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The vertical distribution of some West African mosquitoes (Diptera, Culicidae) over open farmland in a freshwater area of the Gambia

M. T. Gillies and T. J. Wilkes
School of Biological Sciences, University of Sussex, Brighton BN1 9QG, England

Abstract

Mosquitoes flying at low levels over open farmland were sampled by means of electrical suction traps. These were set up at nine levels from ground level up to 6 m. From the vertical profiles obtained it was possible to recognise three patterns of behaviour: (1) a low-flying group with relatively very high densities below 1 m, comprising *Mansonia* (*Mansonioides*) spp., *Aedes* spp. and some species of *Anopheles*; (2) an intermediate group with densities rather evenly distributed at the lower levels but declining above 2–4 m, comprising *A. funestus* Giles, *A. gambiae* Giles and *Culex neavei* Theo.; (3) a high-flying group with catches at 6 m greater, or much greater, than at 1 m, composed of *C. antennatus* (Becker), *C. thalassius* Theo. and *C. poicilipes* (Theo.). For all species, catches after 23.00 h showed an increase in the proportion of mosquitoes taken in traps at the lower levels, this being most marked at ground level and 0·5 m. No influence of either moonlight or wind speed could be detected to account for this. Biting catches on human baits showed a generally similar pattern to suction-trap catches, although differences between baits at 1-m intervals at the higher levels were less than with unbaited traps.

Introduction

The vertical distribution of mosquitoes in equatorial forests in Africa has been relatively well studied (see Snow, 1975), but until recently little attention had been paid to the problem in the more open environment of the savanna. Here, in moving between breeding sites and villages, mosquitoes are exposed to very different conditions compared with those in the forest, particularly in relation to wind speed, illumination and physical obstructions to flight. All of these are likely to affect their vertical stratification. Snow (1975) has described the distribution of mosquitoes in the vicinity of mangrove swamps in the Gambia at levels of up to 9 m. Snow & Wilkes (unpublished) have also shown that the age condition of high-flying and low-flying populations may be different. In the present paper we give an account of similar work on vertical stratification in an inland area of the country where the insects were moving across open farmland between villages and freshwater swamps and rice fields.

Experimental area

The experiments with suction traps were conducted in an extensive area of flat, cultivated land lying between the village of Saruja, MacCarthy Island Division, and rice fields and swamps along the banks of the River Gambia. The vegetation cover of the surrounding land was made up of rice fields, groundnut farms, grassland and low regenerating bush with a few isolated trees up to a height of 6–15 m (Pl. I, fig. 1). The experimental area itself was grass-covered, and this was kept down to a level of 0·3–0·6 m over most of the area. When traps were installed at 0·5 and 1 m the grass was cut down as far as possible to the roots over an area of 18 m radius round the trapping site. Because of regrowth and irregularities in the ground the actual level of the surface of the ground varied by 15–20 cm. In the vicinity of the ground-level traps all vegetation was removed to a distance of 5 m, so that insects approaching them would have been flying over bare ground (Pl. I, fig. 3).

Methods

Aerial densities were estimated with 22·8 cm Vent-Axia fans run at ' boost ' and with the orifices supported horizontally. Mosquito netting cages were fixed to the lower ends of gauze funnels to collect insects blown into them. The fans were supported on frames projecting out from a 1·5-m-square steel tower (Pl. I, fig. 2), and arranged in staggered positions so that the down-draught from the higher traps did not impinge on the lower. To avoid bias due to variation in the efficiency of different fans, the fan units were systematically moved on from one level to another after each night's catch. When traps were used at 0·5 m a pit was dug in the ground under it to prevent rebound from the down-draught interfering with air-flow over the trap. The trap at ground-level was supported in a frame over a 1-m-cube pit at a distance of 12 m from the tower. Tests with smoke showed normal air-flow over both these low-level traps when the fans were running.

Because of constantly light winds during the rainy season we decided that shielding of the cones, as advocated by Taylor (1955), would not be necessary. This assumption was tested by comparing the catch in a trap, the cone of which was shielded with polythene stretched round a frame extending vertically downwards from the mouth of the fan, with that in an exposed trap. Both traps were set up at 5 m and run for 12 nights in two different positions. The mean catch per night for the shielded trap (13·9) did not differ significantly from that in the exposed trap (17·2). On these grounds the use of exposed cones seemed justified.

