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A SURVEY OF FOREST MOSQUITOES IN RELATION TO SYLVAN YELLOW FEVER IN THE PANAMA ISTHMIAN AREA[1]

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The results of immunological surveys of human populations conducted in Mexico, Central America and Panama in the late thirties and early forties have been reported in a series of publications (Sawyer, Bauer and Whitman, 1937; Clark, 1938; Sawyer, 1942; Bustamante, Kumm and Herrera, 1942; Kumm and Crawford, 1943). These authors record that such persons as were found to possess immunity to yellow fever in this region, west of the Canal Zone, were of age groups born prior to 1925. It was generally accepted that the older age groups demonstrating some immunity had been exposed to the disease in its urban form transmitted by *Aedes aegypti*. From 1905 until late in 1948 locally contracted yellow fever had not been clinically recognized in Panama, but the existence of naturally acquired immunity in the younger age groups at several places in Panama east of the Canal Zone was reported by Clark, 1938; Sawyer, 1942; and Kumm and Crawford, 1943. The interpretation of these data was that the sylvan phase of the disease (jungle yellow fever) had been present, and had gone unrecognized in the portion of Panama adjacent to South America and east of the Canal Zone, but that yellow fever was not endemic in Middle America west and north of central Panama and the Canal Zone. The present understanding of yellow fever as primarily a disease of tree-inhabiting anthropoids and possibly certain other mammals, with man only incidentally involved, indicated the desirability of an adequate survey of the forest canopy mosquito fauna in the critical Isthmian area to establish what elements determined the suitability of the forests of eastern Panama and the presumed unsuitability of the forests of western Panama for the propagation of sylvan yellow fever.

The need for such a study was emphasized by the occurrence of several fatal cases of sylvan yellow fever contracted just east of the Canal Zone late in 1948 (Herrera, Elton, and Nicosia, 1949). The writers at first undertook a study of the composition of the forest mosquito fauna in central Panama and the Canal Zone in the area where the new human cases had been recognized (Galindo, Trapido and Carpenter, 1950). Here we found two of the recognized vectors of the disease in South America, *Haemagogus spegazzinii falco* and *Aedes leucocelaenus*, present in some abundance. We also reported on the general distribution, the annual cycle of abundance, and the vertical stratification in the forest of these as well as all other mosquitoes attacking man in the forest in this area. Since this survey had shown the South American vectors to be present, the next year we extended these studies to western Panama and adjacent Costa Rica to establish whether or not there was a zoogeographic shift in the composition of the mosquito fauna of the forest canopy in the Isthmian area, marked by the end of

[1] Studies on the Forest Mosquitoes of Panama, VII.

the range of the South American vectors of the disease, which might be correlated with the supposed absence of the sylvan form of yellow fever from western Panama and Central America. We found at once that the change in the composition of the forest canopy mosquito fauna which, on a theoretical basis we had expected to demonstrate, was in fact lacking. We briefly reported the presence of *Haemagogus spegazzinii falco* in Puntarenas Province, Costa Rica, our westernmost collection station (Galindo, Carpenter and Trapido, 1951 a) but the full account of the findings of this study have been delayed until now by pressure of further field work on this general problem and by other activities. Subsequent to this study, sylvan yellow fever did in fact appear in western Panama and Costa Rica (Elton, 1952), and more recently in Nicaragua and Honduras. Observations on the forest mosquito faunas of these Central American countries will be the subject of later papers.

In Panama there is a considerable gradient in rainfall between the Caribbean and the Pacific drainages, both in terms of the total precipitation, and its distribution through the year. The Pacific slope has less rainfall, and a relatively severe dry season from January through April. On the Atlantic side of the Isthmus the dry season is less marked, and in some places there may be no month with less than four inches of rain. In consequence the Caribbean coast of Panama is largely a trackless tropical rain forest, uninhabited except by small groups of Indians, and accessible only by small coastal boats and by dugout cayucos up the larger rivers. West of the Canal Zone, the Pacific slope with its lesser rainfall and marked dry season is characterized by a lower and more scrubby forest ("deciduous tropical forest" of the plant ecologists) mixed with open grassy savannahs. Here the principal rural population of Panama lives, and there is a road passable at all times of the year from the Canal Zone almost to the Costa Rican border. While it would have been desirable to establish our series of stations for the capture of canopy mosquitoes in the true rain forest of the Caribbean slope, the impossibility of arranging for supply and the transportation of the collections into the laboratory on a routine basis made it necessary to operate for the most part in the best forest which could be found on the Pacific side. Apart from the series of stations located at intervals between the Canal Zone and Puntarenas Province in Costa Rica, we simultaneously set up several stations to the east, between the Canal Zone and Darien Province, adjacent to Colombia, for comparative purposes. We had learned from our previous experience in operating tree stations for a full year in central Panama and the Canal Zone, that most species of canopy mosquitoes, which are dependent for their larval development on accumulations of water in tree holes or epiphytic plants, were rare during the dry season months from February through April. As the present study was intended primarily as a survey, an economy of expenditures was effected by planning to carry on the collections only during the rainy season months between June and December. Certain of the stations, either because they were located in places difficult of access or because they failed to produce a significant catch, were run for shorter periods. At two places where secondary roads gave access to some elevation (Cerro Campana and Chiriqui) the stations

