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THE ABUNDANCE CYCLES OF ARBOREAL MOSQUITOES DURING SIX YEARS AT A SYLVAN YELLOW FEVER LOCALITY IN PANAMA[1]

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INTRODUCTION

The problem of how sylvan yellow fever crossed from eastern Panama through the Canal Zone area and into western Panama and Central America in the period since 1948 has been a subject of much interest. Recent papers which deal with the matter in part have been those of Trapido, Galindo and Carpenter (1955) and Trapido and Galindo (1956a). It has been pointed out that the forest canopy mosquito fauna known to be involved in the transmission of sylvan yellow fever becomes depauperate during the dry season characteristic of the Pacific slope, and that the gap in the mountain system marked by the location of the Panama Canal is an area of transition from the wet and dry deciduous forest conditions of the Pacific slope to the wet rain-forest conditions of the Caribbean slope of western Panama. But on the Pacific side of eastern Panama there is also a gradual transition from tropical deciduous forest in the lowlands and on lower slopes to climatic and vegetation conditions approaching those of tropical rain-forest on the upper slopes (Trapido and Galindo, 1956b). The purpose of the present communication is to present the results of six years of collecting forest canopy mosquitoes at Cerro La Victoria, some 15 miles east of the Panama Canal, and to demonstrate the magnitude of the year to year fluctuations in the populations of these mosquitoes as this may be related to the maintenance of the sylvan yellow fever cycle in the area.

The two stations at La Victoria from which our data are drawn were at elevations of 400 and 1,200 feet, and were thus high enough to be in forest intermediate in appearance between deciduous forest and rain-forest, although the dry season at these localities is sufficiently marked to meet the climatological definition of tropical wet and dry climate associated with deciduous forest. This was an area where sylvan yellow fever occurred late in 1948.

The method of making the collections on which this report is based have been described previously (Galindo, Trapido and Carpenter, 1950). In the initial studies two crews of collectors were used to man the field stations from 8:00 a.m. to 5:30 p.m., but in subsequent years a single crew made collections during the hours when experience had shown the diurnal mosquitoes to be most active, *i.e.*, the hours between 9:00 a.m. and 3:00 p.m.

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So that the population densities from different years might be validly compared, the data from the first year of collecting was reworked to include only the captures made between the hours of 9:00 a.m. and 3:00 p.m. For the present study there are considered only the collections taken attacking human baits stationed on platforms in the forest canopy, because it is in the canopy that the mosquitoes of interest to us are most abundant, and also because it is in the canopy that the sylvan yellow fever transmission cycle is presumed to be carried on among susceptible mammal hosts by arboreal mosquitoes. A full account of the diurnal forest mosquitoes of Panama has already been given (Trapido, Galindo and Carpenter, 1955), and the present paper will deal only with those mosquitoes known or suspected as vectors of sylvan yellow fever. These are five in number as follows: *Haemagogus equinus* Theobald, *Haemagogus lucifer* (H., D. and K.), *Haemagogus spegazzinii falco* Kumm et al., *Aedes leucocelaenus clarki* G., C. and T., and *Sabethes chloropterus* (Humboldt). The nature of the evidence implicating these species in yellow fever transmission has been reviewed recently by Trapido and Galindo (1956a). There is no direct evidence with regard to *Haemagogus lucifer*, but this species is included since it appears increasingly likely that all *Haemagogus* are capable of transmitting the disease under suitable conditions (Galindo, Rodaniche and Trapido, 1956).

As the annual abundance cycles of arboreal forest mosquitoes are dependent on rainfall we will first present these data.

