at all sites on 7 March 1961. Beginning on 20 March, their contents were examined on thirteen occasions at intervals of about a fortnight (range 13–18 days; median 14·7 days), the last collection being on 15 September. On each occasion all mosquito larvae, except species of *Toxorhynchites*, were killed immediately in lactophenol and preserved for subsequent examination. Larvae of *Toxorhynchites* (isolated in separate tubes) and pupae of all mosquitoes were kept alive for the adults to emerge. Other macroscopic animals inhabiting the bamboos were preserved, and watch was kept for any which might be preying on mosquitoes there. All the material was examined and identified by the writer personally, the larvae and pupae being counted and recorded for each bamboo separately. The mosquitoes encountered during this work, and their relative abundance are shown in Table 2, the nomenclature used being that of Stone, Knight & Starcke (1959). Note was taken of leaking or fouled bamboos, thus enabling the total number of bamboos at risk on each occasion to be computed. This

Table 2. *Mosquitoes encountered as larvae or pupae in bamboos during thirteen collections in Zika Forest*

Species	No. of bamboos in which found			No. of larvae and pupae collected		
	Ground	Tower	Total	Ground	Tower	Total
Toxorhynchites (*Toxorhynchites*) *brevipalpis* Theobald subsp. *conradti* Grünberg	82	59	141	92	70	162
T. (*T.*) *kaimosi* (Someren)	12	20	32	12	20	32
Eretmapodites chrysogaster Graham group	1	–	1	3	–	3
Aedes (*Finlaya*) *ingrami* Edwards	1	–	1	3	–	3
A. (*Stegomyia*) *aegypti* (Linn)	51	–	51	1250	–	1250
A. (*S.*) *africanus* (Theobald)	296	73	369	7069	320	7389
A. (*S.*) *apicoargenteus* (Theobald)	79	281	360	1114	4950	6064
A. (*S.*) *simpsoni* (Theobald)	4	–	4	50	–	50
A. (*Aedimorphus*) *stokesi* Evans	1	1	2	1	2	3
Culex (*Neoculex*) *horridus* Edwards	2	–	2	3	–	3
C. (*Culiciomyia*) *macfiei* Edwards	4	26	30	10	120	130
C. (*C.*) *nebulosus* Theobald	161	237	398	7218	5750	12968
Total larvae and pupae				16825	11232	28057
Total bamboos at risk	415	668	1083			
Total bamboos exposed	442	676	1118			

procedure represented a significant improvement upon that followed at Mpanga (Corbet 1961) where the exact incidence of spoiled bamboos was not recorded. At Mpanga the number of times a given species of mosquito occurred had to be expressed as a proportion of the total bamboos containing mosquito larvae (of any kind). Thus percentage occurrence values were strongly influenced by the extent to which a species occurred alone at a given site. The only respect in which this source of error could have modified conclusions drawn from the Mpanga work is mentioned below in connection with *Aedes apicoargenteus* (p. 158).

If counts of larvae and pupae are to be used as an index of oviposition activity in a given site it is necessary to know whether or not predation has occurred since oviposition took place. In the present work the only predators of mosquito larvae recognized were larvae of *Toxorhynchites brevipalpis conradti* and *T. kaimosi.* As intervals between successive collections were less than the minimum duration of the aquatic stages of these two species at Zika (Corbet & Griffiths 1963; Corbet 1963a), it was assumed that in bamboos with *Toxorhynchites* no predation had occurred. Such bamboos were termed *predator-free* and formed the sole basis for computing occurrence values. Among the total bamboos at risk, those which contained a given species were termed *positive*, and the remainder *negative* for that species. Considering predator-free bamboos alone, the following statistics were used to specify the incidence of each species:

$$\text{Percentage occurrence} = \frac{\text{No. positive bamboos}}{\text{No. bamboos at risk}} \times 100$$

$$\text{Average density} = \frac{\text{No. larvae and pupae}}{\text{No. bamboos at risk}}$$

$$\text{Average positive density} = \frac{\text{No. larvae and pupae}}{\text{No. positive bamboos}}$$

For the predators the indices were the same except that they were of course based on all bamboos at risk, and not just on predator-free ones.

In addition to the series of bamboos exposed at ground level and on the tower, test containers were placed at two other sites for shorter periods. These containers comprised two bamboos inside a metal rondavel, the door of which was opened regularly and stood about 3 yd from the forest edge; and seven metal pans (depth 4 in. (10 cm); internal diameter 9½ in. (24 cm)) placed one on each platform of the tower including ground level. These containers were examined at the same intervals as those of the standard series; the information they provided is mentioned in the summaries for separate species, but is not included in the tables of results.

DISTRIBUTION AT GROUND LEVEL

The percentage occurrence of the commoner mosquitoes in different zones is shown in Fig. 4, and their average density in Fig. 5. Figures for average density of *Toxorhynchites* have not been given, since in 87% of positive bamboos only one larva was found (see Table 3); therefore the distributions for percentage occurrence and average density are almost identical. In Figs. 4 and 5 the species have been placed as nearly as possible in order of the degree to which they prefer shaded zones. The raw data on which these diagrams are based appear in Table 3.

When occurrence values for shaded and exposed bamboos, respectively, are compared for each species in each of zones A–D, only two situations reveal differences which may be significant. In the wet forest (zone A) *Aedes africanus* occurred more frequently in exposed bamboos ($P<0{\cdot}02$); and in the outliers (D) both *A. africanus* ($P<0{\cdot}05$) and *Culex nebulosus* ($P<0{\cdot}02$) occurred more often in shaded bamboos. These somewhat unexpected results indicate that, for purposes of comparing the distributions of species between zones, it is valid to combine records from shaded and exposed bamboos within a single zone inside the forest.