TABLE 1

Location and collecting periods at forest mosquito catching stations during 1950

Location	Province	Altitude (in feet)	Inclusive dates	Number of stations	Number of man days collecting		
					Ground	Canopy	Total
Panama							
El Real	Darien	50	3 July to 10 Aug.	4	20	20	40
Candelaria	Colon	200	14 Aug. to 22 Aug.	1	0	8	8
Cacique	Colon	200	19 Oct. to 30 Oct.	1	10	8	18
La Victoria	Panama	400–1,200	7 Feb. to 28 Dec.	2	87	88	175
Panama Viejo	Panama	10	6 July to 21 Dec.	1	17	0	17
Arraijan	Panama	600–800	5 June to 29 Dec.	6	49	103	152
Campanita Abajo	Panama	200	8 June to 30 Nov.	2	23	47	70
Campanita Arriba	Panama	600	28 Aug. to 4 Dec.	2	13	28	41
Campana, 2,000′	Panama	2,000	14 June to 6 Dec.	2	24	50	74
Campana, 2,800′	Panama	2,800	5 June to 21 Nov.	4	28	52	80
La Arena	Veraguas	400	19 Sept. to 28 Sept.	2	10	10	20
Tucue	Cocle	1,000	12 June to 14 Dec.	4	102	101	203
Sante Fe	Veraguas	2,500	25 May to 15 Aug.	3	60	60	120
Chorcha	Chiriqui	300	12 June to 11 Dec.	2	22	43	65
Progreso	Chiriqui	400	16 June to 14 Dec.	2	23	42	65
Bijao	Chiriqui	3,500	13 June to 12 Dec.	2	19	35	54
Palo Santo	Chiriqui	4,600	15 June to 1 Dec.	2	18	35	53
Costa Rica							
Esquinas	Puntarenas	300	6 June to 30 Nov.	4	90	87	177
Totals				46	615	817	1,432

were arranged to give a cross section of the forest fauna at different altitudes above sea level. The locations of the stations, their elevations, and the periods during which mosquitoes were collected at them are given in Table 1. In our previous study (Galindo, Trapido and Carpenter, 1950) collections had been made simultaneously of mosquitoes attacking human subjects on the forest floor, at a platform midway up a tree, and at a platform in the tree canopy. Since the middle platform did not produce species lacking in either the ground or canopy collections, the stations in the present survey were established with only one platform, in the canopy. In the 1949 study we had also operated each station for one half hour each hour from 8:00 A.M. to 5:30 P.M. To operate on this basis two crews of men had been necessary for each station, one for the morning and one for the afternoon. As the mid-day hours were generally the most productive of canopy mosquitoes, in the present study only one crew of men was used for each station, collecting continuously during the six hours from 9:00 A.M. to 3:00 P.M.

In general, each tree station was run one day each week for several months, but at certain of the localities such as Candelaria and Cacique which were difficult of access, and where it was only possible to send in a crew for a short

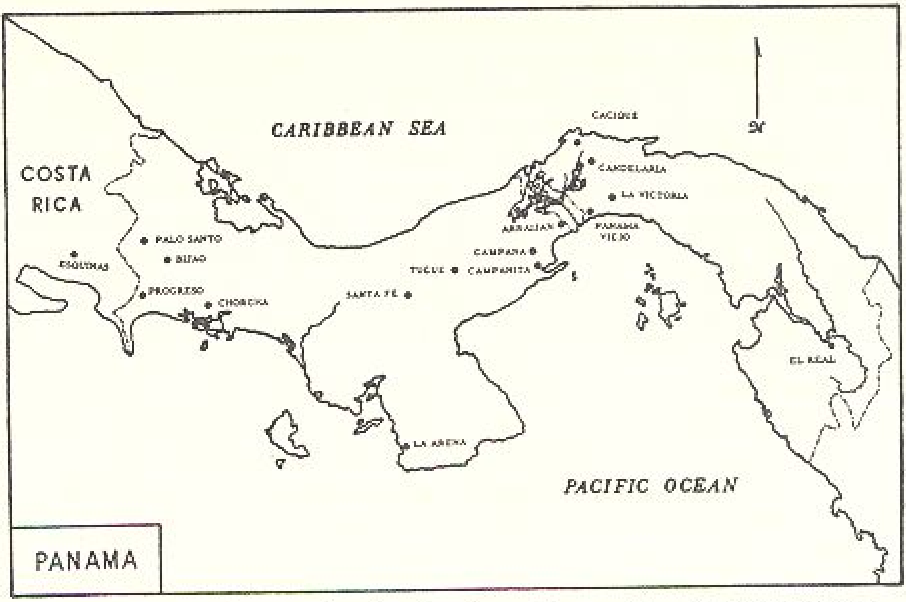

FIG. 1. Map of Panama showing locations of mosquito collecting stations

period, collections were made every day during a short period. In Table 1 are also given the number of man days of collecting, on the ground and in the canopy, at all stations. The geographic locations of the stations are shown in the map (Fig. 1). The method of making the collections has been described in a previous paper (Galindo, Trapido and Carpenter, 1950).

DISTRIBUTION OF SPECIES

In Table 2 are listed the 72 species of mosquitoes identified, arranged according to stations at which they were taken. In all, 72,211 mosquitoes were captured during 8,015 hours of collecting. Of these 31,530 were taken in 4,555 hours of collecting in the canopy and 40,681 in 3,460 hours on the ground.

