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INTRODUCTION

This paper continues the reports we have been making on the forest mosquito fauna associated with the appearance of sylvan yellow fever in Panama. The sequence of yellow fever cases recognized in Panama from 1948 to 1952 has been reviewed by Elton (1952). The present study was undertaken following the histopathological diagnosis of a fatal case of yellow fever contracted near Almirante, Panama, in April 1951.

In February 1951 a group of men were engaged by the "Corporación de Ingeniería" under contract to the government of Panama to survey the route for a projected road from Almirante, a town on the Bahia de Almirante which opens into the Caribbean Sea some 20 miles southeast of the Costa Rican border, to Boquete, a village set in a mountain valley on the southeast side of the Volcan de Chiriqui at an elevation of about 4,000 feet. The air line distance between these two places is only about 40 miles, but the intervening country is composed of a series of mountain ridges so that the length of the projected road was about 100 miles. The slopes of this portion of the Isthmus of Panama facing the Caribbean are covered by tropical rain-forest. While there are scattered groups of Indians living in the region, the route of the proposed road was uninhabited virgin forest only occasionally visited by hunters. It is about ten days by foot from Boquete to Almirante.

On February 7th the engineer in charge of the survey, together with three other men, set out from Boquete to make a preliminary reconnaissance of the terrain between Boquete and Almirante. About a week later, while in the vicinity of a mountain locally known as Cerro Cuna, and at an elevation of about 1,000 feet, the field party came across several dead spider monkeys in the forest. Because of the remoteness of the place where these monkeys were found, and the delay in receiving the report, no investigation of the possibility that the monkey mortality was due to yellow fever was made.

The actual transit survey was begun from Almirante later in February, and by the first week in April had progressed 11.6 kilometers into the forest. Here a clearing was made and a field camp consisting of several palm-thatched "ranchos" was established at an elevation of 625 feet. About thirty men were based here engaged in clearing the path of the transit line and in surveying. Every second Friday afternoon the men walked into Almirante to be paid, returning to the field camp on Sunday afternoon. The second weekend in April, however, the men remained in town until Monday morning the 9th to receive vaccinations for typhoid and yellow fever at the Chiriqui Land Company Hospital there. They

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returned on foot to the field camp on the afternoon of the same day. That night several of the men complained of a mild malaise—presumably a reaction to the typhoid vaccine. By Tuesday night, one of the men was seriously ill, and on Wednesday he was brought into the hospital at Almirante. The patient developed symptoms of yellow fever and died the following Sunday, April 15th. The clinical diagnosis was confirmed at autopsy and by histopathological examination of liver tissue. As the incubation period of yellow fever in man is generally accepted to be three to six days the infection must have been contracted only very shortly before vaccination. Dr. Gustav Engler, Medical Superintendent of the Almirante Hospital, has called to our attention two other recovered cases admitted about the same time which might be considered suspicious for yellow fever. These could not be confirmed by antibody tests as one had a history of having been vaccinated five months previously, and the other was vaccinated after his clinical episode before it was realized his illness might have been yellow fever. The possibility that yellow fever was contracted after vaccination cannot be excluded in light of the subsequent experience of Trejos and Romero (1954) in Costa Rica.

The circumstances under which yellow fever was contracted in the fatal case here reported were typical of the ecology of sylvan yellow fever. The patient had been a rodman with the survey crew. His duties required him to stand still in the lane freshly cleared through the forest. We know that under these conditions the predominantly arboreal mosquitoes attack at ground level.

On May 14, 1951 we went to Almirante to explore the possibility of making a long-term study of the forest mosquito fauna in the immediate area where yellow fever had been contracted. We found that the road survey had been abandoned, but that the palm-thatched shelters in the forest clearing at the survey base camp would be available to us for the establishment of a semi-permanent field camp. Basic supplies were brought into the field camp by mule. Arrangements were made for the simultaneous collection of the mosquitoes attacking human subjects on the ground and in the forest canopy on four days a week, and for the weekly shipment of the mosquito collections from Almirante to the Gorgas Memorial Laboratory in Panama City by air. Four trees were selected for collecting stations. Crossbars were nailed to the trees and platforms constructed in the crotches of the branches. The trees were all located within a half-mile radius of the field camp. The heights of the platforms above the ground were 48 feet, 39 feet, 54 feet and 36 feet. In October 1951 the tree with the 48 foot platform was blown down in a storm and another tree substituted. The replacement platform was 52 feet high. The four stations were located at elevations between 400 and 625 feet above sea-level. Collections were made on one day of each week at each station, with one man acting as both bait and collector on the ground at the foot of the tree station, and another on the platform in the canopy. This routine was followed for a two-year period from May 1951 through April 1953. Collections of all mosquitoes approaching to bite were made between 9:00 A.M. to 3:00 P.M. To obtain, also, some measure of the crepuscular and nocturnal mosquito populations, collections were made from 6:00 P.M. to 10:00 P.M. one evening each week, but only during a part of the study. The general aspect of the study area is shown in Figures 1 and 2.

FIG. 1. The clearing used as a base camp for the two year study of the sylvan mosquito fauna near Almirante, Panama. The density of the vegetation in this region of tropical rain-forest is apparent.

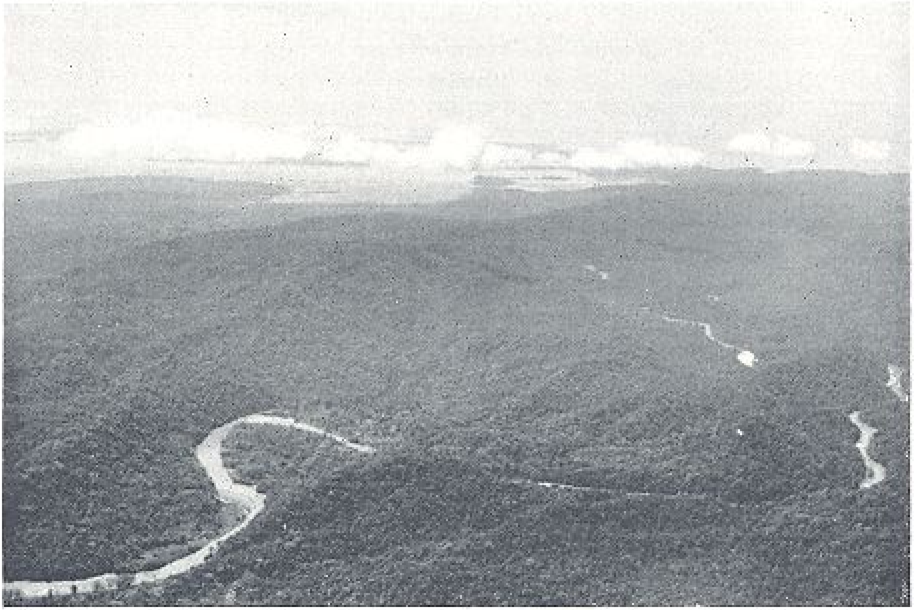

FIG. 2. An aerial view of the unbroken virgin tropical rain-forest inland from Almirante, Panama, where the study reported here was carried out. The Bahia de Almirante may be seen in the distance; the river in the foreground and to the right is the Rio Changuinola. The forest tree stations were located on the ridge in the center of the photograph.

THE ENVIRONMENT

Rainfall. Directly behind Almirante there rises a series of complex ridges culminating in the highest point in Panama, the summit of the Volcan de Chiriqui with an elevation of 11,410 feet. There is thus extreme uplifting of the air mass of the moist northeasterly trade winds moving inland from the Caribbean Sea. In consequence heavy rainfall is experienced throughout the year. Table 1 gives rainfall figures based on the monthly averages of four stations maintained by the Chiriqui Land Company at Changuinola and vicinity for the years 1951 to 1953, the averages for these three years and the averages for a nine-year period. The Changuinola rain gauges are about 15 miles north of the location of the tree stations and at a lower elevation. While the day to day rainfall recorded at these gauges is no doubt different from that which falls at the forest tree stations, the annual distribution is much the same. These data serve to illustrate the lack of any pronounced annual dry season. On the Pacific side of Panama and the Atlantic side in the vicinity of the Canal Zone and the region to the east, where the mountain ridges are low, a distinct dry season occurs during the low-sun period from January through April. The local orographic situation at Almirante modifies this rainfall pattern. It will be seen from the three and nine-year summaries that on the average it is September which has the least rainfall, although there is no really "dry" month.

Vegetation. These rainfall data, together with the temperature data given below, meet the requirements of the "*Af*" or "tropical rain-forest climate" as

TABLE 1

Rainfall at Changuinola and vicinity

(In inches)

	1951	1952	1953	Three year average (1951–53)	Nine year average (1945–53)
January	6.39	13.83	9.75	9.99	8.23
February	19.81	3.70	7.57	10.36	7.51
March	5.44	2.24	3.15	3.61	4.81
April	5.96	5.97	3.31	5.08	6.03
May	5.43	3.85	7.08	5.45	10.34
June	10.45	3.57	7.02	7.01	10.08
July	16.50	8.23	11.42	12.05	11.64
August	12.28	2.62	17.20	10.70	8.36
September	4.65	3.58	1.92	3.38	3.82
October	6.29	13.46	5.83	8.53	5.97
November	7.60	4.41	15.30	9.10	11.02
December	7.00	12.96	9.93	9.96	12.33
Total	107.80	78.42	99.48	95.22	100.14

defined in the Köppen climatic system.[2] Thus, wherever either cultivation by man or special soil conditions have not intervened, the region is clothed in true tropical rain-forest. Such forest is characterized by a dense evergreen broad-leaved canopy, through which very little sunlight penetrates to the forest floor. The ground, therefore, is singularly free of annual herbaceous vegetation except where there may be a break in the canopy such as that caused by a large fallen tree, or along the margins of water courses cutting through the forest.

Climate and microclimate. The ultimate assessment of the ability of a region to maintain yellow fever transmission depends as much on the accurate and detailed measurement and evaluation of the microclimate as it does on the presence of vector and host. In fact, the presence of these also will have been determined in considerable measure by the elements of the climate. Thus we took opportunity at the Almirante stations to record for a typical sylvan yellow fever situation in well-developed tropical rain-forest the details of the climate and microclimate for the period of a year.

The climate and microclimate of an area of tropical rain-forest in Colombia in relation to captures of forest mosquitoes have been studied by Bates (1944 and 1945). Allee (1926) has also given some information on microclimatic differences between the forest floor and the canopy in terms of temperature, evaporation and light for a short period at Barro Colorado Island in the Canal Zone. At the Almirante forest stations we operated a pair of Bendix-Friez hygrothermographs for a fifteen-month period. One instrument was placed three feet above the ground and the other on a platform 40 feet high in the canopy. As it was necessary to protect the instruments from the elements in conventional louvered

[2] A brief exposition of the Köppen world climatic system in English will be found in Trewartha, 1954.

weather shelters, the readings are less extreme than those which would be gotten in the open. Free-flying insects in the sunlight of the canopy would experience higher temperatures and lower humidities than those recorded by the sheltered hygrothermograph. Nevertheless the differences in temperature and humidity conditions near the ground and in the canopy of a tropical rain-forest are nicely illustrated by months for a year's period in Figure 3. The monthly mean figures for temperature and relative humidity are based on bi-hourly readings from the tracings of the recording instruments. The monthly maxima and minima are averages calculated from the daily maxima and minima.