The following series of experiments were run:

(1) October 1973, ten nights with traps at 1, 2, 3 and 4 m.
(2) October–November 1973, ten nights with traps at 1, 2, 5 and 6 m.
(3) July–August 1974, 41 nights with traps at 1-m intervals from 1 to 6 m. Normally four traps were in use each night, the levels being shifted systematically each night. The number of nights on which traps at individual levels were operating varied from 26–29.
(4) August–September 1974, 17 nights with traps as above but with an additional trap at 0·5 m. Individual levels were sampled on 11–13 nights.
(5) September–October 1974, 14 nights with traps at 0·5, 1 and 1·5 m.
(6) October 1974, seven nights with traps at 1, 2 and 3 m.
(7) October 1974, seven nights with traps at 0, 0·5, 1 and 1·5 m.
(8) October–November 1974, ten nights with traps at 0, 0·5 and 1·5 m.

The number of nights on which the traps were operated at different levels was: 0 m (17), 0·5 m (44), 1 m (88), 1·5 m (31), 2 m (66), 3 m (57), 4 m (48), 5 m (47), 6 m (46).

For the biting catches human baits sat on platforms on a scaffolding tower and trapped the mosquitoes with tubes as they settled to bite. Two small towers were used, 30 m apart, set up in a clearing in close proximity to rice fields on one side and open bush with scattered tall trees on the other. Catches were done at one level at a time on each tower and the baits were regularly alternated. A single catch consisted of four 30-min sessions with two baits sitting successively at different levels on each of the two towers. In this way four levels could be sampled by both baits. Catches were done during the period from 20.30–02.00 h on 28 nights. In one series 20 catches were done at levels of 1, 2, 3 and 4 m, while in another 20 catches, biting rates at 1 m were compared with rates at 5 m and 6 m. It was thus possible to compare biting rates at six levels.

Meteorology

The experiments were carried out during the course of two rainy seasons, a time of year when conditions of temperature and humidity are generally equable. Wind speed was measured with a sensitive anemometer at a height of 1·2 m over short grass. Apart from short-lived and sometimes violent squalls that preceded the arrival of thunderstorms, winds are nearly always light at this season. Mean wind speeds for the eight series of experiments were respectively 0·97, 0·84, 1·49, 0·87, 0·81, 0·90, 0·17 and 0·59 m/s. Differences in wind strength during the course of the night were seldom marked, although on average wind speed was 17% greater during the second trapping period. On 12 nights a second anemometer was run at a level of 6 m. This gave a mean reading of 1·69 m/s compared with 1·23 m/s at 1·2 m on the same nights. From the equation given by Geiger (1965), $\log u - \log u_1 = a \log z$, where u = wind speed at height z_1 and u_1 = wind speed at 1 m, it can be calculated that a = approx. 0·20, which indicates a rather flat gradient.

Mosquito fauna

Both African species of the ubiquitous *Mansonia* (*Mansonioides*) were abundant. *M. africana* (Theo.) predominated in the early part of the season, while *M. uniformis* (Theo.) became progressively more common as the season wore on. Some 13 species of *Aedes* were trapped, the commonest being *Ae.* (*Mucidus*) *scatophagoides* (Theo.), *Ae.* (*Aedimorphus*) *punctothoracis* (Theo.), *Ae.* (*A.*) *argenteopunctatus* (Theo.), *Ae.* (*A.*) *fowleri* (Charmoy), *Ae.* (*A.*) *ochraceus* (Theo.), *Ae.* (*A.*) *vexans* (Mg.) and *Ae.* (*Neomelaniconion*) *circumluteolus* (Theo.). As shown by Snow (1975), all Gambian specimens of the *Culex univittatus* Theo. group fall within the range of variation for *C. neavei* (Theo.), as redefined by Jupp (1971), and are designated as such. No identifications of the *Anopheles gambiae* complex were made on material from the experiments, but house catches made in Georgetown, 17 km away, were all determined by Dr G. Davidson as belonging to species A.

Results

Vertical profiles

Table I shows the geometric mean catch (Williams mean) and confidence limits * for 11 species or groups of mosquitoes in all series of experiments. In Table II these results have been converted into ratios of the catch at each level to that at 1 m, and the mean ratio for all species then calculated. In the highly productive catches in series 8 there was no trap at 1 m. So to incorporate these data, the ratio (M_w 0 + 0·5 + 1·5m) Series 7/(M_w 0 + 0·5 + 1·5m) Series 8 was first calculated and the catches in Series 8 then multiplied by this. The corrected values in Series 8 were then expressed as ratios of the catch at 1 m in Series 7. This introduced a possible error into estimation of the ratio of the catch at 0, 0·5 and 1·5 m to that at 1 m, but gave extra information on variation in catches between these levels.