The commonest and most widespread *Haemagogus* species was *equinus* which was taken at all stations, and made up more than half of all the individuals of this genus taken (6,488 *equinus* out of 11,848 *Haemagogus*). Only two specimens were taken in 80 hours of collecting at Panama Viejo, but this station was located in a coastal mangrove swamp and was intended only to establish densities of *H. chalcospilans*. The other stations at which very low numbers of this species appeared were at considerable elevation, Palo Santo being at 4,600 feet and Bijao at 3,500 feet. In the elevation cross section taken at Cerro Campana the highest density was found at the 2,000 foot level, with a fall off in numbers at 2,800 feet. From these data it is apparent that the species is common from near sea-level to 2,000 or 2,500 feet, becoming scarcer above this elevation, and quite rare above 4,000 feet. *Haemagogus lucifer* was also widespread in distribution from near the Colombian border to Costa Rica, but the total number taken was only about half that of *H. equinus*. At the Chiriqui stations and at Santa Fe in Veraguas Province the species was very much less common than *H. equinus*, and at the most elevated station, Palo Santo, none were taken. *Haemagogus iridicolor*, which replaces *lucifer* to the west in Costa Rica, was rare and in all only seven specimens were collected, all at Bijao in Chiriqui Province. *Haemagogus spegazzinii falco* was of special interest since it is a proven vector of sylvan yellow fever in Colombia. The species was the least common of the widely distributed *Haemagogus*, comprising only 6.3 per cent of all the specimens of this genus taken. The only places at which substantial numbers were taken were La Victoria, where it had been found in our previous study, and Tucue in Cocle Province. Its abundance at Tucue might be explained by the fact that this was the only station in western Panama across the continental divide on the Caribbean slope, where the rainfall is higher, and true tropical rain forest better developed. Though none were taken at El Real, the station closest to Colombia, where the species is common, this may be explained by the fact that our station had to be located in second growth, as primary forest was too difficult to reach here. None were found at the 2,800 foot station at Cerro Campana, or the 4,600 foot station at Palo Santo, but there were a few at 3,500 feet at Bijao. It is also remarkable that at Santa Fe, where *H. equinus* was so common, an indication of the suitability of the area for tree hole *Haemagogus* breeding, none were taken. The small number of *spegazzinii falco* taken at Esquinas, Costa Rica (only five in 1,054 hours of collecting) has been interpreted by us (Galindo, Carpenter and Trapido, 1951a) as possibly due to the unsuitability of local conditions, since other *Haemagogus* also were not particularly common at this locality. The Esquinas area has a high and continuous rainfall which may not permit the intermittent drying and flooding of tree holes essential to hatching of *Haemagogus* eggs.

Thirteen species of *Aedes* of three subgenera were identified in the collections. The subgenus *Finlaya* was represented by the three species *leucocelaenus clarki*, *leucotaeniatus* and *terrens*. *Aedes leucocelaenus clarki* was found at stations from near the Colombian border into Costa Rica. More than half the specimens taken, 515 out of 975, were from the station at Tucue, across the divide on the Caribbean slope, which was also the station at which the bulk of the western Panama specimens of *H. spegazzinii falco* were taken. In Chiriqui this mosquito was taken in only very small numbers, but there were a few (five) found at the highest station at Palo Santo. At Cerro Campana they were commonest at 600 to 2,000 feet, and only a few were taken at 2,800 feet. As was the case in our previous study at Cerro La Victoria the total number of *leucocelaenus clarki* (975) approximated that of *H. spegazzinii falco* (750) and was much less than that of the other two *Haemagogus*, *equinus* with 6,488 and *lucifer* with 3,398. *Aedes leucocelaenus* and *H. spegazzinii* are proven vectors of sylvan yellow fever in South America. It is difficult to imagine their being able to maintain the disease on the Pacific slope of western Panama, should it be true that they are also the only vectors in Panama. The relatively high densities of these two species taken at the Tucue station might indicate that the disease could only pass through western Panama on the Caribbean side. The review by Elton (1952) of the location and sequence of

TABLE 2

Summary of diurnal forest mosquito catches during 1950

Station Location	El Real	Candelaria	Cacique	La Victoria	Panama Viejo	Arraijan	Campanita Abajo	Campanita Arriba	Campana 2000′	Campana 2800′	La Arena	Tucue	Sante Fe	Chorcha	Progreso	Bijso	Palo Santo	Esquinas Costa Rica	Total
Number of Hours	235	39	53	927	80	853	404	220	412	447	80	1196	719	360	378	279	279	1054	8015
Tribe Culicini																			
Haemagogus equinus	42	55	44	438	2	865	496	352	930	106	49	1387	1337	147	162	11	2	63	6488
Haemagogus lucifer	85	24	222	464		670	142	131	391	168	10	984	39	45	23				3398
Haemagogus iridicolor																7			7
Haemagogus lucifer—iridicolor																		119	119
Haemagogus spegazzinii falco			6	113								605		12		9		5	750
Haemagogus chalcospilans					1015														1015
Haemagogus argyromeris							55			1		2							58
Haemagogus sp.							3		2							8			13
Total *Haemagogus*	127	79	272	1015	1017	1535	696	483	1323	275	59	2978	1376	204	185	35	2	187	11848
Aedes (Finlaya) leucocelaenus clarki	9	9		84		94	4	44	59	6	93	515		13	37		5	3	975
Aedes (Finlaya) leucotaeniatus		1	3	36		52	3	14	132	32		146	5	3	4		3	1	435
Aedes (Finlaya) terrens		2		10		18	12	4	113	150		139	281	53	96	36	582	39	1535
Aedes (Howardina) allotecnon																	1		1
Aedes (Howardina) quadrivittatus						4	15	38	963	69		14	73	3	17	33	998		2227
Aedes (Howardina) septemstriatus		5		1		2			14	12	1	14		1				1	51
Aedes (Howardina) sexlineatus									14			2							16
Aedes (Ochlerotatus) hastatus														1	6			3	10
Aedes (Ochlerotatus) serratus—group	716			4		8	3					17	102	112	1375	22		110	2469
Aedes (Ochlerotatus) taeniorhynchus	6			82	17	264	49	2				6		1					427
Aedes (Ochlerotatus) angustivittatus	683			1			1		39			8	21	38	222	1		10	1024