The results of comparing the occurrences of the several species *inter se* in zones A–C are given in Table 4. If allowance is made for the unequal sizes of samples, it is evident that the several species usually differ widely from one another in respect of their distribution in the three zones of the forest at ground level. This finding shows that the distributions recorded in Figs. 4 and 5 can be accepted as a valid expression of differences between these species in Zika Forest. The only two comparisons in Table 4 which are not demonstrably different involve *Toxorhynchites kaimosi*, the sample of which was relatively small. Although this fact may have reduced the significance of interzone differences, it is clear that the distribution of this species at ground level must somewhat

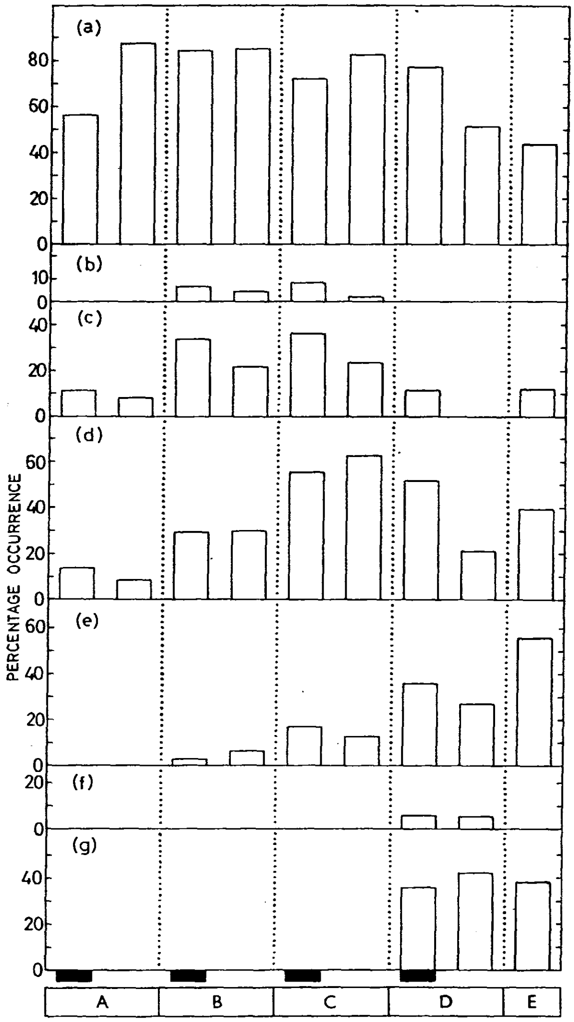

FIG. 4. Percentage occurrence of certain commoner mosquitoes in zones A–E at ground level. Shaded bamboos are recorded to the left of each of zones A–D, as shown at the base of the diagram. (a) *Aedes africanus*; (b) *Toxorhynchites kaimosi*; (c) *T. brevipalpis*; (d) *Culex nebulosus*; (e) *Aedes apicoargenteus*; (f) *A. simpsoni*; (g) *A. aegypti*.

resemble that of *T. brevipalpis* and, to a lesser degree, that of *Aedes africanus*. The rule, however, is for the several species to differ markedly in their distribution at ground level inside forest.

It appears from Figs. 4 and 5 that species also differ considerably in the extent to which they will oviposit outside forest. The outliers (zone D) were chosen as an experimental zone because, though similar in many respects to marginal forest (zone C), they lack continuity with it. Shaded bamboos in the two zones are situated almost identically with regard to incident light and surrounding vegetation, yet those in the outliers are presumably accessible only to females able to venture over open ground to reach them. Exposed bamboos in the two zones differ widely in both respects. Considering only those species found in both zones, and comparing their incidence in shaded bamboos inside and outside forest, and in exposed bamboos inside and outside forest (Table 5), it is found that, with the exception of *A. apicoargenteus*, differences between the exposed bamboos are much the greater, and that only to *Toxorhynchites brevipalpis* are shaded sites in outliers significantly less attractive than those in marginal forest. It may be concluded that, for *Aedes africanus* and *Culex nebulosus*, shade is a more important factor than continuity with forest, and that a site similar in facies to marginal forest is acceptable even though isolated and surrounded by open grassland.

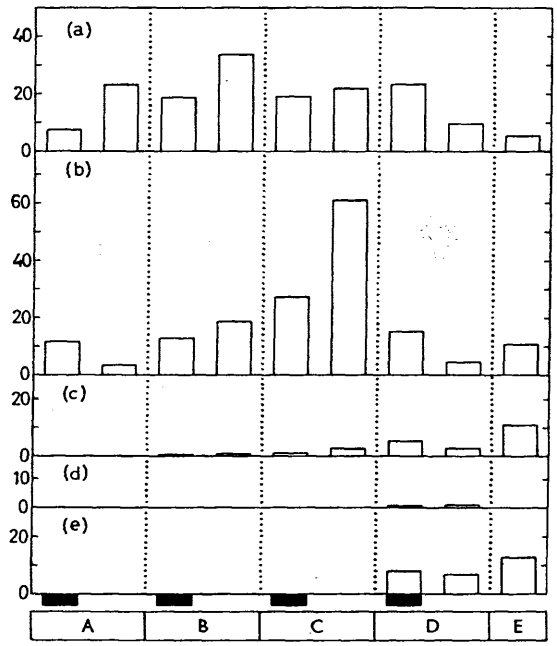

FIG. 5. Average density of certain mosquitoes at ground level. Shaded bamboos shown as in Fig. 4. (a) *Aedes africanus*; (b) *Culex nebulosus*; (c) *Aedes apicoargenteus*; (d) *A. simpsoni*; (e) *A. aegypti*.

So far, the data have been used to discern site preferences for oviposition at ground level, only predator-free bamboos being considered. It is also of interest, however, to obtain a measure of production of each species in the five zones. In Table 6 the incidence of a species is expressed as a percentage of the total larvae and pupae of non-predatory mosquitoes supported by the bamboos in each zone. Values for predator-free and for all bamboos have been computed separately, and are compared in the table. The data emphasize the numerical dominance of *Aedes africanus* at ground level, except in the marginal forest which supports more *Culex nebulosus*, and in the open grassland where *Aedes aegypti* and *Culex nebulosus* are commoner. The production of *Aedes apicoargenteus* at ground level is relatively insignificant in all zones.