Since we unfortunately did not operate a rain gauge at the forest tree station where the hygrothermographs were located, we cannot closely relate rainfall to temperature and humidity conditions. This can be done in a general way, however, by using the rainfall figures from Changuinola.

Annual temperature cycle. For the annual march of temperatures we may refer to the monthly means near the ground. (See Figure 3.) The lowest mean monthly ground temperature, 71.7°F., was in January; the highest, 76.6°F. was in May. The extreme difference during the year was thus but 4.9°F. In terms of the environment experienced by the diurnal canopy mosquitoes the maximum figures are more significant. The variation during the year is not, however, very much greater, though the readings are, of course, in a higher range. The lowest maximum figure was that for January, 75.6°F., the highest maximum in September, 81.0°F.; the difference being 5.4°F. As the station was at about 9°15′N., the effect of latitude is evident but not extreme. The highest temperatures are not in July or August as might be expected from latitude effect alone, since the high rainfall at this time of year exercises a cooling effect.

Comparison of temperatures near the ground and in the canopy. The differences in maximum, mean and minimum temperatures near the ground and in the canopy may also be seen in Figure 3. For the year, the magnitude of the difference in temperatures near the ground and in the canopy was 1.6°F. for the maxima, 1.0°F. for the means, and 0.6°F. for the minima. The greater difference in the case of the maxima is no doubt due to the greater exposure of the canopy instrument shelter to sunlight during the day. The lesser difference in minimum figures is due to the fact that at night, when the minimum temperature conditions are experienced, there is less temperature gradient between the air near the ground and that in the canopy. From the point of view of the diurnal mosquitoes of special interest to us, the maximum temperature figures are the significant ones. The 1.6°F. difference recorded for the daily maxima under sheltered conditions would have been much greater had the recording instruments been unshaded; for then the canopy instrument would have been subject to direct sunlight a good deal of the time, while the instrument near the ground would have been struck only by occasional beams of sunlight penetrating to the forest floor.

Annual relative humidity cycle. Month-by-month differences in relative humidity are less pronounced than those shown by the temperature record. The high for the year, recorded in December, may be related to the high rainfall at

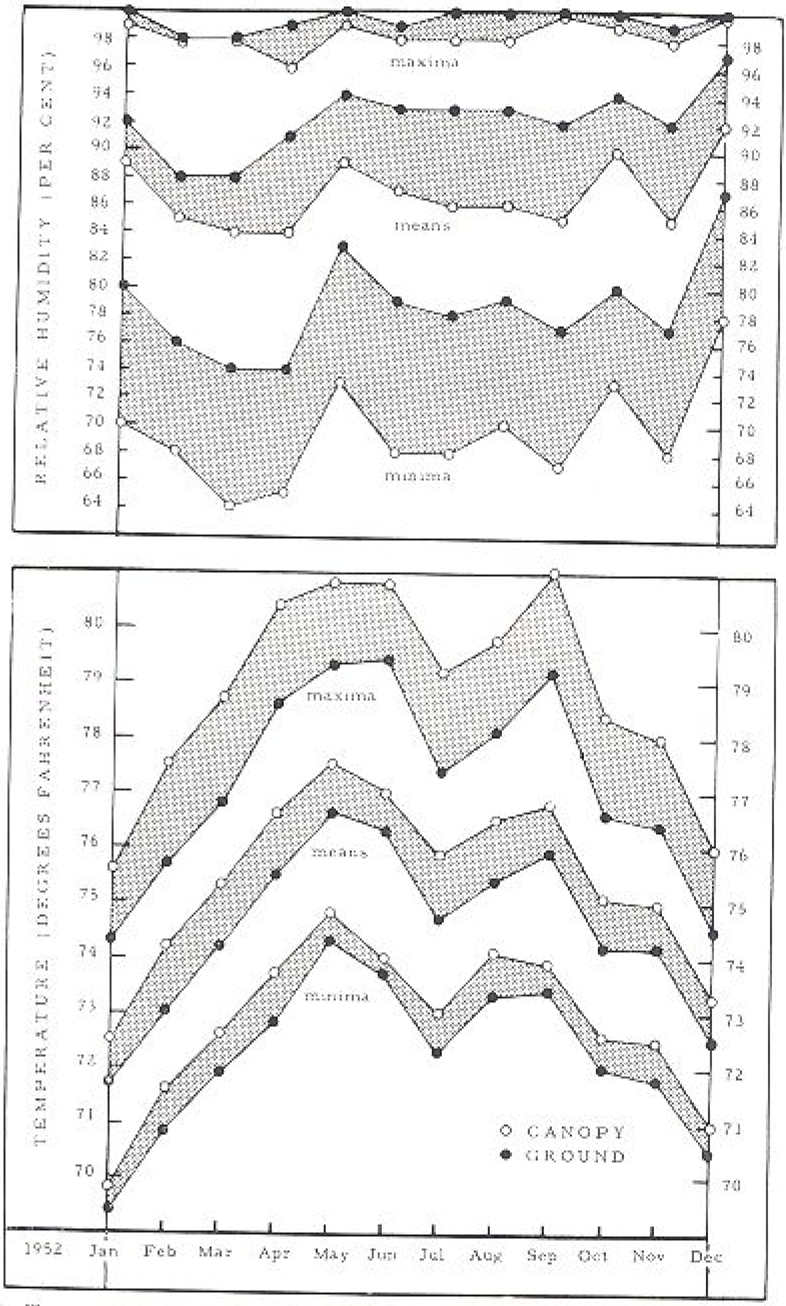

FIG. 3. Temperature and relative humidity during a year period at ground level and in the canopy of the tropical rain-forest near Almirante, Panama.

that time of year. Most striking is the height of the humidity level maintained in this tropical rain-forest. The monthly average of the mean relative humidities near the ground ranged between 88 and 97 per cent. The lowest relative humidity in the canopy was 64 per cent in March. The maximum relative humidity was either at or near saturation throughout the year both at ground level and in the canopy.

Comparison of relative humidities near the ground and in the canopy. The greatest differences in relative humidity readings at ground level and in the canopy appear in the averages determined from the daily minima which occur during the daylight hours when most canopy mosquitoes are active. The average difference in the minima for the year period is 9.3 per cent. The differences in the maxima which occur at night are very slight, the average difference for the year being but 1.2 per cent. It has been suggested that to maintain canopy-inhabiting diurnal *Haemagogus* mosquitoes in captivity it is desirable to keep them at lower humidity levels than those suitable for such crepuscular or night-flying mosquitoes as the anophelines. This has not been our experience with two arboreal mosquitoes, *Haemagogus equinus* and *Sabethes chloropterus*, which we have established in laboratory colonies. The difficulty in the laboratory has been that of maintaining sufficiently high humidity to prevent excessive mortality of adults. While there is a substantial spread between the canopy and ground relative humidity readings as shown by the minima in Figure 3, this spread occurs only during the sunlight hours of the day when, it is true, the canopy mosquitoes are active. But during the night, and during the periods of rain, mist and heavy overcast which account for a good part of the day in the tropical rainforest climate in which these mosquitoes occur, there is very little difference between the relative humidity at canopy and ground level. Even during hours of sunshine, unless the canopy mosquitoes are seeking food or are mating, they probably spend much time at rest in the humid microclimate associated with the surface of leaves and branches. The microclimate of these resting places is at least as important as that which is encountered when they are in flight.

Mosquito captures

Summaries of the diurnal and evening mosquito captures made during the two years of this study are given in Tables 2 and 3. Table 2 also shows for each species the proportion of the catch taken in each yearly period, corrected for the number of man hours of collecting effort. The distribution of the diurnal catch between the canopy and the ground stations is shown in Table 4, and for the evening catch in Table 3. As the evening collections were carried on only once a week during 13 months no breakdown of the catch into yearly periods is made. In all the tabulations the figures refer to numbers of female mosquitoes only. Males which incidentally approached the human baits were not included in the workup of the data.

Haemagogus. The total numbers of *Haemagogus equinus* and *H. spegazzinii falco* were approximately the same, but the proportions taken during each yearly period were different. The *equinus* were taken in approximately equal numbers during each yearly period while the *spegazzinii falco* were about twice as abundant in the first year as in the second. *Haemagogus lucifer* was somewhat less common than the other two species of the genus and the numbers taken during each of the two yearly periods were fairly even. The fact that the numbers of *spegazzinii falco* approximate those of *equinus* we consider significantly related to the climate

TABLE 2

Summary of diurnal mosquito captures at tree stations near Almirante during a two-year period

	May 1951–April 1952	May 1952–April 1953	Two year total	Per cent captured during 1951–52	Per cent captured during 1952–53
Number of man hours collecting	2,036	1,865	3,901		
Tribe Culicini					
Haemagogus equinus	569	582	1,151	47	53
Haemagogus lucifer	576	407	983	56	44
Haemagogus spegazzinii falco	794	347	1,141	68	32
Total *Haemagogus*	1,939	1,336	3,275	57	43
Aedes (Finlaya) leucocelaenus clarki	318	543	861	35	65
Aedes (Finlaya) leucotaeniatus	138	159	297	44	56
Aedes (Finlaya) terrens	40	11	51	77	23
Aedes (Howardina) quadrivittatus	9	19	28	30	70
Aedes (Howardina) septemstriatus	25	7	32	76	24
Aedes (Howardina) sexlineatus	55	79	134	39	61
Aedes (Ochlerotatus) angustivittatus	49	405	454	10	90
Aedes (Ochlerotatus) fulvus	1	4	5	19	81
Aedes (Ochlerotatus) hastatus	0	18	18	0	100
Aedes (Ochlerotatus) serratus group	253	1,518	1,771	13	87
Psorophora (Janthinosoma) ferox	99	2,352	2,451	4	96
Psorophora (Janthinosoma) lutzii	182	735	917	19	81
Psorophora (Grabhamia) cingulata	16	17	33	46	54
Mansonia (Mansonia) indubitans	2	9	11	17	83
Mansonia (Mansonia) titillans	27	6	33	81	19
Mansonia (Rhynchotaenia) arribalzagae	79	11	90	87	13
Mansonia (Rhynchotaenia) nigricans	2	0	2	100	0
Mansonia (Rhynchotaenia) venezuelensis	15	49	64	22	78
Culex (Carrollia) secundus	3	4	7	42	58
Culex (Culex) sp.	4	148	152	3	97
Culex (Melanoconion) sp.	2	23	25	8	92
Culex (Microculex) sp.	0	2	2	0	100
Total Culicini	3,258	7,455	10,713	29	71
Tribe Sabethini					
Trichoprosopon (Trichoprosopon) digitatum	102	46	148	67	33
Trichoprosopon (Ctenogoeldia) magnus	484	184	668	71	29
Trichoprosopon (Isogoeldia) espini	95	77	172	53	47
Trichoprosopon (Rhunchomyia) lampropus	13	5	18	70	30
Trichoprosopon (Rhunchomyia) leucopus	160	289	449	34	66
Trichoprosopon (Rhunchomyia) longipes	36	19	55	63	37
Trichoprosopon (Rhunchomyia) rapax	1	5	6	16	84
Trichoprosopon sp.	20	8	28	69	31
Wyeomyia (Wyeomyia) abebela	1	0	1	100	0
Wyeomyia (Wyeomyia) celaenocephala	50	3	53	94	6
Wyeomyia (Wyeomyia) hemisagnosta	2	0	2	100	0
Wyeomyia (Wyeomyia) mitchelli	2	0	2	100	0
Wyeomyia (Wyeomyia) nigritubus	4	0	4	100	0
Wyeomyia (Wyeomyia) quasiluteoventralis	1	0	1	100	0
Wyeomyia (Wyeomyia) scotinomus	24	0	24	100	0
Wyeomyia (Wyeomyia) sp.	10,230	11,393	21,623	45	55