Aedes (Ochlerotatus) scapularis	1						1		2	2			85	4					95
Aedes (Ochlerotatus) fulvus	796							1						2	71				870
Aedes sp.	25	3		2			3					124	2724	36	129	84	22	11	3163
Psorophora (Psorophora) cilipes	2																		2
Psorophora (Psorophora) lineata	1											7			1				9
Psorophora (Janthinosoma) champerico												70							70
Psorophora (Janthinosoma) ferox	1381	1		13	1	29	13	27	9	57		256	1858	243	1706	51	78	459	6182
Psorophora (Janthinosoma) lutzii	393			23		2				1		28	308	14	81	5		12	867
Psorophora (Grabhamia) cingulata	120	9		1								26	17	2	2		1	4	182
Psorophora sp.				6															6
Mansonia (Mansonia) titillans-indubitans	10			631	9	121	1	6	3	3		7		12	34	2	7	36	882
Mansonia (Rhyncotaenia) venezuelensis	13			10		75								18	9			172	297
Mansonia sp.						9													9
Culex (Culex) sp.	6	1		1								8			1			19	36
Culex (Melanoconion) menytes																		1	1
Culex (Melanoconion) sp.														3	3			11	17
Culex (Carrollia) secundus		1																	1
Culex (Carrollia) urichii												1							1
Culex (Microculex) jenningsi																		1	1
Culex (Isostomyia) sp.												2							2
Orthopodomyia fascipes												1							1
Total *Culicini*	4289	111	275	1920	1044	2213	801	619	2671	607	153	4360	6850	763	3979	269	1699	1080	33712
Tribe Sabethini																			
Trichoprosopon (Trichoprosopon) digitatum		16		2			3	1		1	29	20			4			11	87
Trichoprosopon (Shannoniana) schedocyclius																1			1
Trichoprosopon (Shannoniana) fluviatilis		1														26	16		43
Trichoprosopon (Ctenogoeldia) magnus	2			1		8	1	13	3	1	80	460	177	3687	2442	36	176	1170	8257
Trichoprosopon (Isogoeldia) espini	17						1							63				3	84
Trichoprosopon (Rhunchomyia) longipes	21	11	1	26			47	17	5	1	123	315	10	640	149	20	57	617	2060
Trichoprosopon (Rhunchomyia) cerqueirai												6		2					8
Trichoprosopon (Rhunchomyia) lampropus		4										3	1						8
Trichoprosopon (Rhunchomyia) leucopus		5										17	1					1	24

TABLE 2—*Continued*

Station Location	El Real	Candelaria	Cacique	La Victoria	Panama Viejo	Arraijan	Campanita Abajo	Campanita Arriba	Campana 2000′	Campana 2800′	La Arena	Tucue	Santa Fe	Chorcha	Progreso	Bijao	Palo Santo	Esquinas Costa Rica	Total
Tribe Sabethini—*Continued*																			
Trichoprosopon sp.				8		1						2		10				21	42
Wyeomyia (*Wyeomyia*) *abebela*																13	12		25
Wyeomyia (*Wyeomyia*) *arthrostigma*	14			4					1										19
Wyeomyia (*Wyeomyia*) *celaenocephala*													2		3				5
Wyeomyia (*Wyeomyia*) *florestan*		1																	1
Wyeomyia (*Wyeomyia*) *mitchellii*				2					1	4	10		9			49	24	8	107
Wyeomyia (*Wyeomyia*) *scotinomus*									1										1
Wyeomyia (*Wyeomyia*) *sp.*	132	1079	41	143	13	119	10	49	135	87	164	3167	4777	608	904	1712	638	909	14687
Wyeomyia (*Dendromyia*) *chalcocephala*										1				11	9			1	22
Wyeomyia (*Dendromyia*) *circumcincta*																		1	1
Wyeomyia (*Dendromyia*) *clasoleuca*				1									4						5
Wyeomyia (*Dendromyia*) *jocosa*													140	7		103	11		261
Wyeomyia (*Dendromyia*) *melanocephala*	21											1		1				13	36
Wyeomyia (*Dendromyia*) *aporonoma*	2			29		1			1	2			22	30		50	73	6	216
Wyeomyia (*Dendromyia*) *prolepidis*	1												3						4
Wyeomyia (*Dendromyia*) *sp.*	113	69	15	18	4	41	20	37	49	15	190	3160	841	712	480	442	230	509	6945
Wyeomyia (*Davismyia*) *arborea*													4			16			20
Limatus assuleptus		14		2								174		8		6		5	209
Limatus durhamii	1	8		9			2	6			7	33		38	3	2	5	14	128
Limatus sp.																		4	4
Sabethes (*Sabethes*) *cyaneus*	2	1		30		38	6	12	7	1	29	120	6	65	11		3	18	349
Sabethes (*Sabethes*) *tarsopus*	18	1		18		60	31	33	30	2	23	322	11	52	9		28	18	656
Sabethes (*Sabethinus*) *undosus*												2		2					4
Sabethes (*Sabethoides*) *chloropterus*	35	41	13	280		627	71	177	305	17	161	753	193	105	278	4	11	140	3211
Sabethes sp.				1															1
Total *Sabethini*	379	1251	70	574	17	895	192	345	538	132	816	8555	6201	6041	4292	2480	1284	3469	37531

Tribe Anophelini																			
Anopheles (Anopheles) apicimacula	11	2	18	2		12		3						7	12			161	228
Anopheles (Anopheles) eiseni		6		2					2	1		7	163	4	7	3	6	15	216
Anopheles (Anopheles) punctimacula					3	1									1			22	27
Anopheles (Stethomyia) kompi												6			2				8
Anopheles (Nyssorhynchus) albimanus	17	1			40	6		3						1				75	143
Anopheles (Nyssorhynchus) oswaldoi	3																		3
Anopheles (Nyssorhynchus) strodei	13				3	5								1				97	119
Anopheles (Nyssorhynchus) triannulatus	2																	5	7
Anopheles (Kerteszia) neivai		6		1					3	3			174					2	189
Anopheles (Lophopodomyia) squamifemur		1																	1
Anopheles sp.																		1	1
Chagasia bathanus						6						1	5	1	4			9	26
Total *Anophelini*	46	16	18	5	46	30		6	5	4		14	342	14	26	3	6	387	968
Total All Species	4714	1378	363	2499	1107	3138	993	970	3214	743	969	12938	13393	6818	8297	2752	2989	4936	72211

Serratus-group includes: *serratus*, *oligopistus* and *tormenter*.

recent yellow fever cases in Panama and Costa Rica would confirm this view that the virus passed through western Panama on the Caribbean slope, and was not maintained in Panama on the Pacific slope west of the Canal Zone.