The species have been grouped into three categories: a low-flying group with relatively very high catches below 1 m, an intermediate group rather evenly distributed at lower levels but falling away above 2–4 m, and a high-flying group with catches at

* Estimated as 2·576 × standard error (1%) or 2 × standard error (5%) of the log mean catch +1 for each experiment. In comparing the mean catch in adjacent traps, the mean with the higher variance was used for estimating confidence limits.

TABLE I. *Geometric mean catch of mosquitoes per trap, all experiments*

Species	Series	0 m		0·5 m		1 m		1·5 m		2 m		3 m		4 m		5 m		6 m	Total trapped
Mansonia spp.	1					81·7	.....	*	....	48·8	**	19·9		13·2					2227
	2					67·2	....	**	....	33·3		....	**	....		7·2	**	1·5	1255
	3					26·0	....	**	....	11·8	*	5·9		3·7	**	1·6		1·1	1737
	4			67·5	**	27·6	....	**	....	13·8	**	7·8	**	4·2		2·7		2·1	1645
	5			30·9	**	14·0	**	8·0											924
	6					65·0	....	**	....	31·5	**	17·3							876
	7	378·9	**	121·7		80·4		66·0											4901
	8	292·7	**	81·5	....	*	....	42·7											5675
A. ziemanni	1					2·0				1·9		1·7	*	0·81					68
	2					4·5	....	**	....	1·3						0		0·07	69
	3					1·6	....	**	....	0·69		0·62	**	0·29		0·19		0·15	159
	4			4·4		2·6	....	**	....	1·3		0·74		0·36		0·34		0·2	184
	5			5·1	**	2·5		3·8											241
	6					5·7				4·7		3·2							128
	7	84·8	**	17·3		19·4		23·4											1168
	8	65·6	**	12·8				8·8											1529
A. pharoensis	3					0·43				0·26		0·21		0·29		0·08		0·05	52
	4			2·4	*	0·83				0·74		0·31		0·34		0·20		0·13	97
	5			2·4	*	1·3		1·3											101
	6					2·4				1·3		0·94							46
	7	21·9	**	9·1	*	5·2		5·3											249
	8	9·2	**	1·3				0·75											186
A. squamosus	4			1·9	**	0·48				0·22		0·06		0·06		0		0·06	50
	5			2·1		1·7		1·3											110
	6					2·3				2·0		0·79							63
	7	41·1	**	14·9	**	8·8		8·1											563
	8	13·5	**	1·9				1·9											230

A. funestus	1					2·0				1·1	*	0·28		0·43					50
	2					2·9	....	*	....	1·3						0·15		0·11	79
	3					1·1				0·66	**	0·16		0·16		0·16		0·13	83
	4			2·5		2·4	....	**	....	0·48		1·1	**	0·24		0·36		0·14	123
	5			2·7	*	1·4		1·1											94
	6					4·3				2·7		1·0							85
	7	10·0		10·6		8·3		3·7											285
	8			5·0				2·6											179
A. gambiae	3					1·2				0·86		0·59		0·57		0·35	**	0·05	162
	4			1·8		1·2				0·66		0·90		0·58		0·87	*	0·21	111
Aedes spp.	3					0·44				0·15		0·27		0·27		0·03		0·12	52
	4			1·7		0·99	....	*	....	0·41		0·12		0·34		0·24		0·14	79
	5			1·7	*	0·46		0·37											62
	7	5·7		3·1	**	0·67		0·84											88
C. neavei	1					2·6				3·3		3·1		2·9					225
	2					2·0				1·1						0·78	*	0·22	64
	3					0·83				0·62		0·68		0·93		0·54		0·59	204
	4			0·66		1·1				0·56		0·58		0·74		0·75		0·80	95
	5			0·89		1·4		2·4											99
	6					0·67				1·5		2·1							49
	7	0·84		0·73		0·52		0·86											31
	8	3·4	**	0·58				0·76											62
C. antennatus	3					0·18				0·15		0·28		0·43		0·33		0·36	71
	4			1·0		1·4	....	*	....	0·63		0·35		0·60		0·85		0·97	105
	5			0·77		0·56	**	1·41											57
	6					0·89				1·3		2·2							54
	7	1·2		2·6		3·6	*	6·1											118
	8	0·85		1·4	....	*	....	4·2											90
C. thalassius	3					1·6				0·90		0·52		0·84		0·60	**	2·3	316
C. poicilipes	1					12·9	....	*	....	19·2	**	38·2	**	94·0					1672
	2					2·4				2·3		....	**	....		5·9		8·5	294
	3					1·6				1·4		1·4	**	4·3		3·5	**	9·1	1004
	4			1·8		2·5	....	*	....	1·5		2·1	**	6·4		7·9	**	21·5	638
	5			8·9		10·0		14·2											831
	6					7·5				7·4		16·3							379
	7	27·8	**	12·8	**	20·5		23·3											633
	8	15·8	**	9·0	....	**	....	22·9											582