Table 3. *The occurrence of the commoner mosquitoes in different zones at ground level*

	Ground-level zone								
	A		B		C		D		E
	Shaded	Exposed	Shaded	Exposed	Shaded	Exposed	Shaded	Exposed	Exposed
NON-PREDATORS									
Aedes africanus									
Positive bamboos	13	21	32	40	21	33	24	17	25
No. larvae/pupae	175	552	688	1590	551	876	728	307	304
Culex nebulosus									
Positive bamboos	3	2	11	14	16	25	16	7	23
No. larvae/pupae	270	87	490	877	787	2427	472	139	598
A. apicoargenteus									
Positive bamboos	–	–	1	3	5	5	11	9	32
No. larvae/pupae	–	–	3	17	18	90	176	73	614
A. simpsoni									
Positive bamboos	–	–	–	–	–	–	2	2	–
No. larvae/pupae	–	–	–	–	–	–	18	32	–
A. aegypti									
Positive bamboos	–	–	–	–	–	–	11	14	22
No. larvae/pupae	–	–	–	–	–	–	246	212	723
Total predator-free bamboos at risk	23	24	38	47	29	40	31	33	58
PREDATORS									
Toxorhynchites kaimosi									
Positive bamboos	–	–	4	3	4	1	–	–	–
No. larvae/pupae	–	–	4	3	4	1	–	–	–
T. brevipalpis									
Positive bamboos	3	2	21	14	18	12	4	–	8
No. larvae/pupae	3	2	28	19	23	15	5	–	8
Total bamboos at risk	26	26	63	64	50	52	35	33	66

Table 4. *The significance of inter-zone differences in occurrence within the forest at ground level*

	Culex nebulosus	*Toxorhynchites kaimosi*	*Aedes apicoargenteus*	*Toxorhynchites brevipalpis*
Aedes africanus (4432)	1017·6848 S	2·4127 >0·1	34·2952 S	9·1527 <0·02
Toxorhynchites brevipalpis (90)	26·4136 S	0·7493 >0·1	44·1054 S	
Aedes apicoargenteus (128)	23·0426 S	12·8595* S		
Toxorhynchites kaimosi (12)	6·0604 <0·05			
Culex nebulosus (4938)				

The size of sample is given beneath the name of each species in the left-hand column. The upper value in each cell is that of χ^2. The lower one is the corresponding value of P for 2 degrees of freedom, or in one cell (*) for 1 degree of freedom. S denotes that P is $<0·001$.

Table 5. *The significance of differences in occurrence between zones C and D*

Species	Values of P (1 degree of freedom) for comparison between: Shaded bamboos in C and D	Exposed bamboos in C and D
Aedes africanus	>0·1	<0·01
Toxorhynchites brevipalpis	<0·05	<0·01
Culex nebulosus	>0·1	<0·001
Aedes apicoargenteus	>0·1	>0·1

Table 6. *The occurrence of the commoner non-predatory mosquitoes expressed as a percentage of the total larvae and pupae collected in each zone*

	Ground-level zone					
	A	B	C	D		E
				Shaded	Exposed	
PREDATOR-FREE BAMBOOS						
Aedes africanus	67·05	62·12	30·00	44·31	40·25	13·56
Culex nebulosus	32·93	37·28	67·59	28·73	18·22	26·67
Aedes apicoargenteus	–	0·55	2·27	10·71	9·57	27·38
A. simpsoni	–	–	–	1·10	4·20	–
A. aegypti	–	–	–	14·97	27·79	32·25
Other spp.	–	0·02	0·13	0·18	–	0·13
Total larvae	1084	3666	4755	1643	763	2242
ALL BAMBOOS						
Aedes africanus	70·10	60·25	33·45	44·01	40·25	13·52
Culex nebulosus	29·86	39·21	63·88	29·21	18·22	26·95
Aedes apicoargenteus	–	0·48	2·44	10·10	9·57	28·67
A. simpsoni	–	–	–	1·02	4·20	–
A. aegypti	–	–	–	15·48	27·79	30·72
Other spp.	–	0·04	0·21	0·17	–	0·12
Total larvae	1195	4814	5730	1763	763	2441

VERTICAL DISTRIBUTION

The percentage occurrence of the commoner mosquitoes at different heights is shown in Fig. 6, and their average density in Fig. 7. In these diagrams the most shaded site lies at the bottom and the most exposed at the top; the upper and lower limits of the canopy are indicated in each figure. The species are placed in the same order as before. The raw data on which the diagrams are based appear in Table 7.

Although differences were not large, it appears that mosquitoes did not oviposit at each of the four corners of the tower to the same extent. *Culex nebulosus* was on average commonest in the eastern corner, but *Aedes apicoargenteus* in the southern one. However, as the aspect of a given corner varied from level to level on account of the uneven distribution of shading vegetation (Fig. 2), and as spoiled bamboos were very few (only two out of 104 below the canopy), it is clear that differences between corners cannot have had a significant effect on the patterns in Figs. 6 and 7. Bamboos from all four corners contribute to the distributions shown.

To compare the vertical distributions of the several species inside forest, four strata

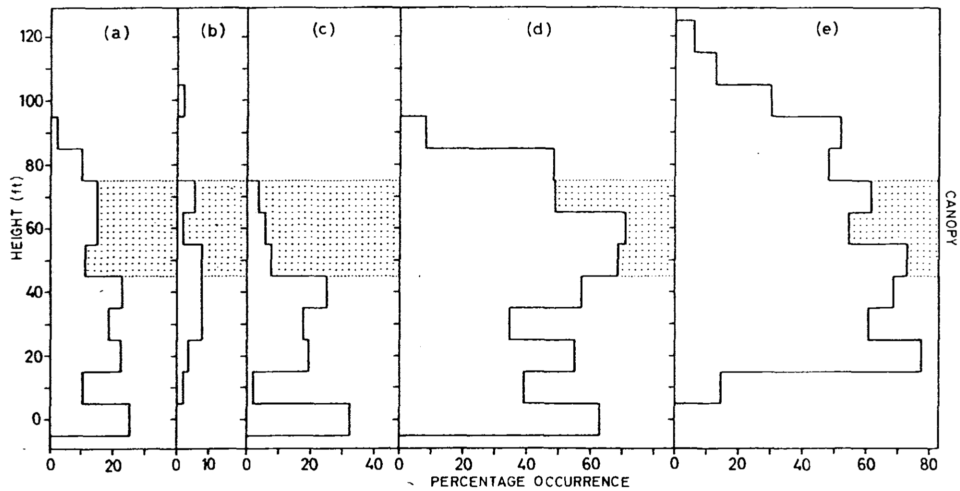

FIG. 6. Percentage occurrence of certain mosquitoes at different levels on the tower. (a) *Aedes africanus*; (b) *Toxorhynchites kaimosi*; (c) *T. brevipalpis*; (d) *Culex nebulosus*; (e) *Aedes apicoargenteus*.