Aedes leucotaeniatus also appears to be distributed throughout the length of Panama, and into Costa Rica although none were taken at the easternmost station at El Real, and only one was captured in 1,054 hours of collecting at Esquinas, Costa Rica. The total number taken was about half that of *leucocelaneus clarki*. The species was most common at Tucue and at the 2,000 foot level at Cerro Campana. Thirty-two specimens were taken at the high station at Cerro Campana and three at 4,600 feet at Palo Santo in Chiriqui. *Aedes terrens*, which had been the least common *Finlaya* in our previous study in central Panama, was found to be rare in eastern and central Panama, but west of Cerro Campana it was, in general, the commonest representative of this subgenus. The numbers taken in western Panama were sufficient to make this the most abundant *Finlaya* taken. Unlike the other *Finlaya*, *terrens* was most abundant at higher elevations. At both Cerro Campana and in Chiriqui Province, the greatest numbers were taken at the most elevated stations. More than a third (582 out of 1,535) of the *terrens* taken were from the 4,600 foot station at Palo Santo.

Four species of the aedine subgenus *Howardina* were taken. Only a single specimen of *allotecnon* was identified, and the numbers of *septemstriatus* and *sexlineatus* were also insignificant. *Aedes quadrivittatus* was not taken east of the Canal Zone, but appeared throughout western Panama. Like *A. terrens* it was most abundant at some elevation, the great bulk of the specimens being taken at the 2,000 foot level at Cerro Campana and at 4,600 feet at Palo Santo in Chiriqui. It was not taken at the low elevation station at Esquinas in Costa Rica.

Of the subgenus *Ochlerotatus* six representatives were taken, and there were probably present in the collections two other species, *Aedes oligopistus* and *tormenter* which were lumped with *serratus* in the routine identification work. The numbers of *Aedes hastatus* were insignificant, but *serratus* was common and widespread, although exhibiting a gap in the Cerro Campana area. The species was commonest at low elevations, with only seven specimens being taken at the 4,600 foot station at Palo Santo. The location of the stations for this study in forest usually remote from the sea did not favor the collection of the coastal tidal marsh breeder, *Aedes taeniorhynchus*, and relatively few specimens were taken. *Aedes angustivittatus* was taken primarily at low elevations. *Aedes fulvus* was abundant only at the El Real station near sea-level in easternmost Panama, while *scapularis* was uncommon, the bulk (85 out of 95) of the specimens being from Santa Fe in Veraguas Province.

Representatives of the three subgenera of the genus *Psorophora* were taken. *Psorophora* (*Psorophora*) *cilipes* and *lineata* were represented by only two and nine specimens respectively. *Psorophora* (*Janthinosoma*) *ferox* was one of the commonest species of all, and was found throughout the length of the country. Relatively few, in terms of the total number taken, were at high elevations. *Psorophora* (*Janthinosoma*) *lutzii* was also generally distributed, but much less abundant. The third *Janthinosoma*, *champerico*, was taken only at the station at Tucue, although in the previous study a few were found at La Victoria. *Psorophora* (*Grabhamia*) *cingulata* was found in small numbers. All were at low elevations except a single specimen taken at the highest station at Palo Santo.

Three species of the genus *Mansonia*, i.e., *titillans*, *indubitans*, and *venezuelensis* were taken. The species *titillans* and *indubitans* were not separated in the routine identification work and they are recorded together in the table.

The genus *Culex* was represented by the subgenera *Culex*, *Melanoconion*, *Carrollia*, *Microculex* and *Isostomyia*, but only insignificant numbers were taken approaching man during the day in the forest. By contrast very great numbers of a large diversity of species may be taken at light traps operated at night, and several species may be taken biting man at night in the forest.

Only a single specimen of *Orthopodomyia fascipes* was collected.

The genus *Trichoprosopon* was represented in the collections by nine species of five subgenera. The most common species was *T.* (*Ctenogoeldia*) *magnus* of which 8,257 specimens were taken. The great bulk of these were from Cocle, Veraguas and Chiriqui Provinces in western Panama and Puntarenas Province in Costa Rica. In this western area it was most abundant at the low elevation stations near extensive stands of *Calathea* in which it breeds. Next in abundance was *T.* (*Rhuncomyia*) *longipes*, of which 2,060 specimens were taken. This species was widespread, having been taken at 16 of the 18 stations. As was the case with *T. magnus*, it was most abundant at the stations in western Panama and adjacent Costa Rica, at low elevations. *Trichoprosopon carqueirai*, *lampropus* and *leucopus*, three other species of the subgenus (*Rhuncomyia*), were rare. Small numbers of *T.* (*Trichoprosopon*) *digitatum* were found distributed from Candelaria in eastern Panama, west into Costa Rica. The subgenus *Shannoniana* was represented by two species, *schedocyclius* and *fluviatilis*, both of which were rare. *Trichoprosopon* (*Isogoeldia*) *espini* was taken in only small numbers at four of the 18 localities, but was present at the easternmost at El Real and the westernmost in Costa Rica.

The genus *Wyeomyia* made up almost a third (22,355) of all the mosquitoes taken. The identification of females of this genus, particularly when specimens have the scales rubbed, is difficult or impossible, so that the great bulk of the material was determined only to subgenus. The relatively small number on which species identifications were made, does not permit generalization about their distribution. On the subgenus *Wyeomyia* six species were identified as follows: *abebela*, *arthrostigma*, *celaenocephala*, *florestan*, *mitchellii*, and *scotinomus*. Seven species of the subgenus *Dendromyia* were determined: *chalcocephala*, *circumcincta*, *clasoleuca*, *jocosa*, *melanocephala*, *aporonoma*, and *prolepidis*. In the course of the study a representative of the South American subgenus *Davismyia* was found and described as a new species, *arborea* (Galindo, Carpenter and Trapido, 1951).