** and * = significant differences between adjacent traps at the 1 % and 5 % levels respectively.

6 m greater than at 1 m. In Fig. 1 the results from Table II have been plotted as horizontal histograms to illustrate, on the left, low-flying species and, on the right, intermediate and high-flying species. In general terms it will be seen that species of *Aedes, Mansonia* and *Anopheles* are mainly flying close to the ground. In the case

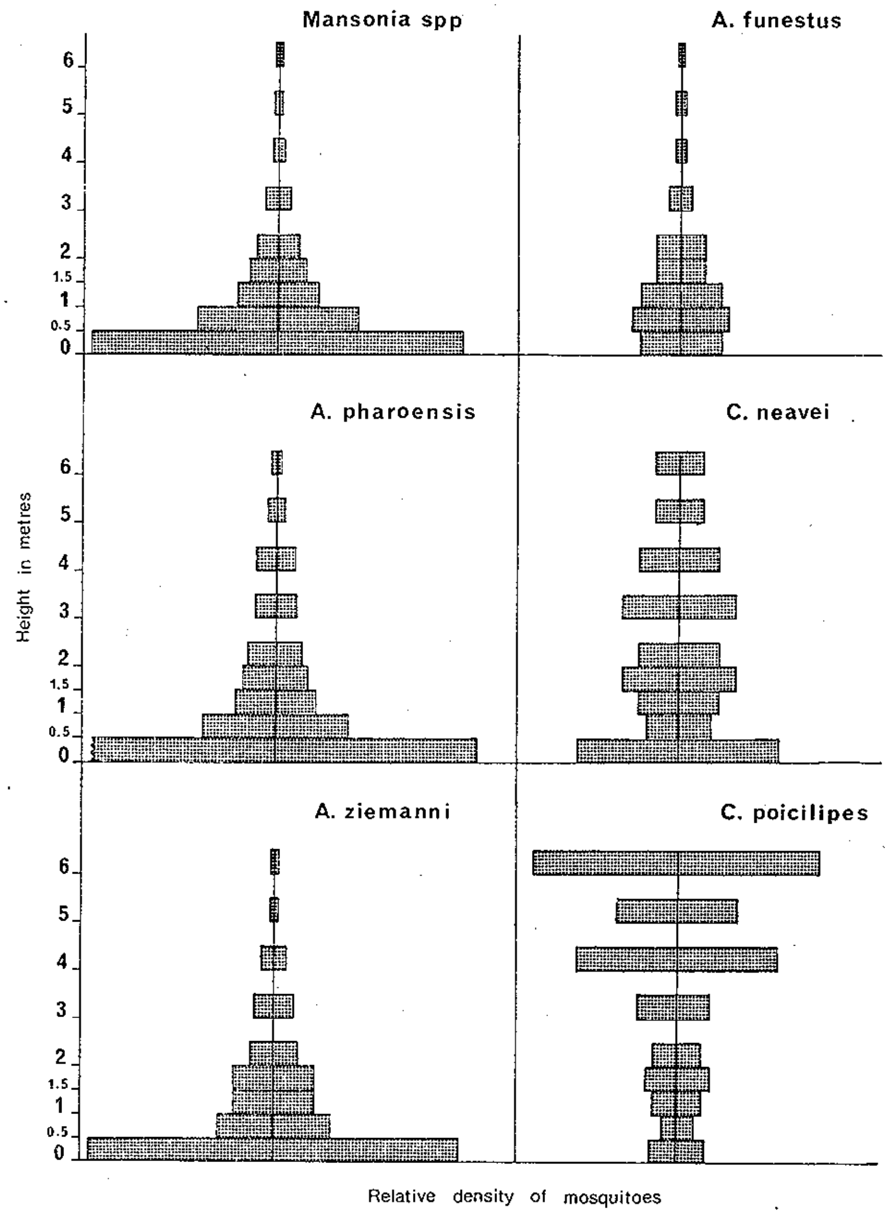

Fig. 1.—Vertical distribution of six species or groups of mosquitoes over open farmland to show low-flying species on the left and intermediate and high-level species on the right. All series combined.