RAINFALL

The available rainfall data are those published by the Section of Meteorology and Hydrography of the Panama Canal Company. We did not, unfortunately, operate rain gauges at the sites of our forest mosquito collecting stations, but it is quite certain that the rainfall there was intermediate in amount between that reported for El Jefe and Balboa Heights. The annual rainfall at El Jefe is more than twice that at Balboa Heights since the former station is much higher than the latter, but the monthly distribution over the year at the two stations is very much the same. The average rainfall for these two stations during the six years of the study, together with the minima and maxima are shown in Table I. The "dry season" is the low sun period from January through April. At El Jefe only 7.3 percent and at Balboa Heights only 6.3 percent of the annual precipitation fell during these four months. From the point of view of our interest in the maintenance of yellow fever transmission we are particularly interested in the rainfall variation during the dry season, the period when arboreal mosquito populations are minimal. Inspection of the data in Table I shows that the magnitude of the fluctuations from year to year is very great. If we take for an example the month of February, we see that at El Jefe during the six year period of the study the rainfall varied from 0.61 inches to 13.10 inches, and at Balboa Heights from only a trace to 2.49 inches. It may be readily appreciated from these data how variable are the conditions from year to year for the production of the tree hole breeding arboreal mosquito populations.

TABLE I

SUMMARY OF VARIATION IN RAINFALL DURING THE SIX YEARS 1949 THROUGH 1954

STATION		JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	YEAR
[1]El Jefe, Panama.....	Max.	9.79	13.10	2.58	6.64	31.69	20.78	21.14	21.47	26.54	24.72	27.51	16.77	169.21
	Av.	2.91	3.25	1.02	3.84	22.51	17.85	15.44	17.59	18.22	21.36	16.59	10.80	151.38
	Min.	0.66	0.61	0.35	1.29	15.61	14.71	13.48	13.75	15.20	16.61	6.08	6.77	132.23
[2]Balboa Heights, Canal Zone.....	Max.	2.66	2.49	1.89	4.89	15.06	13.26	12.14	8.49	9.79	14.81	13.62	13.46	84.03
	Av.	0.92	0.87	0.72	2.12	9.85	8.47	7.64	6.60	7.33	12.49	10.04	6.35	73.39
	Min.	0.15	T	0.11	0.07	8.22	3.97	4.97	2.90	3.79	7.08	6.28	3.80	63.86

[1]Elevation 3,200 feet. [2]Elevation 100 feet.

LONG TERM VARIATIONS IN FOREST CANOPY MOSQUITO POPULATIONS

The results of the forest canopy mosquito collections at Cerro La Victoria are summarized in Table II and in figure 1. These data represent the average capture rates per ten man hours at two stations, with the exception of 1951 when only one of the stations was operated. The collections are unfortunately incomplete for the first five months of certain of the years. In Table II months during which no collecting was done are indicated by dashes. It will be seen in this table that for January there are three years of data, for February, March and April four years, and for May five years.

On reference to figure 1 it can be seen at once that for each species there appears a characteristic average annual abundance cycle. The configuration of these abundance cycles in general follows that reported for the first year of study at these stations (Galindo, Trapido and Carpenter, 1950). The populations of *Haemagogus equinus* are the most rapid in building up after the beginning of the rainy season in May. The peak densities of

Haemagogus lucifer, *H. spegazzinii falco*, and *Sabethes chloropterus* appear somewhat later, in June and July. The apparent low densities of *Aedes leucocelaenus clarki* are somewhat deceptive, since at La Victoria this species is not as arboreal as the others and the data here include only the individuals taken in the canopy.

The principal interest in the data presented concerns the year to year variations in the densities of the monthly captures. Numerical values are shown in Table II, but the magnitude of the variations may best be appreciated by reference to figure 1 in which the monthly maxima and minima (as well as the means) are graphically portrayed. It may readily be appreciated from a review of these data that yellow fever transmission potential must vary greatly from year to year, although it would also appear that if all these species are capable of transmitting the disease there are probably high enough densities of one or the other species during the rainy season months to maintain the cycle. It is evident that the dry season is the critical time of year when the maintenance of the yellow fever transmission cycle must be precarious. During the four dry season months (January through April) *Haemagogus spegazzinii falco* and *Aedes leucocelaenus clarki* were completely lacking. *Haemagogus equinus* and *H. lucifer* were present, although at very low densities, during each of these months in one year or another, but not during all four months in any one year. The only species which appeared during every month in any one year was *Sabethes chloropterus*.