The genus *Limatus* was represented by the two species *assuleptus* and *durhamii*, of which only small numbers were taken.

Sabethes (*Sabethes*) *cyaneus* and *tarsopus* were found to be widely distributed in modest numbers throughout the length of the Republic and into Costa Rica, with *tarsopus* being about twice as abundant as *cyaneus*. Both species were present at the highest station at Palo Santo. *Sabethes* (*Sabethinus*) *undosus*, was very rare, with only four specimens taken. *Sabethes* (*Sabethoides*) *chloropterus* was the most common sabethine found in our previous study in central Panama. In the present study it was also common (3,211 specimens) but was outnumbered by one other sabethine, *Trichoproson magnus* (8,257 specimens). The only station at which *chloropterus* was not taken was Panama Viejo, which was located by a coastal mangrove swamp in which it would not be expected. The species was more common at stations below 2,000 feet than those higher.

The anophelines were not of special interest in this study of diurnal forest mosquitoes but ten species were taken of the genus *Anopheles* and one *Chagasia*. The species collected were the following: of the subgenus *Anopheles*, the species *apicimacula*, *eiseni* and *punctimacula*; of the subgenus *Stethomyia*, the species *kompi*; of *Nyssorhynchus*, the species *albimanus*, *oswaldoi*, *strodei* and *triannulatus*; of *Kerteszia*, the species *neivai*; and of *Lophopodomyia* the species *squamifemur*. Most common were *apicimacula* and *eiseni*, followed in numbers by *neivai* and *albimanus*.

VERTICAL STRATIFICATION

It is now well known that forest mosquitoes show a marked stratification in their vertical distribution. This stratification is most marked in the true tropical rain forest where the tree canopy is dense and the forest floor is deeply shaded and protected from the effects of wind on temperature and humidity. In the more open deciduous tropical forest, characteristic of areas with lower rainfall and a severe dry season, the difference between the microclimate of the canopy and the forest floor is less marked. This results in a less distinct stratification of the mosquito fauna as well. In the present study the stations at which collections were made were by necessity located in the deciduous tropical forest of the Pacific slope, with the exception of that at Tucue which was just across the continental divide in the higher rainfall Atlantic drainage. Thus the data in Table 3 and Figure 2 showing the proportion of each species taken on the ground and in the canopy indicate a less well marked stratification than might be found in true tropical rain forest.

Only species of which 15 or more specimens were taken are included in the table and chart. The percentages of each species taken on the ground and in the canopy are corrected for the numbers of man hours during which the collections were made, and only the numbers of man hours of collecting at the stations at which the species were actually taken were used in the calculations. An examination of the histogram in Figure 2 will show that most of the species of mosquitoes may readily be classified as attacking primarily either at ground level or in the canopy with relatively few being indiscriminate in this regard. More than half the species (25 out of 47) had 20 per cent or less of their numbers taken in the canopy while an additional eight species had 21 to 40 per cent attacking in the canopy. The number of arboreal species is smaller, with only six species being 81 to 100 per cent in the canopy and six falling between 61 and 80 per cent. Only two

TABLE 3

The vertical distribution of diurnal forest mosquitoes

Species	Per cent captured		Number taken
	Canopy	Ground	
Haemagogus equinus	69.1	30.9	6,431
Haemagogus lucifer	67.1	32.9	3,351
Haemagogus spegazzinii falco	80.7	19.3	743
Haemagogus argyromeris	9.7	90.3	58
Aedes leucocelaenus clarki	65.7	34.3	966
Aedes leucotaeniatus	40.1	59.9	434
Aedes terrens	17.4	82.6	1,533
Aedes quadrivittatus	74.3	25.7	2,227
Aedes septemstriatus	14.3	85.7	46
Aedes sexlineatus	10.9	89.1	16
Aedes serratus (group)	9.8	90.2	2,476
Aedes taeniorhynchus	2.0	98.0	632
Aedes angustivittatus	16.7	83.3	804
Aedes scapularis	13.1	86.9	95
Aedes fulvus	10.4	89.6	883
Psorophora champerico	1.5	98.5	70
Psorophora ferox	23.2	76.8	6,180
Psorophora lutzii	23.0	77.0	867
Psorophora cingulata	19.7	80.3	173
Mansonia titillans-indubitans	8.7	91.3	877
Mansonia venezuelensis	24.1	75.9	293
Trichoprosopon digitatum	15.9	84.1	71
Trichoprosopon fluviatilis	11.0	89.0	42
Trichoprosopon magnus	73.0	27.0	8,257
Trichoprosopon espini	60.1	39.9	84
Trichoprosopon longipes	20.8	79.2	2,049
Trichoprosopon leucopus	0.0	100.0	19
Wyeomyia abebela	36.2	63.8	25
Wyeomyia arthrostigma	81.7	18.3	19
Wyeomyia mitchellii	10.1	89.9	107
Wyeomyia chalcocephala	0.0	100.0	21
Wyeomyia jocosa	28.3	71.7	261
Wyeomyia melanocephala	48.6	51.4	36
Wyeomyia aporonoma	2.8	97.2	216
Wyeomyia arborea	100.0	0.0	20
Limatus assuleptus	2.8	97.2	195
Limatus durhamii	14.6	85.4	120
Sabethes cyaneus	87.4	12.6	348
Sabethes tarsopus	87.4	12.6	655
Sabethes chloropterus	75.9	24.1	3,170
Anopheles apicimacula	10.3	89.7	226
Anopheles eiseni	18.1	81.9	210
Anopheles punctimacula	0.0	100.0	24
Anopheles albimanus	8.5	91.5	102
Anopheles strodei	7.1	92.9	116
Anopheles neivai	40.3	59.7	183
Chagasia bathanus	85.8	14.2	26
Total			45,757