TABLE 2—*Continued*

	May 1951–April 1952	May 1952–April 1953	Two-year total	[1]Per cent captured during 1951–52	Per cent captured during 1952–53
Number of man hours collecting	2,036	1,865	3,901		
Wyeomyia (Dendromyia) aporonoma	6	3	9	64	36
Wyeomyia (Dendromyia) circumcincta	2	0	2	100	0
Wyeomyia (Dendromyia) jocosa	28	0	28	100	0
Wyeomyia (Dendromyia) sp.	4,624	2,912	7,536	59	41
Wyeomyia (Davismyia) arborea	14	10	24	56	44
Limatus asulleptus	165	314	479	33	67
Limatus durhami	12	7	19	61	39
Sabethes (Sabethes) cyaneus	201	120	321	61	39
Sabethes (Sabethes) tarsopus	90	141	231	37	63
Sabethes (Sabethoides) chloropterus	1,736	1,879	3,615	46	54
Total Sabethini	18,103	17,415	35,518	49	51
Tribe Anophelini					
Anopheles (Anopheles) apicimacula	6	13	19	29	71
Anopheles (Anopheles) eiseni	7	4	11	62	38
Anopheles (Anopheles) punctimacula	1	3	4	24	76
Anopheles (Nyssorhynchus) albimanus	0	1	1	0	100
Anopheles (Kerteszia) neivai	139	15	154	89	11
Chagasia bathanus	14	8	22	62	38
Total Anophelini	167	44	211	78	22
Total all species	21,528	24,914	46,442	44	56

[1] Percentages corrected for differences in number of man hours of collecting during each year period.

and forest type in which these collections were made. In our previous studies in central Panama and the Canal Zone (Galindo *et al.*, 1950) and throughout the length of the Pacific side of Panama and adjacent Costa Rica (Trapido *et al.*, 1955) we had found *equinus* to be approximately six to eight times as abundant as *spegazzinii falco*. In these previous surveys the numbers of *spegazzinii falco* were found to more nearly approach the numbers of *equinus* in only two circumstances. In the survey reported in 1950 one group of stations near Buena Vista was operated only from October to the beginning of January in an attempt to recover virus in a forest where a fatal case of yellow fever had been contracted. In this instance the number of *equinus* taken was less than twice the number of *spegazzinii falco*. In the study reported in 1955 only slightly less than half as many *spegazzinii falco* as *equinus* were taken at the stations at Tucué. The Buena Vista stations, while in an area of tropical semideciduous forest, were operated only during the fall peak rain period; the Tucué stations were just over the continental divide on the Caribbean slope in an area with vegetation approaching the tropical rain-forest type. It seems clear that populations of *spegazzinii falco* develop best in tropical rain-forest or under climatic conditions approaching those which support forest of this type. Under these conditions

TABLE 3

Summary of evening mosquito captures at tree stations near Almirante during the period July 1951 to May 1953
(Collections made from 6–10 P.M.)

	Total	Per cent captured[1]	
Number of man hours collecting	295	Canopy	Ground
Tribe Culicini			
Haemagogus equinus	2	100.0	0.0
Haemagogus lucifer	1	100.0	0.0
Haemagogus spegazzinii falco	3	100.0	0.0
Total *Haemagogus*	6	100.0	0.0
Aedes (Finlaya) leucocelaenus clarki	2	100.0	0.0
Aedes (Finlaya) leucotaeniatus	2	100.0	0.0
Aedes (Finlaya) fluviatilis	1	0.0	100.0
Aedes (Howardina) sexlineatus	4	100.0	0.0
Aedes (Ochlerotatus) angustivittatus	22	4.4	95.6
Aedes (Ochlerotatus) serratus group	97	14.2	85.8
Psorophora (Janthinosoma) ferox	16	17.1	82.9
Psorophora (Janthinosoma) lutzii	6	47.6	52.4
Psorophora (Grabhamia) cingulata	118	11.4	88.6
Mansonia (Mansonia) indubitans	12	83.3	16.7
Mansonia (Mansonia) titillans	3	47.6	52.4
Mansonia (Rhynchotaenia) arribalzagae	10	51.4	48.6
Mansonia (Rhynchotaenia) venezuelensis	119	33.8	66.2
Culex (Culex) inflictus	1	100.0	0.0
Culex (Culex) sp.	467	70.6	29.4
Culex (Melanoconion) menytes	120	80.3	19.7
Culex (Melanoconion) taeniopus	10	31.2	68.8
Culex (Melanoconion) sp.	206	61.9	38.1
Culex (Microculex) sp.	5	100.0	0.0
Culex sp.	36	83.3	16.7
Orthopodomyia fascipes	2	100.0	0.0
Total *Culicini*	1,265	49.8	50.2
Tribe Sabethini			
Trichoprosopon (Ctenogoeldia) magnus	2	100.0	0.0
Trichoprosopon (Rhunchomyia) leucopus	1	100.0	0.0
Wyeomyia (Wyeomyia) mitchelli	1	100.0	0.0
Wyeomyia (Wyeomyia) scotinomus	2	100.0	0.0
Wyeomyia (Wyeomyia) sp.	14	85.4	14.6
Sabethes (Sabethoides) chloropterus	4	100.0	0.0
Total *Sabethini*	24	91.2	8.8
Tribe Anophelini			
Anopheles (Anopheles) apicimacula	37	11.1	88.9
Anopheles (Anopheles) eiseni	1	0.0	100.0
Anopheles (Kerteszia) neivai	120	100.0	0.0
Anopheles sp.	11	100.0	0.0
Chagasia bathanus	266	99.2	0.8
Total *Anophelini*	435	85.5	14.5
Total all species	1,724	57.8	42.2

[1] Percentages corrected for differences in number of man hours collecting on the ground and in the canopy.

populations of *equinus* are smaller than they are in the more open tropical deciduous forests associated with a rainfall pattern exhibiting a marked dry season such as that experienced on the Pacific side of Panama.

The numbers of *Haemagogus* taken in the evening collections as shown in Table 3 were negligible.

TABLE 4

Vertical distribution of diurnal forest mosquitoes

Tropical rain-forest at Almirante compared with tropical deciduous forest of the Pacific slope of Panama

Species	Almirante (Tropical rain-forest)			Pacific Slope[1] (Tropical deciduous forest)		
	Per cent captured		Number taken	Per cent captured		Number taken
	Canopy	Ground		Canopy	Ground	
Haemagogus equinus	97.8	2.2	1,151	69.1	30.9	6,431
Haemagogus lucifer	98.7	1.3	983	67.1	32.9	3,351
Haemagogus spegazzinii falco	99.6	0.4	1,141	80.7	19.3	743
Aedes leucocelaenus clarki	94.1	5.9	861	65.7	34.3	966
Aedes leucotaeniatus	39.7	60.3	297	40.1	59.9	434
Aedes terrens	10.0	90.0	51	17.4	82.6	1,533
Aedes quadrivittatus	96.5	3.5	28	74.3	25.7	2,227
Aedes septemstriatus	9.2	90.8	32	14.3	85.7	46
Aedes sexlineatus	96.4	3.6	134	10.9	89.1	16
Aedes angustivittatus	2.2	97.8	454	16.7	83.3	804
Aedes hastatus	0.0	100.0	18			
Aedes serratus group	2.0	98.0	1,771	9.8	90.2	2,476
Psorophora ferox	10.9	89.1	2,451	23.2	76.8	6,180
Psorophora lutzii	38.3	61.7	917	23.0	77.0	867
Psorophora cingulata	0.0	100.0	33	19.7	80.3	173
Mansonia titillans	18.4	81.6	33	8.7	91.3	877
Mansonia arribalzagae	2.2	97.8	90			
Mansonia venezuelensis	3.1	96.9	64	24.1	75.9	293
Trichoprosopon digitatum	2.0	98.0	148	15.9	84.1	71
Trichoprosopon magnus	87.5	12.5	668	73.0	27.0	8,257
Trichoprosopon espini	82.7	17.3	172	60.1	39.9	84
Trichoprosopon lampropus	0.0	100.0	18			
Trichoprosopon leucopus	2.4	97.6	449	0.0	100.0	19
Trichoprosopon longipes	0.0	100.0	55	20.8	79.2	2,049
Wyeomyia celaenocephala	9.6	90.4	53			
Wyeomyia scotinomus	17.1	82.9	24			
Wyeomyia jocosa	0.0	100.0	28	28.3	71.7	261
Wyeomyia arborea	95.9	4.1	24	100.0	0.0	20
Limatus asulleptus	0.2	99.8	479	2.8	97.2	195
Limatus durhami	5.2	94.8	19	14.6	85.4	120
Sabethes cyaneus	84.5	15.5	321	87.4	12.6	348
Sabethes tarsopus	99.2	0.8	231	87.4	12.6	655
Sabethes chloropterus	98.1	1.9	3,615	75.9	24.1	3,170
Anopheles apicimacula	0.0	100.0	19	10.3	89.7	226
Anopheles neivai	70.9	29.1	154	40.3	59.7	183
Chagasia bathanus	95.6	4.4	22	85.8	14.2	26
Total			17,008			43,101

[1] Data from Trapido, Galindo and Carpenter, 1955.