have been recognized: ground level to 10 ft (3 m) (amongst ground vegetation); 20–30 ft (6–9 m) (without surrounding vegetation); 40–50 ft (12–15 m) (lower part of canopy); and 60–70 ft (18–21 m) (upper part of canopy). Although the scale is much reduced, such

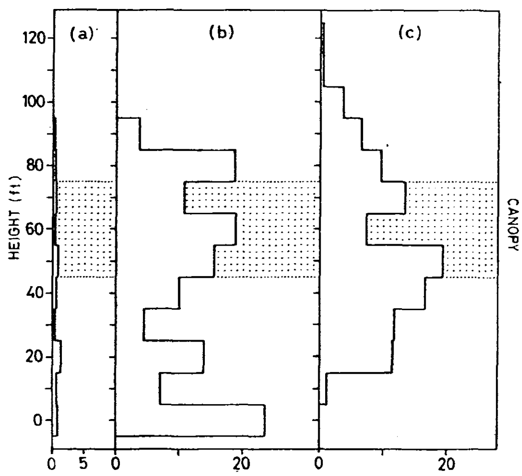

FIG. 7. Average density of certain mosquitoes at different levels on the tower. (a) *Aedes africanus*; (b) *Culex nebulosus*; (c) *Aedes apicoargenteus*.

a comparison is to some extent the vertical counterpart of that made within forest at ground level (Table 4). Results of comparing the occurrences of the several species *inter se* in these four strata are given in Table 8. As at ground level, some of the species

Table 7. *The occurrence of the commoner mosquitoes at different heights on the tower*

	Height (ft)												
	0	10	20	30	40	50	60	70	80	90	100	110	120
NON-PREDATORS													
Aedes africanus													
Positive bamboos	9	5	9	7	8	5	7	7	5	1	–	–	–
No. larvae/pupae	34	36	52	17	25	41	16	28	23	1	–	–	–
Culex nebulosus													
Positive bamboos	22	19	22	13	20	30	34	23	24	4	–	–	–
No. larvae/pupae	815	344	554	169	351	675	900	502	934	173	–	–	–
Aedes apicoargenteus													
Positive bamboos	–	7	31	23	24	32	26	29	24	26	15	6	3
No. larvae/pupae	–	50	461	445	587	842	348	623	479	323	182	22	20
Total predator-free bamboos at risk	35	49	40	38	35	44	48	47	50	50	50	52	51
PREDATORS													
Toxorhynchites kaimosi													
Positive bamboos	–	1	2	4	4	4	1	3	–	–	1	–	·
No. larvae/pupae	–	1	2	4	4	4	1	3	–	–	1	–	·
T. brevipalpis													
Positive bamboos	17	1	10	9	13	4	3	2	–	–	–	–	–
No. larvae/pupae	19	1	15	9	17	4	3	2	–	–	–	–	–
Total bamboos at risk	52	51	52	51	52	52	52	52	50	50	51	52	51

differ widely from one another, and the more prominent differences shown by the data may be accepted as real. The same holds good when the species are compared with regard to their occurrence inside (0–70 ft) and above (80–120 ft; 24–36 m) the forest, respectively (Table 9).

From the figures and tables it can be seen that, with respect to vertical distribution,

Table 8. *The significance of inter-level differences in occurrence within the forest, from ground level to 70 ft*

	Aedes apicoargenteus	*Toxorhynchites kaimosi*	*Toxorhynchites brevipalpis*	*Aedes africanus*
Culex nebulosus (4310)	1017·5634 S	9·1214 <0·05	27·2725 S	32·2266 S
Aedes africanus (249)	518·2018 S	5·2419 >0·1	5·0147 >0·1	
Toxorhynchites brevipalpis (70)	261·9756 S	7·0099 >0·05		
T. kaimosi (19)	2·3965 >0·1			
Aedes apicoargenteus (3356)				

For explanation see Table 4. In Table 8 all values of P are for 3 degrees of freedom.

Toxorhynchites brevipalpis resembles *Aedes africanus*, whereas *Toxorhynchites kaimosi* is more similar to *Aedes apicoargenteus*. The latter two species are exceptional in being absent from ground level. The top of the canopy evidently provides a barrier to *Toxorhynchites brevipalpis* and a significant check to *Culex nebulosus* and *Aedes africanus*; for *A. apicoargenteus*, however, the decline in oviposition activity proceeds fairly smoothly from 50–120 ft and undergoes no obvious change of rate at the canopy. As at ground level (Table 5) the edge of forest presents no effective barrier to this species.

Table 9. *The significance of differences in occurrence above and below the top of the canopy*

	Aedes apicoargenteus	*Culex nebulosus*	*Toxorhynchites brevipalpis*	*Toxorhynchites kaimosi*
Aedes africanus (273)	31·4837 S	22·7639 S	5·3350 $<0·05$	0·7328 $>0·1$
Toxorhynchites kaimosi (20)	28·1428 S	0·4183 $>0·1$	0·4514 $>0·1$	
T. brevipalpis (70)	20·0146 S	16·7098 S		
Culex nebulosus (5417)	12·6448 S			
Aedes apicoargenteus (4382)				

For explanation see Table 4. In Table 9 all values of *P* are for 1 degree of freedom.