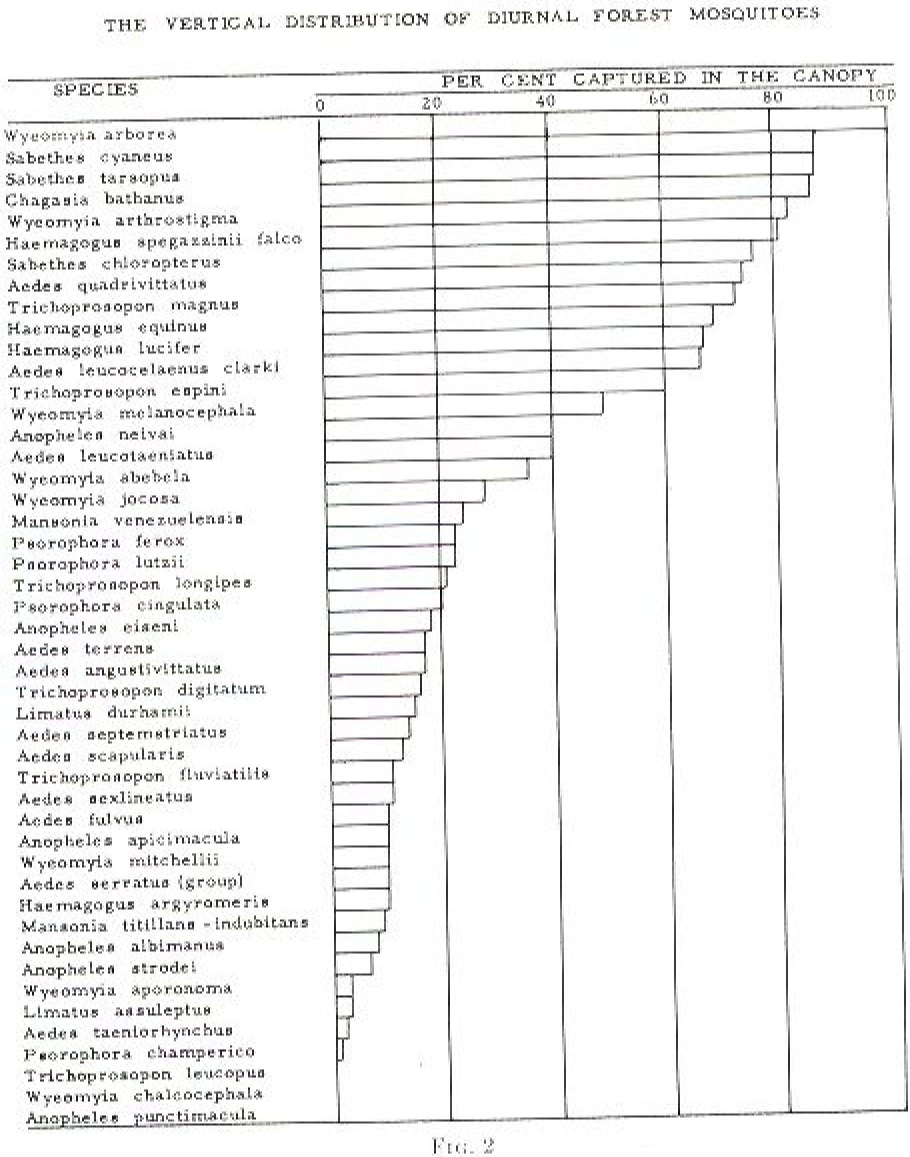

FIG. 2

species appear intermediate with 40 to 60 per cent arboreal. Three species, of which relatively few specimens were taken, were confined completely to the ground level, while one species, the recently described *Wyeomyia arborea*, was taken only in the canopy.

As in our previous study we found that of the *Haemagogus*, the species *spegazzinii falco* was the most arboreal, with 80.7 per cent being taken in the canopy. *Haemagogus argyromeris*, of which very few were taken except in the low, dry, open forest at Campanita Abajo, was the only *Haemagogus* which was not arboreal, with 90.3 per cent being taken on the ground.

Of all the species of *Aedes* the most arboreal was *quadrivittatus*, with 74.3 per cent taken in the canopy, while the other two representatives of the subgenus *Howardina*, *septemstriatus* and *sexlineatus*, were taken primarily on the ground. The three species of the subgenus *Finlaya* were found to be vertically stratified in the same order as in our previous study, with *terrens* being primarily terrestrial, *leucocelaenus clarki* the most arboreal and *leucotaeniatus* intermediate. The *Ochlerotatus* species all were most abundant on the ground.

The *Psorophora* and *Mansonia* also were taken in greatest numbers on the ground.

The most arboreal of the *Trichoprosopon* was the species *magnus* with 73.0 per cent taken in the canopy followed by *espini* with 60.1 per cent in the tree tops. The remaining species taken, *digitatum*, *fluviatilis*, *longipes* and *leucopus* were most abundant on the ground.

Only a very small number of the very numerous *Wyeomyia* were identified to species. The species *arborea*, discovered and described in the course of this study (Galindo, Carpenter and Trapido, 1951) was the one species taken in the study entirely in the canopy. Predominantly arboreal also was the species *arthrostigma* with 81.7 in the canopy. The remaining species had more than 50 per cent of their numbers taken on the ground, but the percentages given in the table and chart would be subject to revision if larger numbers had been identified to species.

The two species of the genus *Limatus* were most abundant on the ground.