Two taxonomic points with regard to the *Haemagogus* at the Almirante stations should be noted. *H. lucifer* is replaced in nearby Costa Rica and in Nicaragua by *Haemagogus iridicolor*, the females of which are indistinguishable from *lucifer*. *H. iridicolor* has also been taken by us along the shores of the Bahia de Almirante in Panama. But a series of males reared from eggs of females taken at the inland forest tree stations were all *lucifer*, and all males taken there were also *lucifer*, so we believe we are correct in assuming that the species in that area is *lucifer*. At the time this study was made *Haemagogus mesodentatus* was known only from the type description based on material from San José, Costa Rica (Komp and Kumm, 1938) and notation of its presence in El Salvador (Kumm and Zuñiga, 1942). The type description did not mention a critical character of the female, namely the presence of a silvery white band of scales at the tip of the mid and hind femora, which is also a primary field character for identifying *H. equinus*; no other Panamanian *Haemagogus* was known to be thus marked at the time. In a substantial topotype series of *mesodentatus* we subsequently obtained at San José we found the white "knee spots" to be present in females as they are in *equinus*. We have also been able to determine more recently that *H. mesodentatus* ranges southeast into Panama in the forests of Bocas del Toro Province between Caldera and Chiriquicito. In unrubbed specimens the females of *mesodentatus* may be readily separated from *equinus* by another character, the silvery grey scales of the mid-tarsi. At the time of the Almirante study we did not suspect the presence of *mesodentatus* in Panama and this was not a character we checked in routine identification work. But after we became familiar with *mesodentatus* we found its distribution to be quite local in the southern part of its range in Costa Rica and Nicaragua. This is a species whose populations in our experience reach their full development far to the northwest in Guatemala and Mexico. Thus it does not follow from the fact that it is present in the area between Caldera and Chiriquicito that it was also present at the forest stations near Almirante. On recently checking a representative sample of white kneed *Haemagogus* which were saved from the Almirante collections we have found all to be *equinus*. While it remains a possibility that *mesodentatus* as well as *equinus* was present at the Almirante forest stations we are inclined to think that we did not overlook it there.

Aedes. Four species of the subgenus *Finlaya* were taken at the Almirante forest stations. Most abundant of these was *Aedes leucocelaenus clarki*. This is a species of particular interest since it, like *H. spegazzinii falco*, has been proven to be a vector of sylvan yellow fever in South America (See Whitman, 1951). In previous surveys in Panama this species had been about as abundant as *H. spegazzinii falco*, but at Almirante it was outnumbered by the latter. As in the case of *spegazzinii falco*, approximately two-thirds of the specimens were taken in one year and one-third in the other. But, curiously, the greater number was taken in the 1952–53 year period while *spegazzinii falco* was more abundant in 1951–52. We have no explanation of why this should be so. This shows, however, that the factors which govern the production of tree-hole-breeding mosquitoes are complex. A rainfall pattern which yields a high production of one tree-hole-breeding species in a particular year does not necessarily affect other tree-hole-breeding species in the same way. *Aedes leucotaeniatus*, which is very closely related to *leucocelaenus clarki*, was much less abundant than the latter species. What currently goes under the name *Aedes terrens* is more than one species. The lowland form does not attack man readily and was not very common in the Almirante collections. Although the numbers of *Finlaya* taken in the evening collections was insignificant, it was in the evening that one specimen of *Aedes fluviatilis* was taken.

Three species taken of the *Aedes* subgenus *Howardina* were *quadrivittatus*, *septemstriatus* and *sexlineatus*. These also breed in water containers; *septemstriatus* in tree holes and the other two species in bromeliads. They were not abundant in the collections attacking man. Only *sexlineatus* appeared in the evening collections.

Four ground pool breeders of the subgenus *Ochlerotatus* were taken: *angustivittatus*, *fulvus*, *hastatus* and the *serratus* group. The mosquitoes of the *serratus* group were not identifiable as to species on the basis of the females taken attacking man. Light traps operated at the Almirante stations during a portion of this study took males of several species in this group. They will be dealt with in another paper specifically treating taxonomic and distributional problems. Only the *serratus* group and *angustivittatus* were common. All four species illustrate how irregular the hatches of these mosquitoes may be in nature. The bulk of the collections appeared in the 1952–53 year period. Only the commoner forms, *angustivittatus* and the *serratus* group were taken in the evening collections

Psorophora. Psorophora lutzii and *ferox* were both abundant, with about three times as many *ferox* as *lutzii* being taken. These ground-pool-breeding species were much more abundant in the second year of the study than they were in the first, as was the case with the ground-pool-breeding *Aedes*. Both species are diurnal as may be seen by comparison of the numbers caught during the day in Table 2 with the numbers caught at night given in Table 3. *Psorophora cingulata*, on the other hand, was uncommon in the diurnal collections but much outnumbered the other two *Psorophora* in the evening collections. This species is clearly crepuscular or nocturnal unlike *lutzii* and *ferox*.

Mansonia. The *Mansonia* mosquitoes which are primarily crepuscular and nocturnal, and breed attached to the roots of vegetation in swamps were not very abundant at the Almirante forest stations which were on elevated slopes. Five species of two subgenera were taken: *indubitans* and *titillans* of the subgenus *Mansonia*, and *arribalzagae*, *nigricans* and *venezuelensis* of the subgenus *Rhynchotaenia*. *M. venezuelensis*, in the evening collections, was the commonest species.

Culex. As the identification of the *Culex* depends primarily on characters of the male terminalia few of these were determined to species. Only one form was identified to species in the diurnal collections, *Culex secundus*. In the evening collections the three species *inflictus*, *menytes* and *taeniopus* were determined. It was not previously realized that the species *menytes* and *taeniopus* bite man.

Trichoprosopon. *Trichoprosopon* of four subgenera and seven species were taken. In order of greatest to least abundance in the diurnal catch the species were *magnus*, *leucopus*, *espini*, *digitatum*, *longipes*, *lampropus* and *rapax*. Only the first four species were moderately abundant. The relatively large numbers of *Trichoprosopon magnus*, a species breeding in a *Calathea* characteristic of swampy situations, is explained by the presence of a small open spring-fed bog in the forest near the tree stations. This species is of some interest in the epidemiology of sylvan yellow fever as it was the commonest arboreal mosquito present during an epizootic of the disease investigated on the north coast of Honduras in 1954 (Trapido and Galindo, 1955). *Trichoprosopon* were rare in the evening collections, only two specimens of *magnus* and one of *leucopus* being taken.

Wyeomyia. The identification of female *Wyeomyia* to species is difficult or impossible if the scales are rubbed; thus these mosquitoes were for the most part determined only to subgenus. Of the few which were identified further, there appeared 11 species of the three subgenera *Wyeomyia*, *Dendromyia* and *Davismyia*. Of interest is the large number of this genus in comparison with the total catch. At the Almirante tropical rain-forest stations the *Wyeomyia* comprised more than 60 per cent of the total catch, while in the survey made in the deciduous tropical forest of central Panama (Galindo *et al.*, 1950) they made up only about three per cent of the catch. This may be explained by the fact that most mosquitoes of this genus breed in water-holding plants, primarily epiphytes, which are more abundant in the tropical rain-forest than in the tropical deciduous forest. The *Wyeomyia* are diurnal mosquitoes, and only insignificant numbers were taken in the evening collections.

Limatus. Two species of *Limatus* were present in the diurnal collections, *asulleptus* and *durhami*, with the former far more abundant than the latter.

Sabethes. *Sabethes chloropterus*, the most abundant representative of this genus at these stations as elsewhere in Panama, was fairly evenly distributed during the two years of the survey. Much less common were *Sabethes cyaneus* and *tarsopus*. Both these species demonstrated an irregular annual distribution, about two-thirds of the collections being taken in one year and one-third in the other. But as in the case of two other tree hole breeding species, *A. leucocelaenus clarki* and *H. spegazzinii falco*, *cyaneus* was more abundant in the first year while *tarsopus* was more abundant in the second year. This again illustrates how differently the same climate cycle may affect species with apparently similar breeding habits. The *Sabethes* are diurnal species and only insignificant numbers of the common *chloropterus* were taken in the evening.

Anophelini. There were five species of *Anopheles* in the collections: *apicimacula*, *eiseni*, *punctimacula*, *albimanus* and *neivai*. Only the bromeliad breeding *neivai* of the subgenus *Kerteszia* was present in substantial numbers either in the diurnal or evening collections. It is of interest that so large a number of this species was taken biting in the daytime collections, and also that the bulk of the daytime captures were made during the first year of the survey. In the traverse survey made from Caldera to Chiriquicito in 1955 another *Kerteszia* was taken, *Anopheles boliviensis*, which was previously known only from South America (see Lane, 1953). As we kept the *Kerteszia* specimens from the Almirante forest stations, it has been possible to check them to be sure we did not overlook *boliviensis*.

None were present in the Almirante collections. This serves to confirm our belief that the finding of *H. mesodentatus* on this same traverse survey between Caldera and Chiriquicito does not necessarily imply that this species was present at the Almirante forest stations also.

Fairly common in the evening collections was *Chagasia bathanus*. It was rare in the diurnal catches, and may properly be considered crepuscular or nocturnal as are the other anophelines in general.

Vertical stratification

The data from the Almirante stations, located as they were in virgin tropical rain-forest, are particularly valuable for illustrating how forest type affects vertical stratification of the mosquito fauna. The summary for the Almirante stations is given in Table 4, and for comparison there are included in this table the data from the series of stations operated in the tropical deciduous forest of the Pacific side of Panama during 1950, which were reported in a previous paper (Trapido *et al.*, 1955). The 1950 survey included one station, Tucué, which was just across the continental divide in the Caribbean drainage. But because of the relatively low elevation of the divide there the tropical rain-forest rainfall pattern was not as well developed as at the Almirante stations, and the forest was intermediate between the tropical-rain and tropical deciduous types. All the other Pacific side stations were located in either tropical deciduous or semi-deciduous forest. The data from the 1950 collections may thus be validly compared with those from Almirante to demonstrate the difference in the vertical stratification of the catch in different forest types. In the case of both sets of figures the percentages shown in Table 4 were obtained by making correction for the number of hours expended in collecting on the ground and in the canopy. Per cent captures in the canopy and on the ground were calculated only for those species of which more than 15 specimens were taken. In the case of the Almirante collections there were 36 species which met this requirement, while 31 of the same species appeared in the 1950 survey.

It has been shown by such authors as Bates (1944) and Haddow (1954) that the vertical stratification of the forest mosquito fauna shifts during different hours of the day and between wet and dry season. We believe the comparisons we here make between the stratification at the Almirante stations and those of the Pacific side of Panama to be valid for the following reasons. At both sets of stations the collections were made between 9 A.M. and 3 P.M. The Pacific side collections were made from June to December, the rainy season months, while the Almirante work was carried on throughout a two-year period. But since at Almirante there is no pronounced dry season, the collections were made under rainfall conditions in general similar to those of the rainy season of the Pacific slope. The collections were made over such long periods that effects produced by minor weather fluctuations would be smoothed out in the general averages.