Table 10. *The occurrence of the commoner non-predatory mosquitoes expressed as a percentage of the total larvae and pupae collected at each level*

	Level (ft)					
	0–10	20–30	40–50	60–70	80–90	100–120
PREDATOR-FREE BAMBOOS						
Aedes africanus	5·25	3·95	2·62	1·82	1·24	–
Culex nebulosus	86·89	41·36	40·69	58·00	57·27	–
Aedes apicoargenteus	3·75	51·83	56·67	40·17	41·49	100·00
Other spp.	–	0·11	–	–	–	–
Total larvae	1334	1748	2521	2417	1933	224
ALL BAMBOOS						
Aedes africanus	6·58	3·53	2·65	1·93	1·24	–
Culex nebulosus	86·09	36·13	41·83	56·06	57·27	–
Aedes apicoargenteus	3·42	57·31	55·51	42·02	41·49	100·00
Other spp.	3·90	3·02	0·04	–	–	–
Total larvae	1460	2153	2836	2537	1933	224

The production of larvae of the commoner non-predatory species in different strata is shown in Table 10. Two species, *Culex nebulosus* and *Aedes apicoargenteus*, provide more than 89% of the total at all levels. Between 20 (6 m) and 90 ft (27 m) production of these two is about the same; below this *Culex nebulosus* predominates, and above, *Aedes apicoargenteus*. Production of *A. africanus* is insignificant at all levels.

The findings will now be discussed separately for each species. Certain references to earlier work, mentioned in connection with the study at Mpanga (Corbet 1961), will not necessarily be repeated here.

SUMMARIES FOR SEPARATE SPECIES

Toxorhynchites brevipalpis conradti Grünberg

Oviposition occurs mainly inside marginal and raised forest, in which the more shaded sites appear to be slightly preferred (Fig. 4c). Ground level is favoured most, but oviposition occurs regularly up to the canopy, within which it declines abruptly (Fig. 6c). At Zika no larvae were found above the canopy, although a few had been recorded in this situation at Mpanga. The preferred site was in a shaded bamboo in raised forest (Fig. 1, T). Larvae were three times found in metal pans on the tower—at ground level and 20 ft.

T. brevipalpis leaves forest more readily near the ground than at canopy level, but nevertheless does so infrequently. Unlike *Aedes africanus*, which it otherwise resembles

Table 11. *Association of various prey species with* Toxorhynchites *in different zones expressed as percentage of occurrences*

Accompanying species	*Toxorhynchites brevipalpis*							*T. kaimosi*		
	Ground-level zone					Tower		Ground-level zone		Tower
	A	B	C	D	E	Ground	Above ground	B	C	Above ground
Aedes africanus	80	74	70	50	63	18	14	100	80	5
Culex nebulosus	–	40	63	50	50	29	33	43	100	35
Aedes apicoargenteus	–	–	20	25	63	–	57	14	20	55
Culex macfiei	–	–	3	–	–	–	–	14	–	10
Aedes aegypti	–	–	–	25	38	–	–	–	–	–
None	20	11	7	25	38	65	33	–	–	25
Total occurrences	5	35	30	4	8	17	42	7	5	20

most, it is considerably less common in shaded outliers than in similiar sites in marginal forest (Figs. 4a and 4c, Table 5). That exposure, rather than absolute height, is limiting its vertical distribution to the canopy is indicated by the fact that, in the Ivory Coast, this species oviposits up to 42 m when this is the height of the canopy (Doucet 1960). Of all the commoner species encountered, *Toxorhynchites kaimosi* probably included, *T. brevipalpis* is the one most confined to forest. At Zika the recorded distributions indicate that the main prey of *T. brevipalpis* at ground level comprises *Culex nebulosus* and *Aedes africanus*, and above the ground *Culex nebulosus* and *Aedes apicoargenteus*. *A. aegypti*, though occurring commonly in situations only a few feet from *Toxorhynchites brevipalpis*, is exposed to much less predation from this species on account of its failure to enter forest. This is evident from data in Table 11 which shows the proportion of times various prey species were found in the same bamboo as *T. brevipalpis*. Following Bick (1951) association values have been expressed as percentages to facilitate comparison, but it should be stressed that numbers of occurrences were small in several zones. It is noteworthy that, considering the ground-level transect as a whole, *T. brevipalpis* occurs most frequently in the two zones (B and C) in which the absolute numbers of prey species are greatest, although its distribution shows a poor correspondence with that of any one of them (Figs. 4

and 5). At Zika the preference shown by this species for ground level can be readily rationalized in terms of absolute abundance of prey. On the tower above the ground 14/42 positive bamboos contained larvae of *T. brevipalpis* without accompanying prey; and in 12/14 of these cases only a single *T. brevipalpis* larva was present. At ground level, however, only 8/82 positive bamboos lacked accompanying prey, and in 6/8 of these cases two or more *T. brevipalpis* larvae coexisted in a single bamboo. It appears probable that a single *T. brevipalpis* larva had exhausted its supply of prey in 12/42 or 29% of cases on the tower, but in only 2/66 or 3% of cases at ground level ($P<0.001$). Thus the observed oviposition preferences of this species accord well with the distribution and availability of its prey, as judged by numerical abundance.

T. kaimosi (Someren)

Inside forest this species prefers to oviposit above ground level, the favoured stratum being 30–50 ft (Fig. 6b). Its preferred site was at 50 ft on the northern corner of the tower. Some indications of a preference for ovipositing at higher levels were noted for this species in Kaimosi Forest, Kenya by Garnham, Harper & Highton (1946).

At ground level in Zika Forest *T. kaimosi* has a distribution most similar to that of *T. brevipalpis*, favouring the raised and marginal forests, but vertically its distribution differs markedly and more closely resembles that of *Aedes apicoargenteus*. It appears likely that the main prey of *Toxorhynchites kaimosi* and *T. brevipalpis* will be the same near the ground, but that *T. kaimosi* will feed to a greater extent on *Aedes apicoargenteus* at higher levels.

Eretmapodites chrysogaster Graham group

A few larvae occurred once in a shaded bamboo at ground level in marginal forest, and twice in metal pans at ground level. As larvae of this group had predominated in bamboos at Mpanga, particularly near the ground, their extreme scarcity at Zika constituted one of the more striking differences between the two forests. It is tempting to see a causal relationship between this and the exceptional rarity of tree-hole-breeders such as those of the subgenera *Stegomyia* and *Finlaya* at Mpanga.

Eretmapodites oedipodius Graham group

A few larvae occurred once in a metal pan at ground level.

Aedes ingrami Edwards

Although adults were known to be common while collections were being made, larvae were encountered only once, in a bamboo in open grassland 2 yd from the forest margin. Garnham *et al.* (1946) experienced similar difficulty in collecting larvae in Kaimosi Forest, and considered this species to be less sylvan in habit than many others found in forest.