TABLE II

SIX YEAR ABUNDANCE CYCLES OF FIVE MOSQUITOES KNOWN OR SUSPECTED AS SYLVAN YELLOW FEVER VECTORS
CERRO LA VICTORIA, PANAMA
(SHOWN AS NUMBER OF EACH SPECIES PER TEN MAN HOURS OF COLLECTING IN THE FOREST CANOPY.)

SPECIES	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
Haemagogus equinus	1949	—	0.0	0.0	2.0	13.1	41.8	18.3	3.6	8.2	1.8	4.4	0.9
	1950	0.4	0.0	0.0	0.4	14.8	20.5	9.2	4.6	1.7	4.6	4.0	1.8
	1951	—	—	—	—	—	9.5	0.8	0.0	1.9	0.8	1.9	0.0
	1952	—	—	—	—	73.2	42.1	22.2	5.7	8.6	8.6	6.4	9.7
	1953	3.0	4.9	0.0	1.1	38.0	16.3	14.7	3.4	12.2	16.1	6.6	1.5
	1954	0.0	0.0	0.8	0.0	56.9	29.5	13.3	13.1	1.4	1.9	2.8	1.4
	Av.	1.1	1.2	0.2	0.9	39.2	26.6	13.1	5.1	5.7	5.6	4.4	2.6
Haemagogus lucifer	1949	—	0.0	0.0	0.0	10.8	20.9	35.7	13.0	19.7	17.1	25.4	7.2
	1950	0.8	0.0	1.3	0.2	4.6	8.3	12.8	8.3	3.8	3.5	3.6	2.9
	1951	—	—	—	—	—	2.7	3.3	2.6	1.9	0.8	5.4	0.5
	1952	—	—	—	—	17.7	25.3	24.1	6.6	7.7	6.7	6.6	6.4
	1953	1.8	0.8	0.0	0.3	9.7	10.1	16.3	10.1	17.3	12.1	15.6	13.1
	1954	1.7	0.0	0.0	0.0	17.8	14.4	26.3	18.8	4.0	4.4	7.8	3.4
	Av.	1.4	0.2	0.3	0.1	12.1	13.6	19.8	9.9	9.1	7.4	10.7	5.6
Haemagogus spegazzinii falco	1949	—	0.0	0.0	0.0	0.0	14.5	16.1	2.6	8.3	4.7	10.2	3.9
	1950	0.0	0.0	0.0	0.0	0.7	3.3	5.9	1.8	1.3	0.5	1.1	0.6
	1951	—	—	—	—	—	1.4	1.7	0.9	1.4	0.0	0.8	0.0
	1952	—	—	—	—	3.8	6.8	2.1	0.7	0.4	0.9	0.9	0.3
	1953	0.0	0.0	0.0	0.0	0.9	1.0	3.3	1.0	1.3	4.3	2.2	1.8
	1954	0.0	0.0	0.0	0.0	3.1	11.7	2.4	3.8	0.6	0.8	1.0	0.4
	Av.	0.0	0.0	0.0	0.0	1.7	6.5	5.3	1.8	2.2	1.9	2.7	1.2
Aedes leucocelaenus clarki	1949	—	0.0	0.0	0.0	2.2	2.4	3.9	2.2	2.2	2.2	1.1	1.7
	1950	0.0	0.0	0.0	0.0	0.0	0.3	0.6	1.6	1.3	0.4	1.2	0.0
	1951	—	—	—	—	—	0.5	0.4	0.4	5.2	1.5	7.7	1.1
	1952	—	—	—	—	1.0	3.5	4.6	1.1	0.9	0.7	0.8	0.3
	1953	0.0	0.0	0.0	0.0	0.0	0.3	1.9	2.6	2.1	6.9	4.1	3.1
	1954	0.0	0.0	0.0	0.0	0.0	2.8	5.3	4.8	1.3	1.0	1.0	0.6
	Av.	0.0	0.0	0.0	0.0	0.6	1.6	2.8	2.1	2.2	2.1	2.7	1.1
Sabethes chloropterus	1949	—	0.0	0.4	1.4	6.3	30.9	32.2	32.0	12.2	8.6	11.8	3.8
	1950	1.8	0.0	1.5	1.5	3.2	7.7	16.4	10.4	4.5	2.0	1.2	1.8
	1951	—	—	—	—	—	5.0	1.3	1.3	2.4	0.4	2.3	1.1
	1952	—	—	—	—	5.2	17.9	51.1	29.9	19.0	9.9	3.6	6.8
	1953	2.0	0.5	0.5	0.3	8.6	9.1	22.8	16.3	10.0	9.7	4.1	1.8
	1954	0.2	0.0	0.0	0.2	5.4	19.5	29.1	19.1	4.1	1.2	3.4	1.2
	Av.	1.3	0.1	0.6	0.9	5.7	15.0	25.5	18.2	8.7	5.3	4.4	2.8