The results from the Almirante stations differ in a number of particulars from those obtained in our first study of the forest mosquito fauna in central Panama and the Canal Zone done in 1949 (Galindo *et al.*, 1950). At that time, however, we collected at platforms midway up the trees as well as in the canopy and on the ground. Under these conditions there was diversion of a portion of the catch, and the results may not be readily compared with those obtained at the stations at which only canopy and ground collections were made. Thus we will not attempt to make comparisons with these data.

The generalization which emerges from a study of the data in Table 4 is that species which are predominantly arboreal in tropical deciduous forest are more distinctly so in tropical rain-forest, while those predominantly taken at ground level in tropical deciduous forest show this tropism in more extreme fashion in the rain-forest. That is to say, in general, the stratification of the mosquitoes between canopy and ground is much more pronounced in rain-forest than it is in deciduous forest.

Arboreal species. Of the 31 species occurring at both sets of stations, 12 were taken in the canopy of the tropical deciduous forest more than 60 per cent of the time. The percentage of these taken in the canopy of the rain-forest was substantially higher in the case of ten of these 12 species. The two exceptions were *Wyeomyia arborea* and *Sabethes cyaneus*. In the case of the extremely arboreal *Wyeomyia arborea* (we named this species in recognition of this characteristic, Galindo *et al.*, 1951), 100 per cent were taken in the canopy of the deciduous forest so that a greater percentage could not possibly have been gotten in the canopy of the rain-forest. The numbers taken at both sets of stations were small, so that the percentage shown for the rain-forest stations (95.9) represents only a single specimen taken on the ground. This exception to the general rule given above is therefore not significant. *Sabethes cyaneus* thus remains as an exception to the generalization made above, although the percentage taken in the canopy of the deciduous forest was only slightly higher (2.9 %) than in the rain-forest. Striking increases in the percentages taken in the canopy are shown by the three species of *Haemagogus*, *Aedes leucocelaenus clarki* and *quadrivittatus*, *Trichoprosopon magnus* and *espini*, *Sabethes tarsopus* and *chloropterus*, and *Chagasia bathanus*. As an example of an extremely arboreal species we may take *H. spegazzinii falco*. Of 1,141 specimens taken, 99.6 per cent were in the canopy at the Almirante rain-forest stations while but 80.7 per cent of 743 specimens were collected in the canopy of the deciduous forest. The stratification of this species was also more marked at the Almirante stations than at two localities where it had been studied in Colombia (Bates, 1944) and Brazil (Causey and Dos Santos, 1949). The most extreme increase in preference for the arboreal habitat was shown by *H. lucifer* with 67.1 per cent in the canopy of the deciduous forest and 98.7 per cent arboreal in the rain-forest, an increase of 31.6 per cent.

These data nicely illustrate an important point in the epidemiology of sylvan yellow fever. In the virgin tropical rain-forest near Almirante the vector species of *Haemagogus* and *A. leucocelaenus* are so completely arboreal that human beings could probably pass through this forest in the presence of a raging epizootic among monkeys in the canopy, without danger of being infected on the ground. In tropical deciduous forest the vertical stratification of the mosquitoes is pronounced but much less so than in the case of rain-forest. Where the canopy of the rain-forest is broken by clearing, or even the felling of a single large tree, the microclimate of the canopy is brought near the ground and there is real danger of being bitten by arboreal mosquitoes. It was a circumstance of this sort which produced the yellow fever case near Almirante. We routinely make use of this fact when engaged in rapid surveys of canopy mosquitoes. Where it is not feasible to climb into the canopy for collecting we fell several trees, letting the sunlight through to the forest floor. Samples of mosquitoes taken attacking in the fresh opening in the forest then include the arboreal species. This technique has been used for some years by our colleague, Dr. Jorge Boshell. In deciduous forest it is often not necessary to disturb the canopy to obtain a sample of the essentially arboreal mosquito fauna at ground level, though an exception to this generalization would be such a species as *Wyeomyia arborea*.

Of the mosquitoes taken in some numbers in the evening collections there were three predominantly arboreal species, *Culex menytes*, *Anopheles neivai* and *Chagasia bathanus*. As the gradients of light, temperature and humidity between canopy and ground are much less marked during the evening and early night hours during which these collections were made, there is indication that factors other than the microclimatic ones discussed earlier in this paper are involved. Some evidence of height orientation based on factors other than light has previously been suggested by the laboratory experiment of Bates (1947). Another factor which should be considered as concerned in determining vertical stratification is that of host preference. That is, a species with a strong preference for feeding on primate blood would need to seek out the forest canopy to find its host. The strong arboreal preference of the anophelines, *A. neivai* and *Ch. bathanus*, may be of significance in a disease problem other than yellow fever, *i.e.*, the transmission of the monkey malaria parasite, *Plasmodium brazilianum*, which occurs in forest primates in this area as well as in South America.

Ground level species. Sixteen of the diurnal species in the deciduous forest were taken more than 60 per cent of the time on the ground. Thirteen of these were taken with greater relative frequency on the ground than in the canopy under rain-forest conditions at Almirante. These species were *Aedes terrens*, *septemstriatus*, *angustivittatus* and the *serratus* group, *Psorophora ferox* and *cingulata*, *Mansonia venezuelensis*, *Trichoprosopon digitatum* and *longipes*, *Wyeomyia jocosa*, *Limatus asulleptus* and *durhami*, and *Anopheles apicimacula*. Exceptions were *Mansonia titillans* and *Trichoprosopon leucopus* of which slightly higher proportions were taken on the ground in the deciduous forest. But the numbers of the former (33) were small in the rain-forest and the numbers of the latter (19) were small in the deciduous forest, so that the comparisons probably are not very significant. Substantial numbers of *Psorophora lutzii* were taken in both types of forest, and the failure of this species to demonstrate increased ground-oriented stratification in the rain-forest is a plain exception to the generalization that stratification is more extreme in rain-forest. *Psorophora cingulata* which was more abundant in the evening than in the daytime collections showed strong preference for the ground in both circumstances.

Five species were taken at the Almirante rain-forest stations for which comparative stratification figures from the Pacific slope deciduous forest stations are not available. These species, *Aedes hastatus*, *Mansonia arribalzagae*, *Trichoprosopon lampropus*, *Wyeomyia celaenocephala* and *scotinomus*, were all preponderately present in the ground level collections.

Indifferent species. Only a single species, *Aedes leucotaeniatus*, appears to be relatively evenly distributed between the canopy and the ground level, though slightly favoring the ground. The proportions taken at canopy and ground level in both types of forest were almost exactly the same. As this species is very closely related to *A. leucocelaenus clarki* it is of interest to note how differently it stratifies in the forest.

Species showing inconsistent behavior. Two species demonstrate "switches" in their relative abundance in the canopy and near the ground in the two types of forest, *Aedes sexlineatus*, and *Anopheles neivai*. Both appeared predominantly in the canopy at the rain-forest stations and predominantly at ground level in the deciduous forest. The number of *A. sexlineatus* was small (16) in the deciduous forest and the ground preference shown in this habitat is probably not significant. The samples of *A. neivai* in both types of forest were large enough to have produced a consistent pattern. We have no ready explanation of why this species showed preference for the ground level in the deciduous forest and the canopy in the rain-forest. Its arboreal predominance in the daytime while marked was much exceeded by that shown in the evening collections in which 100 per cent of 120 specimens were taken in the canopy.

Insects other than mosquitoes. Other biting insects taken in forest canopy have been *Phlebotomus* sandflies and Tabanids. Our colleague, Dr. Graham Fairchild, has discussed the vertical stratification of the Tabanidae (Fairchild, 1953); and Fairchild and Hertig (1952) have noted the arboreal tendency of *Phlebotomus trapidoi* which was taken in numbers in the evening collections at Almirante.

SUMMARY

The clear cut nature of the vertical stratification of the mosquito fauna of the tropical rain-forest is well illustrated if we eliminate the one "indifferent" species and the two species which "switched" their distribution in the two forest types, and then enumerate the remaining 33 species in ten per cent groups. In the case of the 12 canopy mosquitoes nine species were 90 per cent or more, and three from 80 to 90 per cent in the canopy. Of the remaining 21 species 17 were 90 per cent or more at ground level, three from 80 to 90 per cent at ground level, and only one in the 60 to 70 per cent bracket.

Daily activity cycle

The daily activity cycle as we deal with it here concerns only activity as measured by mosquitoes approaching a bait to bite. This subject deserves careful study not only for itself but also for its importance in any basic understanding of the disease transmission cycles in which these mosquitoes may be involved. In the present fluid state of our knowledge of the dynamics of daily mosquito activity cycles any serious attempt to analyze the mass of data accumulated at

Almirante on a causal basis would require a lengthy and involved presentation. The difficulties inherent in the various methods of collecting the data and analyzing them, as well as those of interpreting the results, have recently been pointed out by Haddow (1954). As our purpose in this paper is to give the overall picture of the activity of the mosquito fauna of a rain-forest yellow fever area, we will confine ourselves to a general summary of the findings on the daily periodicity or "biting cycle."

Haddow (1954) has warned of the pitfalls in drawing conclusions with regard to biting cycles based on anything less than 24-hour catches. While his point is well taken, we are confident that such species as the *Haemagogus*, the *Aedes* of the subgenus *Finlaya*, the *Trichoprosopon* and *Sabethes* are distinctly diurnal. The several individuals of these species taken in the evening collections were taken before the hour of nightfall. This does not hold, of course, for such species as *Psorophora cingulata* and *Anopheles neivai* which were present in substantial numbers during the evening and early night as well as during the day. The diurnal collections were confined to the hours 9 A.M. to 3 P.M., as this period could be handled by a single crew of men, and since it was our empirical impression that these hours were the ones of greatest activity of the diurnal forest mosquitoes known or suspected to transmit yellow fever. The evening collections were made only incidentally, and at times irregularly, and they are therefore not suited to analysis of periodicity.

For the interpretation of daily biting cycles Haddow (1954) considers the geometric mean a better measure of central tendency than plain averages (arithmetic means), particularly when dealing with data drawn from a small series of days. This is because the results are "apt to be unduly influenced by extreme values, due to individual catches" (Haddow, 1954, p. 219). In the case of our data, however, we believe the averages to be meaningful since we are dealing with a very long series of days, and since large hourly peaks were not frequent. This may be illustrated by the example of *Haemagogus equinus*. The activity cycle shown for this species in Table 5 is based on 1,944 hours of collecting during 258 days, when the maximum number taken during any one hour was only eight specimens.