A. aegypti (Linn)

Adults reared from larvae belonged to the form *formosus*. In the area covered by the transect most oviposition occurred in the open grassland, the preferred site being 187 yd (168 m) from the forest edge and 50 yd (15 m) from the nearest occupied hut (see Fig. 1, G). In the outliers no discernible preference was shown for either shaded or exposed bamboos, an unexpected finding in view of the preference this species shows for shaded sites in similar situations in Nigeria (Surtees 1960). At Zika, larvae were never found inside forest though frequently encountered on the grassland within a few feet of the forest margin. That shade alone cannot be determining this site selection is evident from the fact that eggs were laid in shaded bamboos in zone D, but not in zone C. It is noteworthy also that no larvae were found on the tower, even above the canopy. It appears that, at Zika, *A. aegypti* was neither entering, nor flying over, the forest margin to oviposit.

A similar reluctance to enter forest by this species has been recorded by McClelland (1956) at Lunyo Forest, near Entebbe, and by Thomas (1960) in Sierra Leone: in both localities *A. aegypti* very seldom oviposited in forest and if so in the drier parts or during the dry season. It is significant that in Nigeria, where both *A. africanus* and *A. aegypti* breed in tree-holes and enter villages to bite man, *A. africanus* breeds mainly inside forest but *A. aegypti* outside (Boorman & Service 1960). Although Garnham *et al.* (1946) found *A. aegypti* breeding a mile or more inside the Kaimosi Forest in Kenya, the favoured sites were on the edges of clearings; when bamboos were placed inside forest to test the penetration of this species, no larvae were found in them. Two records which cannot at present be reconciled with the known habits of *A. aegypti* elsewhere are those of Haddow (1945) and Doucet & Cachan (1962) who encountered larvae in climax rain forest in western Uganda and the Ivory Coast, respectively; in the former locality larvae were in tree-holes, and in the latter in bamboos at heights between 5 and 42 m.

A. africanus (Theobald)

Inside forest oviposition is virtually restricted to ground level, where little discrimination is shown between shaded and exposed sites, save in the wet forest where exposed sites are slightly preferred. As the microclimate surrounding the shaded bamboos in wet forest was probably moister than that around exposed ones (at least at the time of day when oviposition takes place) it is possible that oviposition declines abruptly near the transition to the swamp forest, into which the transect could not be extended. Occasionally, eggs are laid up to a height of 90 ft (27 m) in forest, but the number above ground level is negligible, and far smaller than in any situation investigated at ground level. The preferred site for *A. africanus* at Zika was in an exposed bamboo near the lower margin of the raised forest (Fig. 1, F). *A. africanus* frequently oviposited in the hut by the forest margin, and also occasionally in metal pans at 0–30 ft.

Although oviposition declines in frequency in ground-level sites beyond the shade afforded by marginal forest or outliers, it still persists at a level significantly exceeding that in forest only 10 ft above the ground. In open grassland, without shelter of any kind, larvae were encountered about twice as frequently and in much greater numbers than at any site above 10 ft inside forest. This indicates that the distribution of oviposition is related to height *per se* and not to the equable microclimate which is a feature of ground-level situations in forest (Haddow & Corbet 1961). This does not conform with earlier interpretations of the observed distribution of oviposition in this species (Laarman 1958; Corbet 1961). *A. africanus* typically shows its greatest biting activity in the canopy of forest or woodland (Haddow, Gillett & Highton 1947; Haddow 1961a); the fact that in the same habitats oviposition is markedly concentrated near the ground should sound a caution against using any single activity as a basis for general conclusions on microhabitat selection or vertical stratification of a species.

In view of what is known of the behaviour of *A. africanus* near Entebbe, the regularity with which females oviposited in open grassland was an unexpected finding. No specimens were taken biting man on open grassland 90 yd (82 m) from the forest margin at

Zika during a series of ten catches designed to discern such behaviour, although many were taken biting inside forest at this time (Snow & Corbet 1959). More recently the writer has taken a single female biting man in this situation (at 25–30 min after sunset), but such an event is obviously exceptional at Zika. This is possibly a local behaviour trait, since both in Tanganyika (Smith 1955) and in West Africa (Kerr 1933; Boorman & Service 1960; Boorman 1960) females bite man commonly over open ground.

The fact of oviposition occurring outside forest in a markedly sylvan population of *A. africanus* raises the question of the time of day at which it occurs. Inside Zika Forest oviposition is strictly diurnal with a peak 3–4 h before sunset; outside forest, however, environmental conditions are relatively severe at this time, and it is therefore of interest to note that eggs are laid over open ground during the hour after sunset (Corbet 1963b). Evidently there is more movement of this species outside forest than baited catches indicate. Once again, however, the strong relationship of oviposition with ground level is evident. Though biting females are known to be common in and above the canopy at sunset (Haddow 1961b), oviposition was never recorded above 90 ft, the height of the highest emergent trees near the tower.

A. apicoargenteus (Theobald)

Most oviposition occurs in forest above ground level, between 20 ft and the top of the canopy. The preferred site was at 50 ft on the western corner of the tower. The canopy does not form an effective barrier, and oviposition continues, though with declining intensity, up to 120 ft (36 m), the highest level sampled. Oviposition occurred occasionally in the hut, very commonly in the metal dishes at 0–60 ft, and once at 80 ft.

The low incidence of oviposition in exposed marginal sites at ground level demonstrates that the distribution of this activity is determined to a large extent by height *per se* and not simply by the greater exposure associated with higher sites. This finding is somewhat unexpected since work by Laarman (1958) on oviposition habits of this species in the Congo led to the conclusion that a direct response to light intensity might determine its vertical distribution; and subsequent observations based on its biting activity in nature (Haddow 1961c) and its oviposition activity in the laboratory (Haddow, Corbet & Gillett 1960) have favoured this interpretation. The present results demonstrate, however, that the spatial distribution of oviposition activity cannot be simply rationalized thus, and further that the exogenous factors controlling biting and oviposition appear to be different, and not the same as previously suggested. Although heights of 30–50 ft are favoured by *A. apicoargenteus* for both biting and oviposition, the diel rhythms of these two activities in nature at a single site are quite different. Biting occurs as a broad wave with an ill-defined maximum which usually falls shortly after noon (Haddow 1961c); and oviposition occurs shortly after sunrise and before sunset (Corbet 1963b).