TABLE II. *Vertical distribution of flying mosquitoes expressed as ratios of catch at each level to that at 1 m; all series of experiments combined*

		0 m	0·5 m	1 m	1·5 m	2 m	3 m	4 m	5 m	6 m
Low-flying group	*Aedes* spp.	8·56	3·33	1	1·02	0·37	0·36	0·47	0·15	0·20
	Mansonia spp.	4·59	2·03	1	0·71	0·51	0·25	0·15	0·09	0·04
	A. ziemanni	4·61	1·38	1	1·14	0·64	0·52	0·24	0·09	0·07
	A. pharoensis	5·02	1·84	1	0·83	0·67	0·42	0·54	0·21	0·14
	A. squamosus	5·17	1·94	1	0·82	0·68	0·24	0·12	0	0·12
Intermediate group	*A. funestus*	0·96	1·26	1	0·56	0·50	0·25	0·16	0·12	0·07
	A. gambiae		1·52	1		0·63	0·62	0·47	0·51	0·07
	C. neavei	2·51	0·80	1	1·35	1·09	1·42	0·97	0·57	0·51
High-flying group	*C. antennatus*	0·35	0·86	1	2·02	0·91	1·42	1·40	1·22	1·35
	C. thalassius			1		0·57	0·33	0·53	0·38	1·43
	C. poicilipes	1·19	0·69	1	1·33	0·98	1·71	4·19	2·52	5·91

of the two important malaria vectors, *A. gambiae* Giles and *A. funestus* Giles, this low level pattern is less marked. Species of *Culex* are generally flying at higher levels, this being particularly striking in *C. poicilipes* (Theo.) in which mean catches at 6 m are almost six times greater than those near the ground. It is clear from this that a large section of the population of *C. poicilipes* would have been flying above the highest level we were sampling and that the vertical profile illustrated is highly incomplete. Statistical analysis of the combined data is not possible, so that the significance of small differences in Table II cannot be estimated. However, the overall picture of differences between species is very clear.

A closer analysis of the shape of the profile within single species or groups can be made on the data in Series 4 in which traps were operated at seven levels from 0·5–6 m. Figure 2 shows the distribution of catches of *Mansonia* and *C. poicilipes* plotted on a log/log scale. The data for *Mansonia* (1643 mosquitoes) show a close fit to the regression line corresponding to $b = -1{\cdot}467$. The distribution for *C. poicilipes* (638 mosquitoes) shows no such simple relationship, although from 2 m to 6 m the distribution of densities is approximately linear ($b = +0{\cdot}381$).

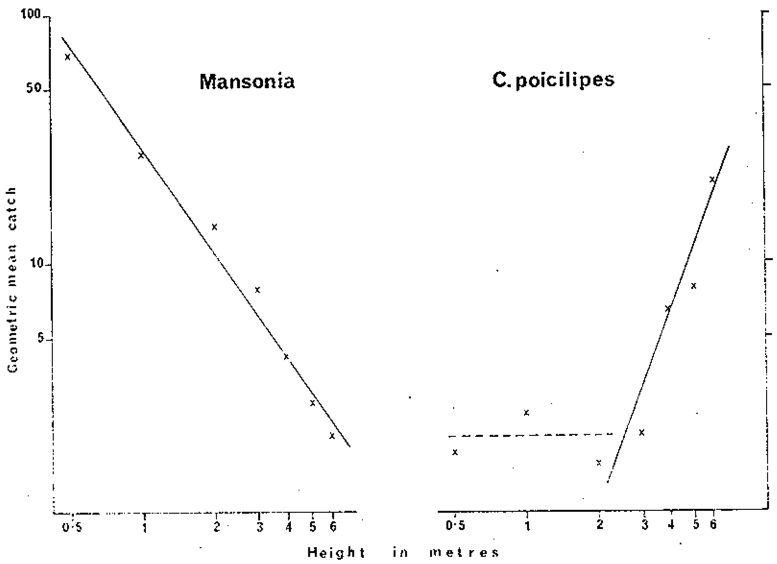

Fig. 2.—Vertical distribution of mosquitoes, Series 4 only.