The hourly distribution of the 19 species of which more than 100 specimens were taken during the two-year period of the survey are shown in Table 5. In arriving at these figures we eliminated from consideration any days on which no specimens of a particular species were taken, and for the remaining days determined the number of specimens present per ten man-hours of collecting. Hours during which for some reason, such as heavy rain, the collectors were not at their stations, were also eliminated in arriving at the catch per ten man-hours. For ready comparison of the hourly occurrence of the different species, the attack rates per ten man-hours were converted into percentages of the catch made during each of the six one-hour periods between 9 A.M. and 3 P.M. To give some idea of the relative reliability of the results the size of the sample is shown for each species. Where 90 per cent or more of the catch of a particular species was taken at either canopy or ground level the averages were derived from the

TABLE 5

Comparison of the hourly attack rates of forest mosquitoes given as the percentages of the total number attacking between 9 A.M. and 3 P.M.

Species	0900–1000	1000–1100	1100–1200	1200–1300	1300–1400	1400–1500	Where taken	[1]Number taken
Haemagogus equinus	11.7	15.7	17.3	18.4	16.1	20.9	Canopy	1,126
Haemagogus lucifer	14.0	14.0	17.3	18.3	16.4	20.0	Canopy	970
Haemagogus spegazzinii falco	12.3	16.2	17.9	18.8	16.5	18.3	Canopy	1,136
Aedes leucocelaenus clarki	14.6	18.3	17.8	15.5	14.9	18.9	Canopy	810
Aedes leucotaeniatus	22.7	21.6	14.8	15.9	11.4	13.6	Can. & Gr.	297
Aedes sexlineatus	27.4	16.4	17.8	17.3	8.2	12.8	Canopy	129
Aedes angustivittatus	28.1	13.4	14.1	12.4	14.1	17.9	Ground	444
Aedes serratus group	21.6	14.3	16.5	18.7	12.7	16.2	Ground	1,735
Psorophora ferox	11.4	13.6	15.9	18.1	20.0	21.0	Can. & Gr.	2,451
Psorophora lutzii	11.0	13.8	22.0	19.3	16.3	17.6	Can. & Gr.	917
Trichoprosopon digitatum	13.0	10.8	15.7	20.0	23.1	17.3	Ground	145
Trichoprosopon magnus	19.9	17.6	15.9	14.5	15.5	16.6	Can. & Gr.	668
Trichoprosopon espini	35.3	17.4	13.7	12.6	6.3	14.7	Can. & Gr.	172
Trichoprosopon leucopus	20.0	17.6	18.0	14.4	14.8	15.2	Ground	438
Limatus asulleptus	10.2	22.0	21.0	18.5	14.6	13.7	Ground	478
Sabethes cyaneus	11.3	13.6	22.6	16.9	15.8	19.8	Can. & Gr.	321
Sabethes tarsopus	12.8	16.8	15.7	15.7	12.8	26.2	Canopy	229
Sabethes chloropterus	14.9	16.1	17.6	16.7	15.8	18.9	Canopy	3,545
Anopheles neivai	23.5	15.7	14.7	18.1	9.3	18.6	Can. & Gr.	154

[1] Hourly attack rates have been calculated only for those species of which more than 100 specimens were taken during the two year period of the study.

catches in that one situation. Where the vertical stratification was less extreme, *i.e.*, species with less than 90 per cent of their numbers at either canopy or ground, the data from the two environments were combined. Which set of data was used for each species is indicated in the table.

Examination of the results summarized in Table 5 first reveals that the variations by hours in the capture rates for most species are not of very great magnitude. As the collections were distributed among six one-hour periods, the proportion taken in any one-hour period, if the mosquitoes were uniformly active between 9 A.M. and 3 P.M., would be one-sixth of 100 per cent or 16.7 per cent. In the case of only one species, *Trichoprosopon espini*, was this theoretical average more than doubled; while but two species, *T. espini* and *A. neivai* had hour periods during which less than half the theoretical average was taken. While the differences in magnitude are slight, three patterns of activity may be detected.

1. Species with the least activity during the first hour (9–10 A.M.) and the most activity during the last hour (2–3 P.M.).

Six species met these conditions as follows: *Haemagogus equinus* and *lucifer*, *Aedes leucocelaenus clarki*, *Psorophora ferox*, *Sabethes tarsopus*, and *chloropterus*. *H. spegazzinii falco* also follows this pattern although the 12–1 P.M. collection was slightly higher (0.5 per cent) than the 2–3 P.M. collection. All of these species also showed a slight decline in the 1–2 P.M. collection with the exception of *P. ferox*. The calculations for all these species except *P. ferox* are based on the canopy collections only, as they were species of which more than 90 per cent were taken in the canopy.

2. Species with the most activity during the first hour (9–10 A.M.).

This category included eight species as follows: *Aedes leucotaeniatus*, *sexlineatus*, *angustivittatus* and the *serratus* group, *Trichoprosopon magnus*, *espini* and *leucopus*, and *Anopheles neivai*. All but the following three showed some decline during the 1–2 P.M. period as in the case of the first group: *A. angustivittatus*, *T. magnus* and *leucopus*. With the exception of *A. sexlineatus*, a canopy species, the data used were either from the ground collections or combined ground and canopy collections. *A. neivai*, not exclusively a diurnal species, was most abundant in the hours closest to darkness, 9–10 A.M. and 2–3 P.M., though it also had a secondary peak near midday, noon to 1 P.M.

3. Species most active at an intermediate hour.

The remaining four species had their greatest activity at some intermediate hour. The peak hour for *Limatus asulleptus* was 10–11 A.M., for *Psorophora lutzii* and *Sabethes cyaneus* 11–12 A.M., and for *Trichoprosopon digitatum* 1–2 P.M. With the exception of *T. digitatum* the least active hour for these species was the first hour of collecting, 9–10 A.M., as in the first group. The data for these species were drawn from either the ground or the ground and canopy collections combined.

Whether the slight differences which appear in the daily activity cycles are significant, we think must remain in doubt. Comparable data taken in other parts of Panama reveal somewhat different cycles, though this may be due to differences in forest type and weather. Further analyses of these data by other means may be made at a later date. For the present, one can only generalize that a substantial portion of the biting by the diurnal mosquitoes in the Almirante rain-forest occurred during each of the hours between 9 A.M. and 3 P.M.

Regularity of attack rates

The effectiveness of a mosquito species as a vector of yellow fever is a function of the extrinsic incubation period of the virus at the temperatures to which the mosquito is subjected in nature, and also the relation of this incubation period to the natural life span of the mosquito. But also of importance is the regularity of contact made by the species with susceptible hosts over long periods of time. A species which multiplies virus slowly, but which is long-lived and consistently and frequently bites susceptible hosts throughout the year may be of as much importance in maintaining the transmission cycle as a species which mutiplies virus more rapidly and with greater regularity but which is in less frequent contact with susceptible hosts during some part of the year. The annual abundance cycles presented in the next section throw light on this point, but it is also of interest to examine certain relationships expressed in Table 6. We have selected for illustration in this table the data obtained for the three species of *Haemagogus*, *Aedes leucocelaenus clarki* and *Sabethes chloropterus*, because of their known or suspected roles in the transmission of sylvan yellow fever, and for *Psorophora*

TABLE 6

Various measures of biting activity

	Haemagogus equinus		*Haemagogus lucifer*		*Haemagogus spegazzinii falco*		*Aedes leucocelaenus clarki*		*Sabethes chloropterus*		*Psorophora ferox*	
	Canopy		Canopy		Canopy		Canopy		Canopy		Ground	
Total no. of mosquitoes taken	1,126		970		1,136		810		3,545		2,185	
No. per 10 man-hrs. of collecting	5.8		5.0		5.8		4.2		18.2		11.2	
Proportion of each canopy sp. taken (%)	15		13		15		11		47		—	
Total no. of days of collecting	338		338		338		338		338		342	
Total no. of hrs. of collecting	1,944		1,944		1,944		1,944		1,944		1,957	
Max. no. of mosquitoes per 1 hr. period	8		9		12		6		21		68	
	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%	Nos.	%
Regularity of attack												
Days during which mosquitoes were taken	258	76	242	72	226	67	234	69	324	96	133	39
Hrs. during which mosquitoes were taken	685	35	602	31	591	30	558	29	1,345	69	427	22
Grouping of mosquitoes attacking												
Mosquitoes taken per hr.												
1	434	39	388	40	355	31	397	49	501	14	173	8
2	290	26	262	27	236	21	208	26	706	20	120	6
3	174	15	132	14	144	13	111	14	540	15	120	6
4	104	9	92	9	104	9	44	5	452	13	116	5
5	70	6	50	5	80	7	20	2	400	11	110	5
6–10	54	5	46	5	183	16	30	4	718	20	458	21
over 10	0	0	0	0	34	3	0	0	228	6	1,088	50

ferox to illustrate certain differences in activity pattern. *H. spegazzinii falco* and *A. leucocelaenus clarki* are well established vectors (Whitman, 1951). It has also recently been established in the laboratory (Galindo *et al.*, 1957) that Middle American *H. equinus* and *S. chloropterus* are capable of transmitting yellow fever, and virus has been recovered from these species in nature (Johnson and Farnsworth, 1956). As it appears increasingly likely that all *Haemagogus* are capable of transmission, we include also *H. lucifer*.

We see in Table 6 (lines 1 to 3) the relative abundance of these species. *S. chloropterus* was approximately three to four times as abundant as the other four canopy species. It is of interest to compare the densities of the populations of two of these species with those reported from sylvan yellow fever areas in Colombia (Bates, 1944 and 1945) and Brazil (Causey and Dos Santos, 1949). (Bates' *Haemagogus capricornii* is now known as *spegazzinii* and his *Sabethoides imperfectus* is the same as our *chloropterus*.) The average density over a year period found by Bates (1945) for *spegazzinii* was 58.8 per ten man hours, for *chloropterus*, 7.8 per ten man hours. Comparison of these figures with those in Table 6 (line 2) reveals that the relative densities of these two mosquitoes is reversed, *spegazzinii* being more abundant in Colombia and *chloropterus* more abundant at Almirante. The density of *spegazzinii* in Colombia was about ten times that at Almirante and three and a half times that of all three species of

Haemagogus combined at Almirante. Bates (1944) records attack rates for *spegazzinii* in the canopy as high as 140 per man hour while Causey and Dos Santos (1949) took as many as 39 *spegazzinii* per man hour. At Almirante the greatest number of *spegazzinii* taken in any one hour was 12 (Table 6, line 6), and this number was attained during only one hour of the 1,944 hours during which collections were made in the canopy. The maximum hour catch for the other two *Haemagogus* at Almirante was eight for *equinus* and nine for *lucifer*. Of all the *Haemagogus* taken at Almirante only 34 were gotten at rates in excess of ten per man hour (Table 6, line 15).

The different balance between the numbers of *Haemagogus* and *Sabethes* in Colombia and Panama suggests that there may be a difference in the relative role of the two kinds of mosquitoes in the transmission of sylvan yellow fever in the two areas. It is of interest therefore to examine further certain numerical relationships between the populations of *Sabethes chloropterus* and the *Haemagogus* species at Almirante. As is pointed out above, the regularity of biting, day by day, may be of as much importance for disease transmission as the actual numbers present. In Table 6 we have also shown the proportions of the total days and hours of collecting during which the various species attacked.