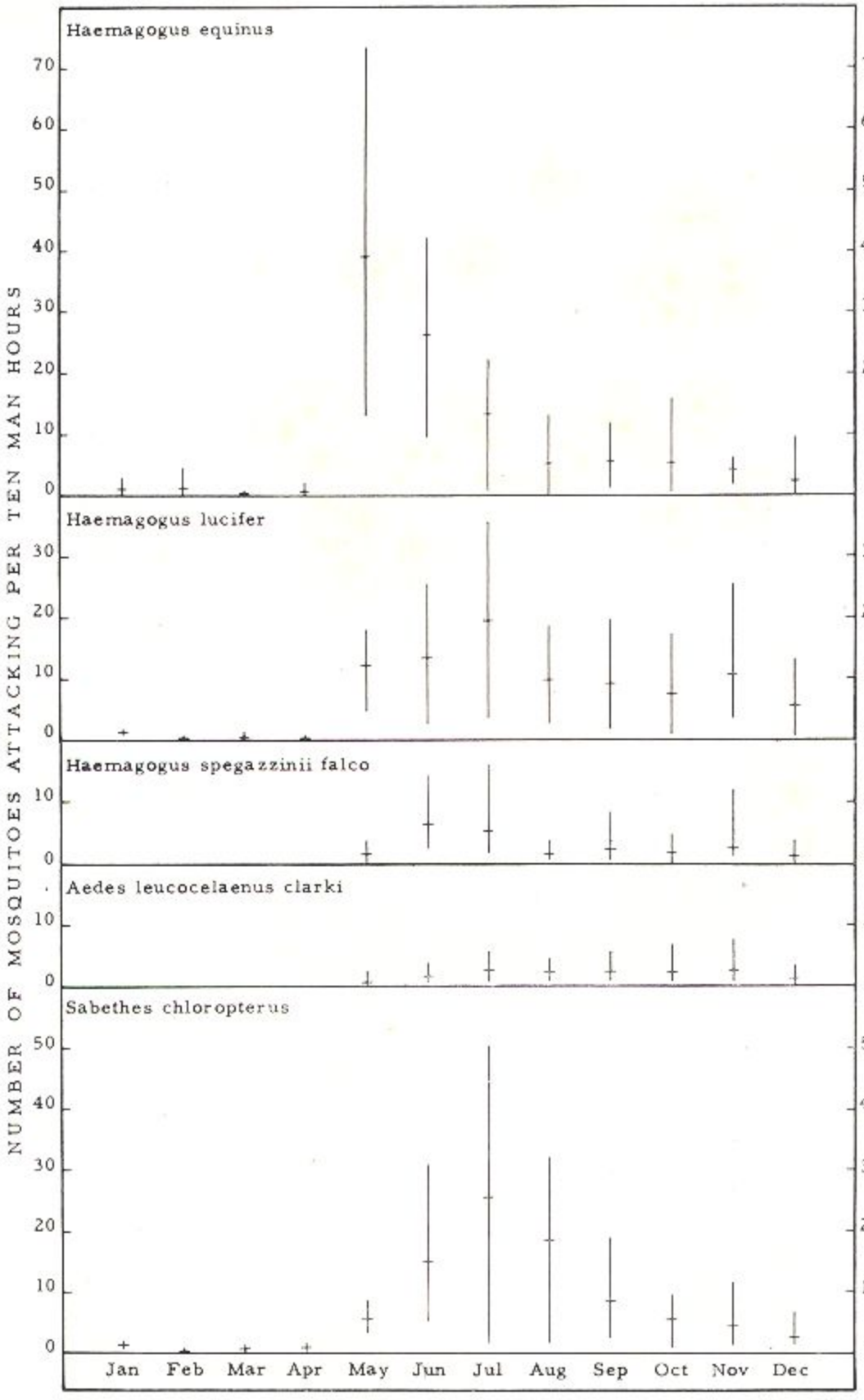

FIGURE 1. Annual abundance cycles of five arboreal tree hole breeding mosquitoes known or suspected as sylvan yellow fever vectors, based on six years of collecting. Shown are the maximum, minimum and mean numbers taken per ten man hours, by months.

The three species of *Haemagogus* and *Aedes leucocelaenus clarki* are aedine mosquitoes with eggs which resist desiccation, and their survival during the dry season in this state poses no special problem. But as the present understanding is that there is no transovarian passage of yellow fever virus (Whitman, 1951) the means by which the virus is maintained through dry season is a very live issue.

Sabethes chloropterus also utilizes rot holes in trees for breeding, but the eggs do not resist desiccation. For survival through the dry season this species must either find breeding places or else be so long lived as to persist as adults from one rainy season to the next. We have previously shown that this species does possess a mechanism for breeding through the dry season (Galindo, Carpenter and Trapido, 1951). That is, the species lays its eggs preferentially in tree holes which have a small aperture opening into rot holes with a large water holding capacity. Such water containers are protected from the desiccating winds of dry season and are able to retain water through this unfavorable time of year. This finding has been confirmed in the laboratory by two of the authors (P. G. and H. T.) who have succeeded in colonizing the species. Even under caged conditions it has been found that *chloropterus* will only lay eggs in numbers in water containers which are closed at top and have a small aperture on the side (*i.e.*, covered bamboo sections with a hole one inch in diameter in the side). The colony experience has also been that *Sabethes chloropterus* is longer lived than the species of *Haemagogus* which have been studied in the laboratory. Thus it appears that both means of surviving the dry season mentioned above, are utilized.