Temporal differences

In the course of this work it became apparent that there were striking differences in the numbers caught at lower levels between the early catches (19.30–23.00 h) and the later catches (23.00–05.00 h). This behaviour was exhibited by all species. Catches of four of them were analysed in detail. Table III shows the ratios of geometric means at each level to the catch at 1 m for the two periods of the night separately. Catches at 1·5, 2 and 3 m and at 4, 5 and 6 m have been combined. The table shows that, in all four species, the catch at ground level is relatively much greater during the later period of the night. At 0.5 m this effect is much less marked and is indeed absent in the case of *A. funestus*. At the two higher levels there is no apparent difference in the distribution of catches during the night except in the case of *C. poicilipes* where there is a well-marked reduction at the highest level (4–6 m) after 23.00 h.

TABLE III. *Ratios of catch at each level to that at 1 m for early (19.30–23.00 h) and late (23.00–05.00 h) periods of the night*

	Period	0 m	0·5 m	1 m	1·5–3 m	4–6 m
Mansonia spp.	Early	3·22	1·29	1	0·57	0·10
	Late	9·97	2·76	1	0·47	0·09
A. ziemanni	Early	2·59	1·12	1	0·73	0·11
	Late	10·56	1·93	1	0·80	0·15
A. funestus	Early	0·85	1·26	1	0·50	0·15
	Late	2·27	1·32	1	0·33	0·10
C. poicilipes	Early	0·74	0·61	1	1·51	5·90
	Late	4·65	1·09	1	1·07	3·02

To test whether moonlight was responsible for this difference in flight level, catches were separated into moonlit and moonless periods. Moonlight was defined as present or absent when it was above or below the horizon for at least two-thirds of the trapping period. No account was taken of the phases of the moon or of cloud cover. The results of this analysis showed that the difference for the ratio of catches at 0 : 0·5 m was virtually uninfluenced by the moonlight factor. The differences in this ratio for the two periods were highly significant (χ^2 test, $P < 0{\cdot}001$) in all four species whether moonlight was present or not. Thus no evidence was found of any gross effect of moonlight on flight level.

Similar analysis was carried out to see if wind speed during the two periods could account for the differences in flight behaviour. During 16 nights, when traps were run at 0 m and 0·5 m, wind speed in the second period averaged $0{\cdot}51 \pm 0{\cdot}107$ m/s compared with $0{\cdot}38 \pm 0{\cdot}079$ m/s in the first. On seven nights when this slight difference in wind speed was reversed, that is, when the wind was equal to or greater during the first than in the second period, the ratio of catches of *Mansonia* at 0 : 0·5 m was 1·63 for the first and 3·31 for the second period. This shows that the same pattern of behaviour was followed independently of changes in wind speed in the two periods of the night. Further analysis was made of catches on 23 nights when traps were run at 0·5 and 1 m. Catches of *Mansonia* were separated into three categories according to whether the wind was less than 0·3 m/s, 0·3–0·9 m/s or 0·9–1·9 m/s. When the data were standardised for wind speed in this way, the ratio of catches at 0·5 : 1 m in the first period of the night was 1·66, 1·50 and 1·66 for the three grades. In the second period there were no occasions when the wind averaged less than 0·3 m/s; for the two higher categories the 0·5 : 1 m ratios were 3·03 and 2·71, respectively. Again this shows that the difference in flight pattern for the two periods was uninfluenced by variation in wind speed. It also shows that, within the range of wind speeds encountered, the level of flight of mosquitoes near the ground was not primarily determined by this factor.

A short series of temperature readings was taken near the ground on seven nights when low-level traps were operating. Maximum and minimum thermometers were fixed horizontally above dry, bare earth at levels of 50 cm and 10 cm and read at 19.00, 23.00 and 05.00 h. Maximum and minimum readings (to the nearest 0·5°C) were virtually identical at both levels at 27°C and 17°C, respectively. The observations did not exclude the possibility that finer temperature gradients were present, but they gave no evidence of any marked stratification of temperatures at these levels.

Biting catches

Table IV shows the results of 28 nights' biting catches. It will be seen that the vertical distribution of biting mosquitoes resembles that obtained by suction traps in the overall picture, but differs in detail. Thus *Aedes* and *Mansonia* have the highest proportion biting at 1 m, *A. gambiae* is active rather evenly up to 5 m, while the attack by *C. thalassius* Theo. and *C. poicilipes* increases with height above the ground. On the other hand, the numbers of *Mansonia* are much more evenly distributed at the higher levels and show no regression with height as with the suction trap catches.