We see that in terms of days (Table 6, lines 4 and 7) all the canopy species were present at least two-thirds of the time; *spegazzinii falco* was least frequent (67 per cent of the days) and *chloropterus* most frequent (96 per cent of the days). The demonstration of the ability of *chloropterus* to transmit yellow fever, together with the above evidence of the regularity with which it attacks in the canopy, cannot but impress one with the possibility that this species may play a role in the maintenance of yellow fever in arboreal primates.

The relative lack of regularity in the appearance of *spegazzinii falco* is also shown by comparison of the data for this species with that for *equinus* and *leucocelaenus clarki* (Table 6, lines 1 and 7). *Leucocelaenus clarki* (810 specimens) was substantially less abundant than *spegazzinii falco* (1,136 specimens), but appeared on a slightly greater number of days: *clarki*—234 days; *falco*—226 days. The numbers of *spegazzinii falco* (1,136) and *equinus* (1,126) were almost the same; but the former was taken attacking during fewer days: *falco*—226 days; *equinus*—258 days. As the *spegazzinii falco* were taken during fewer days, it follows that it attacked in larger numbers on the days when it was present. This may be confirmed by examining the figures for the distribution of the catches by attack rate per hour shown in Table 6, lines 9 to 15. Thus, if regularity of attack is significant in assessing the transmission role, as it would seem to be, then *spegazzinii falco* would appear to be of lesser importance than the other species, other factors such as life span, rate of virus multiplication, *etc.*, being equal.

A further measure of the regularity of attack is that gotten by determining the proportion of the total number of collecting hours during which each of the species was taken (Table 6, lines 5 and 8). In these terms the difference between *chloropterus* and the other species is proportionately more pronounced. The proportion of the hours during which *chloropterus* attacked (69 per cent) was about twice that of the other canopy species (29 to 35 per cent).

TABLE 7

Comparison of the annual cycles of diurnal forest mosquitoes during a two-year period, by months, per ten man-hours of collecting

Species	[1]Year period	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	[2]Where taken	Number taken
Haemagogus equinus	1951–52	6.1	9.6	7.7	4.7	2.4	2.4	11.2	3.1	8.5	4.3	1.3	6.0	Canopy	554
	1952–53	5.1	13.5	8.8	4.8	1.5	6.5	5.3	2.5	13.9	4.2	3.9	0.6	Canopy	572
Haemagogus lucifer	1951–52	15.0	5.7	11.3	6.6	5.0	4.0	4.7	2.8	3.8	7.5	3.4	2.5	Canopy	571
	1952–53	1.8	6.7	6.4	6.4	2.2	3.2	3.1	4.0	6.5	3.0	5.0	0.9	Canopy	399
Haemagogus spegazzinii falco	1951–52	10.0	13.5	23.1	11.6	6.6	1.5	7.0	7.7	3.4	6.2	2.3	1.0	Canopy	792
	1952–53	2.7	9.6	7.5	4.4	3.7	1.9	2.2	3.8	4.4	0.5	0.0	0.6	Canopy	344
Aedes leucocelaenus clarki	1951–52	1.9	1.9	3.5	4.4	2.3	2.9	5.0	4.4	3.3	3.5	1.1	1.2	Canopy	297
	1952–53	1.1	2.9	6.9	5.8	4.6	5.1	9.3	10.3	8.9	7.2	4.2	1.3	Canopy	513
Aedes leucotaeniatus	1951–52	0.6	1.0	1.0	0.9	0.6	0.1	1.5	0.6	0.7	0.4	0.2	0.7	Can. & Gr.	138
	1952–53	0.8	3.0	1.9	0.5	0.3	0.3	0.2	0.3	1.0	0.3	0.5	0.1	Can. & Gr.	159
Aedes sexlineatus	1951–52	0.6	1.4	1.8	0.5	0.2	0.3	0.0	0.0	0.5	0.3	0.1	0.0	Canopy	52
	1952–53	0.0	1.8	2.4	0.1	0.9	0.5	0.6	0.6	1.3	0.5	0.3	0.1	Canopy	77
Aedes angustivittatus	1951–52	0.0	0.2	0.9	1.4	0.1	0.0	0.1	1.6	0.6	0.1	0.0	0.1	Ground	47
	1952–53	0.5	0.1	2.4	14.2	7.0	1.6	8.6	9.2	6.1	3.0	0.0	0.0	Ground	397
Aedes serratus group	1951–52	1.1	0.9	5.9	5.4	2.5	0.5	3.0	3.1	1.1	3.5	0.4	0.4	Ground	242
	1952–53	0.5	3.1	22.7	52.5	5.0	0.3	49.7	16.3	21.9	9.9	0.4	0.0	Ground	1,493
Psorophora ferox	1951–52	0.0	1.0	1.1	1.8	0.1	0.1	0.0	0.1	0.7	0.0	0.0	0.0	Can. & Gr.	99
	1952–53	0.6	0.9	44.8	21.9	1.9	1.1	42.5	7.8	7.9	1.4	0.0	0.0	Can. & Gr.	2,352
Psorophora lutzii	1951–52	0.4	0.5	1.8	3.6	0.0	0.0	0.0	0.2	2.5	0.0	0.0	0.3	Can. & Gr.	182
	1952–53	0.1	0.3	2.0	9.5	0.0	0.1	35.6	0.1	0.9	0.1	0.3	0.0	Can. & Gr.	735
Trichoprosopon digitatum	1951–52	0.8	2.1	0.8	0.9	0.2	0.3	1.1	0.5	1.4	1.1	0.2	2.0	Ground	100
	1952–53	1.0	0.7	0.7	0.6	0.4	0.0	0.0	0.5	0.0	0.0	0.1	1.2	Ground	45
Trichoprosopon magnus	1951–52	1.5	1.9	2.0	1.1	0.5	3.6	3.0	3.8	1.5	3.3	2.8	3.8	Can. & Gr.	484
	1952–53	3.6	0.9	1.3	0.5	1.2	0.2	0.5	0.8	0.9	0.4	0.2	0.9	Can. & Gr.	184
Trichoprosopon espini	1951–52	0.0	0.4	0.8	0.1	0.2	0.3	0.7	0.9	0.6	0.8	0.4	0.6	Can. & Gr.	95
	1952–53	0.6	0.5	0.4	1.3	0.7	0.0	0.5	0.1	0.2	0.2	0.0	0.1	Can. & Gr.	77
Trichoprosopon leucopus	1951–52	0.0	0.1	0.0	0.0	0.2	1.9	2.8	2.1	0.8	2.9	6.0	2.1	Ground	157
	1952–53	1.8	3.9	9.9	5.2	3.5	0.3	1.2	3.5	1.3	1.2	0.2	0.4	Ground	281

Limatus asulleptus	1951–52	0.0	1.4	0.1	1.0	2.4	1.2	3.0	1.3	1.8	2.9	2.7	1.7	Ground	165
	1952–53	2.6	9.5	6.3	5.9	3.1	2.1	1.9	2.9	0.6	1.0	0.8	0.5	Ground	313
Sabethes cyaneus	1951–52	0.8	0.5	0.7	0.4	0.6	1.6	1.2	1.8	0.9	0.9	1.4	1.0	Can. & Gr.	201
	1952–53	0.4	0.2	0.1	0.4	0.8	0.5	0.5	0.8	1.2	0.9	1.1	0.9	Can. & Gr.	120
Sabethes tarsopus	1951–52	1.1	1.1	0.8	1.0	1.8	0.8	0.5	1.0	0.4	0.8	0.7	0.7	Canopy	90
	1952–53	1.9	0.9	0.8	1.9	1.5	0.3	1.2	1.3	1.5	2.1	2.4	2.0	Canopy	139
Sabethes chloropterus	1951–52	11.1	22.1	16.3	16.5	27.0	26.6	10.9	16.1	9.8	11.7	10.3	15.0	Canopy	1,722
	1952–53	15.8	17.9	12.6	13.6	24.8	20.3	19.9	32.5	25.7	33.5	18.5	13.6	Canopy	1,823
Anopheles neivai	1951–52	0.4	0.9	2.8	1.2	0.3	0.3	0.6	0.2	0.6	0.3	0.1	0.0	Can. & Gr.	139
	1952–53	0.1	0.2	<0.1	0.1	0.0	0.1	0.1	0.2	0.0	0.1	0.1	0.1	Can. & Gr.	15

[1] As the work was begun in May 1951 the "year periods" extend from May 1951 to April 1952 and from May 1952 to April 1953.

[2] Annual abundance cycles have been calculated only for those species of which more than 100 specimens were taken during the two year period of the study.

Finally, if we examine the data showing the numbers of each species attacking at various rates per hour of collection (Table 6, lines 10 to 16) we find another characteristic of *chloropterus*. That is, aside from the fact that *chloropterus* was more regularly present, as shown above, it was more often present in groups rather than singly as were the other species. In Table 6, lines 10, 11 and 12, we see that for the three species of *Haemagogus* and *leucocelaenus clarki* the numbers taken at the rate of two or three per hour were less than the numbers taken at the rate of one per hour. But *chloropterus* attacked more frequently at rates of two or three per hour than at rates of one per hour. Many more were also taken at rates in excess of five per hour. Thus we see that the greater abundance of *chloropterus* is expressed both in greater regularity of attack and also greater numbers attacking per hour. It might be thought that this relationship must be expected in the case of a species so much more abundant than the others. But it is possible for a species to be abundant and yet not express this abundance both in terms of regularity of appearance and large grouping of individuals.

We include data for *Psorophora ferox* in Table 6 to illustrate this point. This species was about two-thirds as common as *chloropterus* but the maximum catch in a single hour period was more than three times that of *chloropterus* (Table 6, line 6). The clustering of the catch is also shown by the fact that 50 per cent of those taken were in groups in excess of ten per man-hour while only six per cent of the *chloropterus* were taken in such aggregations (Table 6, line 15). The lack of regularity of attack by *P. ferox*, on the other hand, is brought out by the fact that it was taken on only 29 per cent of the days and 22 per cent of the hours of collecting; *chloropterus* being present on 96 per cent of the days and 69 per cent of the hours (Table 6, lines 7 and 8). Although two to two-and-a-half times as abundant as the species of *Haemagogus* and *Aedes leucocelaenus*, *ferox* was taken on substantially fewer days and hours than these species (Table 6, lines 7 and 8).