As mentioned on p. 146 the figures given for the vertical distribution of *A. apicoargenteus* on the tower at Mpanga are not directly comparable with those for Zika, since at Mpanga occurrence was expressed as a percentage of bamboos containing mosquito larvae, not of the total at risk. This inflated occurrence values of *A. apicoargenteus* above the canopy, where it was often the only species present. The raw data (Corbet 1961, p. 277) show that oviposition was commonest above the canopy, and that it declined in frequency towards ground level; therefore the two main conclusions which were reached remain unaffected. The qualification which must now be added is that oviposition probably declined also above 110 ft (33 m). Thus the preferred level was not the highest sampled, as implied by the figure, but a stratum between 80 and 110 ft.

A. simpsoni (Theobald)

This was encountered only in zone D, on four occasions. On three, larvae occurred in a shaded bamboo next to a group of *Dracaena ugandensis* plants, in the axils of which *Aedes simpsoni* is known to oviposit (Gibbins 1942; Haddow 1948). During subsequent work, larvae were once found in zone E, in the site most favoured by *A. aegypti*. *A. simpsoni* is known from previous work to oviposit readily in bamboos (Harris 1942; Bailey 1947; McClelland 1958).

A. stokesi Evans

This occurred in an exposed bamboo in marginal forest and in the east corner of the tower at 30 ft. The species is known to breed in tree-holes (Hopkins 1952) and was found in a bamboo at ground level by Doucet & Cachan (1962) in forest in the Ivory Coast during the rainy season. Larvae are reputedly found only after heavy rain (Hopkins 1952); those at Zika were collected on 1 and 15 Sept. 1961, a week or two after the 'short rains' had begun.

Culex horridus Edwards

There were two occurrences only, in shaded bamboos in outliers, 26 and 100 yd from the forest margin.

C. macfiei Edwards

Oviposition occurred occasionally at ground level in raised and marginal forest, ana frequently on the tower at 0–40 ft. The preferred site (occurrence 73%; average density 4·3) was at 10 ft in the southern corner of the tower. Larvae also occurred in metal pans at 0 and 10 ft, which suggests that the species may not breed exclusively in tree-holes in nature (see Hopkins 1952).

C. nebulosus Theobald

This species showed its characteristically wide valency, occurring in every site except those on the tower above 90 ft. Nevertheless it exercised a distinct preference for ovipositing in exposed bamboos in marginal forest, and to a lesser degree in, and just above, the canopy. The preferred site was an exposed bamboo at ground level in zone C, 64 ft (19 m) from the grassland margin (Fig. 1, N). Larvae occurred twice in the hut and occasionally in metal pans on the tower at 0–60 ft. The greatest number of larvae and pupae found coexisting in one bamboo was 588.

The distributions in Figs. 5(b) and 7(b) indicate that for *C. nebulosus* the forest margin restricts oviposition to about the same extent at ground level and the canopy. In the Ivory Coast it oviposits up to 42 m when the canopy is at this height (Doucet 1960); therefore exposure, more than absolute height, probably determines its vertical distribution.

OTHER INHABITANTS OF BAMBOOS

Three other animals found in bamboos merit brief mention. Larvae and pupae of the psychodid fly, *Telmatoscopus albipunctatus* (Williston) occurred in all zones at ground level, though mainly inside the forest. On the tower they occurred frequently at 0–50 ft, and occasionally up to 90 ft. They were found in metal pans at 0 and 40 ft. This insect is commonly encountered in moist rooms of houses at Entebbe, a situation which probably closely resembles certain parts of forest with respect to light, temperature and humidity. The species is now circumtropical, and breeds commonly in sewage beds and pit latrines (see Lewis 1958). Adults of this family can be a nuisance in dwellings if abundant (Smart 1956) and two species of *Psychoda* have been incriminated as causative agents in allergic bronchial asthma in man (Ordman 1946). A few larvae of the tipulid fly, *Limonia (Limonia) congoensis* Alexander, occurred in bamboos at ground level in raised and marginal forest, on the tower at 70 ft and in a metal pan at 60 ft. Two frogs, probably *Afrixalus fulvovittatus* (Cope) (Polypedatidae), were found in a shaded bamboo in an outlier 100 yd from forest, and in a bamboo in grassland 40 yd from forest. The gut contents of each individual consisted entirely of terrestrial arthropods (mainly Hemiptera–Homoptera and spiders), no mosquitoes being represented.

PREDATION BY *TOXORHYNCHITES*

It was hoped that the work on oviposition preferences would yield quantitative information on the effects of predation by *Toxorhynchites* in Zika Forest. The existence of a few, abundant prey species and the apparent scarcity of other predators were both factors making the ecological picture a relatively simple one. As obligate predators inhabiting the small-container habitat, species of *Toxorhynchites* have received much attention as possible agents of biological control. Their ability to survive long periods without food (Wigglesworth 1929), their catholic oviposition behaviour (Paine 1934), and their habit of wantonly destroying other animals shortly before they pupate (Corbet & Griffiths 1963) are all features which would seem to fit them for such a role. On the other hand, the fights to the death which occur between full-grown larvae must provide a rapid and efficient means of maintaining *Toxorhynchites* populations at a fairly low density.

The amount of predation achieved by *Toxorhynchites* in any locality will depend to a large extent on the densities of predator and prey, and on their temporal and spatial coincidence in the available breeding sites. Variables such as these will confine the application of estimates of predation to the time and place in which they were made. In addition to these factors, the feeding behaviour of *Toxorhynchites* must be taken into account if the practical significance of estimates is to be understood.