The figures for the *Sabethes* are somewhat at variance with those obtained in our previous study. In the present study *cyaneus* and *tarsopus* were equally abundant in the canopy (87.4 per cent) with *chloropterus* somewhat less so (75.9 per cent). In our earlier study the positions of *cyaneus* and *chloropterus* were reversed with *chloropterus* appearing to be more arboreal than *cyaneus*.

As the present collections were made during the daylight hours the number of anophelines taken was not large. All the species of the genus *Anopheles* were either completely or primarily taken on the ground with the exception of the epiphytic plant breeding representative of the subgenus *Kerteszia*, *neivai*, of which 40.3 per cent were in the canopy. As was found in our previous study, *Chagasia bathanus* was taken most often in the canopy, with but 14.2 per cent of the catch on the ground.

DISCUSSION AND CONCLUSIONS

It is evident from the preceding review of forest mosquito collections made throughout the length of Panama and into Costa Rica, that there is no consistent shift in the composition of this fauna which might be used in explanation of the failure of sylvan yellow fever to appear west of the Canal Zone prior to 1950. The known vector species in South America, *Haemagogus spegazzinii falco* and *Aedes leucocelaenus clarki* were found in western Panama and Costa Rica. The other species of *Haemagogus*, the *Aedes* of the subgenus *Finlaya*, and the *Sabethes* which might be considered suspect as vectors on epidemiological grounds, all continue their ranges through the Isthmian region, with the exception of *Haemagogus lucifer* which is replaced in westernmost Panama and Costa Rica by *H. iridicolor*. The significant positive finding for the area under study is that the mosquitoes which are the known South American vectors of yellow fever and their ecological associates were only abundant at the Atlantic drainage station at Tucue, where the forest is most representative of the true tropical rain forest type of the Amazon and Orinoco basin in which sylvan yellow fever permanently persists. Related to this fact is the circumstance that the proven yellow fever fatalities west of the Canal Zone in Panama during 1950 and 1951 (Elton, 1952) were contracted in this Atlantic slope rain forest, while yellow fever failed to appear in the western provinces of the Pacific side. The critical factor would thus appear to be not geographical but ecological.

In our introduction we mentioned the rainfall differential between the Atlantic and the Pacific slopes of the Isthmus, and the consequent difference in forest type in the two drainages. We might add that as a result of the gap in the mountain system in the Canal Zone area, the northeasterly trade winds here spill across the Isthmus to the Pacific side, so that just east of the Canal Zone in the La Victoria area and just west of the Zone at Arraijan, the forest while not so well developed as the Atlantic side rain forest, is at least intermediate between rain forest and deciduous forest. When we review the data presented here we find that the known South American vectors and their ecological associates were most abundant in the best developed rain forest, at Tucue, secondary in numbers in the transitional forest at such places as La Victoria and Arraijan, and sparse, rare, or wholly absent in deciduous or scrub forest at such places as Campanita Abajo and Arriba which are in the rain shadow of Cerro Campana.

This leaves us still with the question of why, if the immunity surveys conducted in Panama, Central America and Mexico (cited above) are taken at face value, sylvan yellow fever was confined in the past decades to the area of Panama east of the Canal Zone, contiguous with South America. The data presented here for the Pacific slope of western Panama are ample to show the incidence of known vectors to be too low to be considered capable of maintaining virus. But what of the Atlantic slope forest and the fact that sylvan yellow fever did finally pass through this area in the period 1949 to 1951? The explanation would be this. The gap in the mountain system in the Canal Zone area, as mentioned above, results in a spilling of moisture onto the Pacific slope which would otherwise fall in the Atlantic drainage. This is inadequate in amount and annual distribution to produce true rain forest on the Pacific slope, but also deprives the Atlantic side of the moisture necessary to maintain this ecological situation. The conditions for the vector species, *Haemagogus spegazzinii falco* and *Aedes leucocelaenus clarki*, are in consequence only marginal in the area. The ability of the virus to cross this marginal zone would thus depend on the coincidence of the approach of the virus from the east with a year of particularly favorable rainfall conditions which would result in an optimum production of the vector species at the critical time. This interpretation would gain substance if it could be demonstrated that there are long term as well as annual cycles of abundance of these mosquitoes. That such long term cycles, which are well known among anophelines, also occur in forest dwelling, tree hole breeding mosquitoes such as *Haemagogus* and *Aedes* (*Finlaya*) has been suggested by Causey and Dos Santos (1949) in Brazil.

Subsequent to the studies reported here, the observations at the La Victoria stations were continued, so that we now have data on the abundance cycle of these mosquitoes over a period of years. These data will be the subject of a separate paper, but it may be said now that they do support the hypothesis advanced here.

SUMMARY

Collections of forest mosquitoes totaling 72,211 individuals were made on the ground and in the canopy during the rainy season of 1950 at 18 localities throughout the length of Panama and into Costa Rica, in seeking an explanation for the failure of sylvan yellow fever to appear west of the Canal Zone prior to that time.

It was found that the known South American vectors of the disease, *Haemagogus spegazzinii falco* and *Aedes leucocelaenus clarki* occurred sparingly west into Costa Rica, but the only station at which they were present in substantial numbers was one located in the well developed tropical rain forest of the Atlantic slope.

The vertical stratification of the mosquitoes taken in the forest is summarized for each species of which more than 15 individuals were taken. These data are of importance in assessing the possible role of each species in terms of its contact with the arboreal mammals which are the intermediate hosts of the yellow fever virus.

It is suggested that physiographic and meteorologic conditions in central Panama and the Canal Zone area produce a forest cover which is intermediate between tropical rain forest favorable for the production of substantial numbers of tree hole breeding vector mosquitoes, and tropical deciduous forest in which conditions are less favorable. It is further suggested that since conditions are marginal in this critical area, it would take a particularly favorable rainfall pattern to produce the mosquito population necessary to carry the virus across into the Atlantic side rain forest of western Panama as happened in 1949 and 1950.

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