While it is true that the five mosquitoes dealt with here are predominantly arboreal, the forest at Cerro La Victoria has a more open aspect than is seen in true tropical rain-forest, and the vertical stratification of these species is not so marked as in forest of the latter type. The dry season is the period of maximum leaf loss at Cerro La Victoria. At this time of year the difference between the microclimate in the canopy and at ground level is least pronounced, and there is some tendency for the arboreal species to appear less well stratified in the forest. This phenomenon had been noted by Bates (1944) for *Haemagogus* in Colombia. At Cerro La Victoria we found this to be particularly true of *Sabethes chloropterus* in some years. It was most clearly shown in 1949 at a time when collections were made at platforms midway up the trees as well as on the ground and in the canopy. The decline in the catch in the canopy and the increase in the catch at ground level and at the middle platform during dry season may be seen in the following tabulation in which the proportions of the *chloropterus* in catch at the three levels are shown as percentages.

	Ground	Middle Platform	Canopy Platform
Dry Season.....	23%	61%	16%
Rainy Season.....	8%	46%	46%

DISCUSSION AND SUMMARY

The data here summarized demonstrate that in an area of Panama through which sylvan yellow fever passed, where the vegetation cover is transitional between tropical deciduous forest and tropical rain-forest, there are substantial year to year fluctuations in rainfall and correspondingly great fluctuations in the densities of the arboreal mosquitoes known or suspected to be yellow fever vectors. During the dry season characteristics of this forest type the arboreal mosquito fauna becomes rare. But it is shown that there is enough variation in mosquito populations so that during the four month dry season at least some of the vector species are present during each month in some years. The tendency toward a lesser vertical stratification of the arboreal mosquito fauna in dry season means that these mosquitoes are actually not quite so scarce as the tabulations of the canopy catch summarized might indicate. Of the mosquitoes known or suspected as vectors of sylvan yellow fever, *Sabethes chloropterus* was the one species taken in the canopy during all months in any one year.

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