Two phases of prey destruction can be recognized during the life of a *Toxorhynchites* larva. During the first phase, lasting until 2–3 days before pupation, prey is killed solely for food; *T. brevipalpis conradti* needs the equivalent of about 250 *Aedes aegypti* larvae, as a minimum, during this phase (Corbet 1963a). During the second phase, shortly before pupation occurs, mosquito larvae are killed if encountered, but few or none of these are eaten. This killing response is a compulsive habit found in several species of *Toxorhynchites* and appears to be an adaptation directed towards protecting the relatively vulnerable pupa against attack by another *Toxorhynchites* larva which may occupy the same container (Corbet & Griffiths 1963). During the second phase, a larva of *T. brevipalpis conradti* can kill at least 150 fourth-instar *Aedes aegypti*; therefore in nature it is probable that all the other mosquito larvae in a tree-hole are usually killed at this time. Destruction of prey will accordingly be independent of prey density in the first phase but strictly dependent upon it in the second.

At Zika, intervals between successive collections in bamboos were almost always several days less than the minimum duration of the larval stage of *Toxorhynchites* (Corbet & Griffiths 1963; Corbet 1963a), and therefore killing had not yet commenced in the bamboos; any reduction of prey can therefore be ascribed to predation during the first phase.

If it be assumed that, in a given site, the percentage occurrence of prey is initially the same in both predator and predator-free bamboos, then the reduction due to the presence of *Toxorhynchites* should be equivalent to the difference in positive average density between the two series. The validity of such an estimate of predation will depend on the extent to which predators and prey are randomly distributed among samples; if they show a preference for the same individual bamboos in the series, the estimate will be too low, and if they show a preference for different ones, it will be too high. Accordingly, the best way of deploying bamboos in order to minimize errors due to these causes would be either to make long series of collections from single bamboos or to expose several at the same spot. During the present work the second condition was partly fulfilled by having four bamboos at each level of the tower, none being more than 9 ft distant from any of the other three. Therefore, the reduction of prey in bamboos with *Toxorhynchites* can be computed for those bamboos on the tower for which predator-free collections (Table 7; Fig. 6) show both predators and prey to be regularly coincident. These comprise bamboos at 0–70 ft for both *Aedes africanus* and *Culex nebulosus*, and 20–70 ft for *Aedes apicoargenteus*.

To compare the average positive density of prey in predator and predator-free bamboos, it is first necessary to adjust the denominator of this fraction (p. 147) for the predator bamboos to allow for those in which prey was originally present but has since been destroyed *in toto* by the predator. This can be done by assuming that the percentage occurrence of prey was initially the same in bamboos of both categories. The occurrence of *A. apicoargenteus* at 50 ft may be taken as an example to illustrate this. In predator bamboos its observed occurrence was 3/8 or 37·5%. To conform with the 68·1% occurrence recorded in the forty-four predator-free bamboos at this level, its occurrence in predator bamboos must be adjusted from 3 to 5·82. By adjusting occurrence values in this way, *separately for each level* on the tower within the range of predator–prey coincidence, the average positive density for predator bamboos in this range can be obtained from:

$$\frac{\text{No. larvae and pupae (all levels combined)}}{\text{Adjusted No. positive bamboos (all levels combined)}}$$

Between 20 and 70 ft this value for *A. apicoargenteus* is 568/38·91 or 14·60. For predator-free bamboos in this range the comparable value is 20·04, and accordingly the reduction of average positive density in the presence of *Toxorhynchites* is 5·44/20·04 or 27%. The comparable reductions computed for *Culex nebulosus* and *Aedes africanus* between 0 and 70 ft on the tower were 38 and 30%, respectively.

It must be stressed that these provisional estimates refer only to first-phase predation by *Toxorhynchites* between 20 and 70 ft, and 0 and 70 ft, in Zika Forest during March through September 1961.

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SUMMARY

1. The preferred oviposition-sites of tree-hole-breeding mosquitoes were determined by exposing bamboo sections along horizontal and vertical transects in a strip of lake-side forest (Zika) in Uganda. Bamboo sections in the horizontal transect extended from wet forest to open grassland, those inside the forest being arranged in pairs, one of each pair being more shaded than the other. Those in the vertical transect were placed at 10 ft (3 m) intervals, from ground level to 120 ft (36 m), on a steel tower which passed through the top of the canopy of raised forest at 70–80 ft (21–24 m). Thirteen collections at regular intervals between March and September 1961 yielded 28 057 larvae and pupae of twelve species of mosquito.

2. Oviposition preferences were deduced from the frequency and density of larval occurrences, allowance being made for possible predation by *Toxorhynchites*. All the commoner species differed markedly from each other in their horizontal and vertical distributions. In the degree to which they preferred shaded oviposition sites, the commoner mosquitoes fell in the following order: *Aedes africanus*, *Toxorhynchites brevipalpis conradti*, *Culex nebulosus*, *Aedes apicoargenteus*, *A. simpsoni*, *A. aegypti*.

3. In *Toxorhynchites brevipalpis* and *Culex nebulosus* the degree of exposure to light apparently determined the observed distributions. In other cases height above ground *per se* played the main role. Both inside and outside forest, *Aedes africanus* predominated near the ground but *A. apicoargenteus* at higher levels. Accordingly these two species competed very little for breeding sites though inhabiting the same small patch of forest.

4. Generalizations concerning adult preferences for microhabitat or level cannot validly be based upon one activity alone. Although *A. apicoargenteus* bites and oviposits mainly at understorey level, *A. africanus* bites in the canopy but oviposits near the ground.

5. In Zika Forest the main prey of *Toxorhynchites brevipalpis conradti* at ground level comprised *Culex nebulosus* and *Aedes africanus*, and above the ground *Culex nebulosus* and *Aedes apicoargenteus*. *A. aegypti* largely escaped predation on account of its failure to enter forest to oviposit.

6. Two phases of prey-destruction are recognized during the life of a *Toxorhynchites* larva; in the first it kills only for food; in the second, which immediately precedes pupation, it compulsively destroys all animals it encounters in its tree-hole. A provisional estimate was attempted of predation during the first phase, within certain strata of the forest. This indicated that larval populations of *Aedes apicoargenteus*, *A. africanus* and *Culex nebulosus* were suffering reductions of 27, 30 and 38% during the period of the investigation.

7. The abundance of species of *Aedes* (*Stegomyia*) at Zika (relative to Mpanga Forest, the site of an earlier study) may perhaps be causally related to the marked scarcity of larvae of the *Eretmapodites chrysogaster* group in small containers there.

8. Other animals encountered in the bamboo sections are briefly mentioned.

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