Annual abundance cycle

An important reason for making the collections at the Almirante stations over a two-year period was that of obtaining a picture of the long-term abundance cycle of the forest mosquitoes in a typical tropical rain-forest which supported the yellow fever transmission cycle. We were interested not only in the relative abundance of the various species from year to year, but also how they might vary from month to month within the period of a year. The gross differences in the numbers of the various species taken during each year period have been shown in Table 2. But for the 19 species of which more than 100 individuals were collected we have calculated the catch per ten man-hours for each month during the two year period. The results are summarized in Table 7. To portray the fluctuations graphically and to facilitate comparisons of species illustrating particular points, the monthly ten man-hour capture rates were converted to percentages of each year's catch taken each month. The annual abundance cycles determined in this way for six selected species are shown in the accompanying circle graphs.

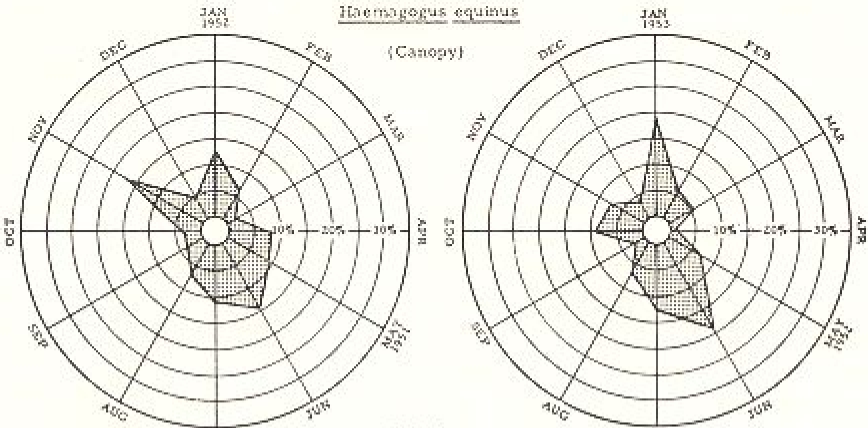

FIG. 4

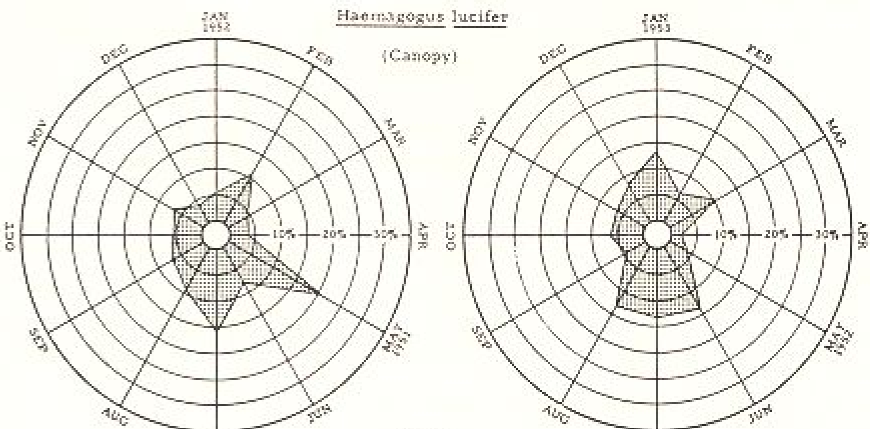

FIG. 5

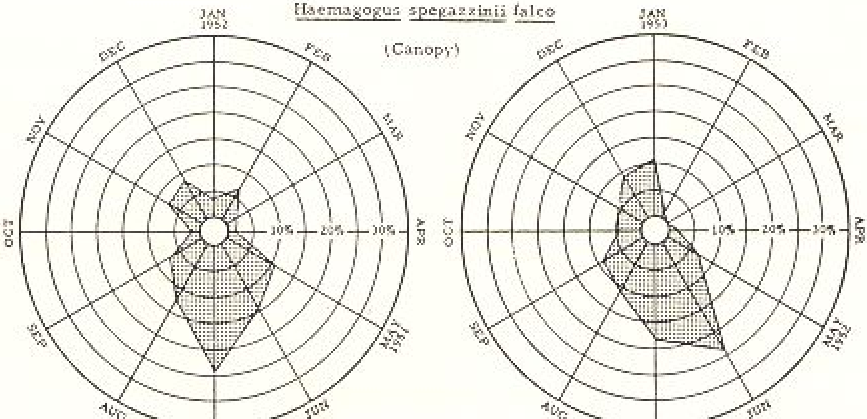

FIG. 6

FIGS. 4, 5, and 6. Annual abundance cycles of three species of *Haemagogus* during a two year period in the tropical rain-forest near Almirante, Panama.

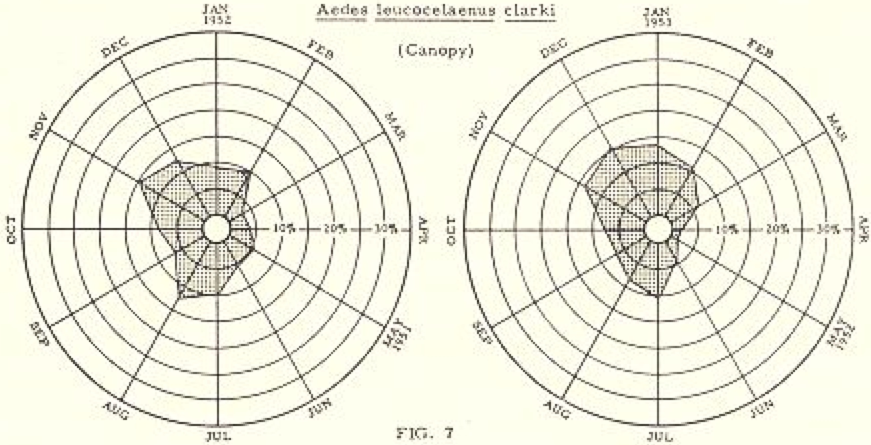

FIG. 7

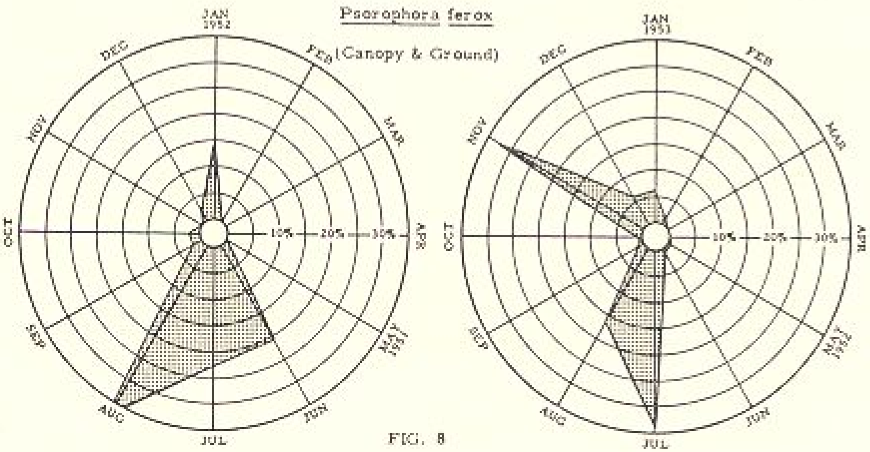

FIG. 8

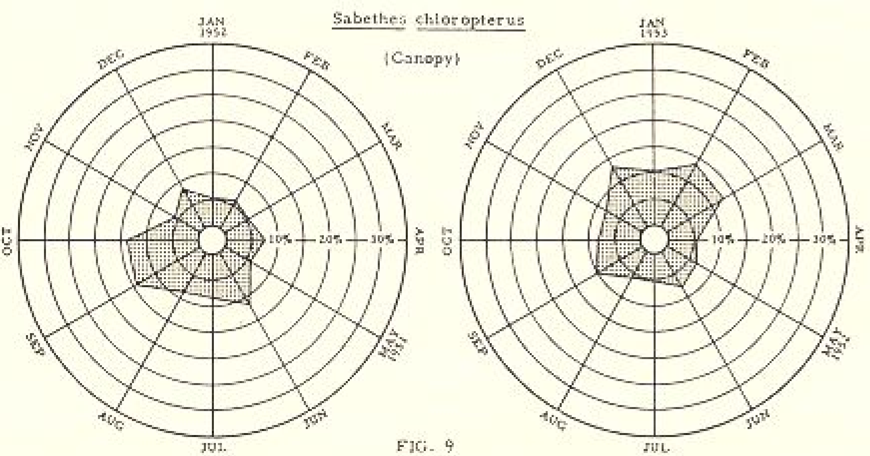

FIG. 9

FIGS. 7, 8, and 9. Annual abundance cycles of three species of mosquitoes during a two year period in the tropical rain-forest near Almirante, Panama.

The irregularity of the details of the annual distribution is apparent on study of Table 7 and the accompanying graphs. In the case of only one species, *Aedes sexlineatus*, was the month of maximum abundance the same (July) during both years. Six other species had their month of maximum abundance one month apart: *Haemagogus lucifer* and *spegazzinii falco*, *Aedes leucocelaenus clarki*, *Psorophora ferox*, *Sabethes cyaneus* and *Anopheles neivai*. The mosquitoes demonstrating the greatest variation in the annual abundance cycle were the ground-pool breeding species of *Aedes* and the *Psorophora*. This is graphically illustrated for one of these species, *P. ferox*, in Figure 8. In such species there are a number of months in which there is no catch at all and there are peaks of abundance when more than 30 per cent of the year's catch is taken in a single month.

The three species of *Haemagogus* (Figures 4, 5 and 6) have pronounced peaks, but these are much less extreme than those of the ground-pool breeding species. The largest peaks for any particular month reach only 20 per cent of the year's catch, and there are no months during which these species are wholly absent. The cycle is even more uniform in the case of *leucocelaenus clarki* (Figure 7) with no peak exceeding 15 per cent. Most uniform in distribution throughout the two-year period was *chloropterus* (Figure 9). A substantial portion of the catch was taken during all months. There was no month in which less than five per cent or more than 15 per cent of the annual catch appeared.

The relative uniformity of the month-by-month catch of the tree-hole-breeding arboreal mosquitoes in this tropical rain-forest must be an important factor in maintaining the chain of yellow fever transmission. In forests which experience a pronounced dry season, as do those of the Pacific versant of Panama, the annual abundance cycles are very different. The contrasting of the cycles in the two types of forest has been made the subject of a separate paper (Trapido and Galindo, 1957b).

SUMMARY

An analysis has been made of the composition of the sylvan mosquito fauna of a well developed virgin tropical rain-forest in which yellow fever appeared in 1951. The results are based on two years of collecting mosquitoes attacking human baits on the ground and in the forest canopy, during the daylight and evening hours. The circumstances under which yellow fever occurred are given, and the climate and microclimate of the rain-forest summarized. It is shown that in true rain-forest the vertical stratification of the sylvan mosquito fauna is much more pronounced than in open deciduous forest. The daily activity cycles of 19 species are illustrated, and an analysis made of the regularity of attack in the case of five species known or suspected as sylvan yellow fever vectors. In addition the annual abundance cycles of 19 species are given.

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