TABLE IV. *Vertical distribution of biting mosquitoes expressed as ratios of catch* (M_w) *at each level to catch at 1 m*

	1 m	2 m	3 m	4 m	5 m	6 m	Total caught
Aedes spp.	1	0·20	0·24	0·18	0·33	0·16	220
Mansonia spp.	1	0·34	0·25	0·23	0·24	0·23	5586
A. gambiae	1	1·67	1·32	1	1·47	0·53	450
C. thalassius	1	1·26	0·92	1·1	1·23	3·25	334
C. poicilipes	1	1·90	2·09	2·33	10·61	5·68	229

Discussion

The problem we were studying concerned the dispersal at night of mosquitoes at low levels across a kilometre or two of flat, open terrain between breeding grounds and feeding sites. Although some females were undoubtedly newly emerged and not ready to feed, the bulk would have been engaged in search flights in the sense of Haskell (1966). This is evident from the similarity between the profiles for insects caught on human bait and those in suction traps. Their objective would, therefore, be warm-blooded hosts, and the stimuli that would convert search flights into upwind approach flights would be the physical and chemical components of the host-stream (Gillies & Wilkes, 1969). Their readiness to be 'distracted' by the appropriate stimuli shows that their flight cannot be described as migration as defined by Johnson (1969).

One of the most striking features of these results is the very high density of many species of mosquitoes flying just above the ground in the layer of air from 0 to 15 cm above the ground. It is noteworthy that the wind in the rainy season is nearly always light. In the extreme example of Series 7 the mean wind over six nights at 1·2 m was 0·17 m/s, yet catches of *Mansonia* and certain *Anopheles* at ground level during this period exceeded those at 1 m by a factor of more than 4. Under these conditions the boundary layer, that is, the layer of slower moving air near the ground within which wind speed is less than the flight speed of the insect (Taylor, 1958), should be relatively deep. So it would not appear that avoidance of unfavourable wind-speeds was primarily responsible for this behaviour. Then there is no evidence to suggest that, in flying between breeding grounds and villages, mosquitoes might settle periodically on ground vegetation. This factor is therefore also unlikely to affect flight level. It is possible that visual cues from the pattern of the ground underneath them might be important for orientation through optomotor mechanisms (Kennedy, 1940); but in the absence of any information on their direction of flight the point cannot be discussed further.

Without this information our understanding of the significance of the sort of vertical profiles that these studies reveal will remain limited.

The earliest observations on flight levels of African mosquitoes were made by Laarman (1959) who, using rotating nets, reported Anophelines as flying at heights not greater than 60 cm above the ground. Snow (1975), working near the coast in the Gambia, found that *Anopheles melas* (Theo.) (a member of the *A. gambiae* complex), *A. squamosus* (Theo.) and *Aedes* spp. were commonest at the lowest levels, while *C. thalassius* was more generally distributed up to 3 m and with a peak at 9 m. Although Snow was trapping at different intervals and up to a greater height than we were, the results from the two areas are in general agreement with each other. In particular, the behaviour of the banded species of *Culex*, *C. thalassius* and *C. poicilipes*, is strikingly different from other groups of mosquitoes. The latter species shows a more or less inverted profile with catches from 4 m upwards greater than at 1 m or below. At lower levels densities are rather evenly distributed right down to ground level.

The natural hosts of many mosquitoes are large mammals, including man. The large numbers caught by a ground-level (1 m) human bait in our experiments relative to those at 2 m, as shown in Table IV, suggest that the host has a fairly deep host-stream, probably extending down to ground level. Thus an insect should have equal chances of locating the host whether it flies just above the ground or up to a metre above it. Flight just above the ground cannot, therefore, be regarded as adaptive from the point of view of host-seeking. In the case of the high-flying group, exemplified by *C. poicilipes*, it might be thought that this would facilitate the locating of birds, especially those roosting in trees. It is known that this mosquito feeds on a wide range of hosts (P. F. Boreham, pers. comm.; Hamon *et al.*, 1964), including both mammals and birds. But on the evidence available it can hardly be described as a primarily ornithophilic species. In this respect also, explanation of vertical distribution does not find much support from feeding habits.

Most of our experiments were done with small numbers of traps, so that the figures of vertical distribution illustrated (Fig. 1) are composite ones, compiled over an extended period of time. This makes it difficult to compare our findings with the detailed analysis of a large number of taxa flying over open ground in England that were carried out by Taylor (1974). This showed that, when plotted on a log-log scale, profiles of nearly all insects revealed a discontinuity at a level below 1 m. Above this, density regressed steeply with height. Our data for *Mansonia* from the series in which traps were run at seven levels within the range 0·5–6 m (Fig. 2) show a similar regression ($b = 1{\cdot}467$). This is comparable to Taylor's figures for crepuscular (non-blood-sucking) Nematocera. It is also similar to the profiles for woodland mosquitoes given by Service (1971). On the other hand, *C. poicilipes* shows a reversed pattern with a regular increase in density from 2 m up to 6 m. This makes it clear that, even within a fairly homogeneous group like mosquitoes, differences in behaviour patterns between species may be more important determinants of vertical profiles than purely aerodynamic considerations. This conclusion is strengthened by a comparison of two species of *Anopheles*, *A. funestus* and *A. ziemanni* Grünb. The former with a wing length of 2·5–3 mm was one of the smallest mosquitoes trapped in these experiments, while *A. ziemanni*, with a wing of 5–5·5 mm, was one of the largest. If, for a given wind speed, flight speed was the main factor in determining level above the ground, it would have been expected that *A. funestus* would have been flying lower than *A. ziemanni*, whereas in fact the reverse was true.

We have to leave unresolved the problem of the lowering of flight levels in the later part of the night. That this applied to all groups of mosquitoes suggests that environmental factors were involved. Analysis is hampered by the fact that catches were only segregated into two periods of 3–4 and 6 h duration. Within these rather crude time divisions no effect of moonlight or wind speed could be demonstrated to account for the difference in behaviour. Snow (1975) also failed to find any lunar effect on vertical distribution in his studies. On calm nights temperature inversions in the lower atmosphere undoubtedly occurred; but it is doubtful whether, within the shallow layer of air we were sampling, this could be important. This is supported by the few temperature measurements we made below 1 m, where the greatest change in mosquito distribution was occurring and where no temperature stratification of the air could be demonstrated.

These studies demonstrate that groups of mosquitoes differ rather widely in the vertical profiles they adopt in flying across open country. The reasons for these differences remain obscure. But their existence suggests that the responses of mosquitoes to topographical features such as windbreaks and vegetation barriers will be at least partly influenced by species- or group-specific patterns of behaviour.

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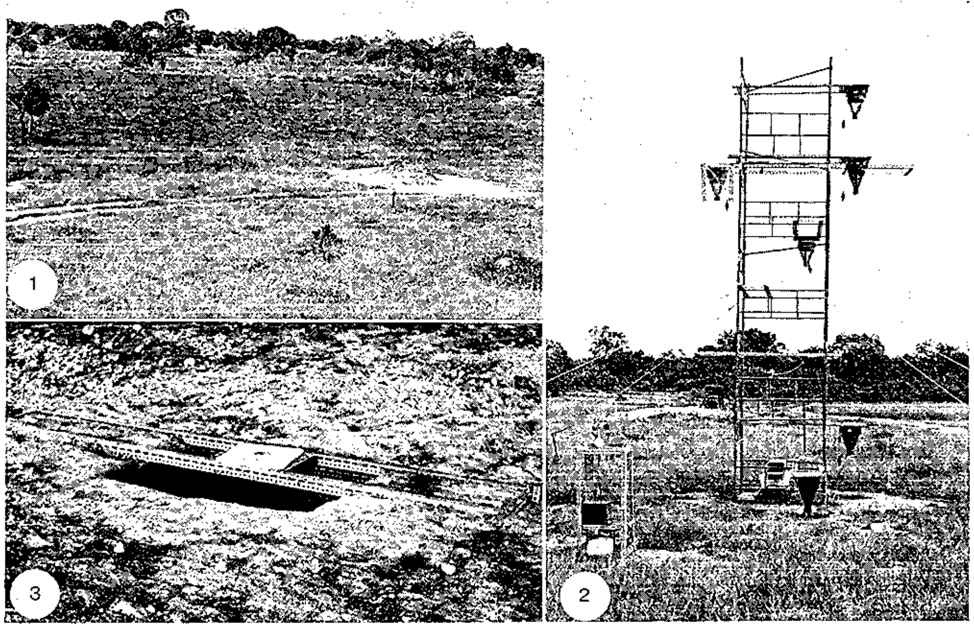

Fig. 1. General view of experimental area towards the village of Saruja. Fig. 2. Suction traps mounted on tower at levels from 0·5 to 6 m with shielded and unshielded traps at 5 m. Regenerating bush in the background. Fig. 3. Suction trap at ground level.