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FOREST MOSQUITOES ASSOCIATED WITH SYLVAN YELLOW FEVER IN NICARAGUA

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During 1952 and 1953 eleven human yellow fever fatalities from Nicaragua were reported in the Weekly Epidemiological Reports of the Pan American Sanitary Bureau (Trapido and Galindo, 1956 a). During these two years there were also numerous reports of monkey fatalities received by the Nicaraguan Ministry of Public Health, following similar reports during 1951 in Costa Rica. A number of the forest primate deaths in Costa Rica were shown to have been due to yellow fever (Vargas-Mendez and Elton, 1953). Dr. Jorge Boshell, yellow fever consultant to the Pan American Sanitary Bureau, investigated the Nicaraguan reports and was able to obtain livers from recently dead monkeys in the Rivas Isthmus area in 1952. These gave histopathological evidence of having been due to yellow fever. In 1953 monkeys were reported to have been dying on the Pacific slope, south and southwest of Managua, but tissues from freshly dead animals in which the lesions of yellow fever could be demonstrated were not obtained. While these fatalities may well have been due to yellow fever, definite proof of this is lacking. Previous to these events yellow fever in its sylvan form had not been recognized in Nicaragua.

Because of the appearance of sylvan yellow fever in Nicaragua it seemed desirable to make a survey of the forest mosquito fauna which had not been studied before. In 1953 arrangements were made to collect forest mosquitoes during the rainy season near Villa Somoza in Chontales Province, east of Lake Nicaragua, where both human and monkey fatalities had occurred the previous year. The area selected was along the Rama Road 14 to 32 kilometers east of Villa Somoza where the plateau east of Lake Nicaragua slopes down to the Caribbean coastal plain in the basin of the Rio Mico. As this slope is exposed to the northeasterly trade winds it is an area of relatively high rainfall, and the heavy broad-leaved forest has the aspect of tropical rain-forest. Five sites at elevations between 700 and 1,350 feet were selected as collecting stations.

The collecting method used was similar to that previously employed in Panama (Trapido *et al.*, 1955). That is, a pair of men were stationed in the forest to make collections of mosquitoes which approached to attack, on the ground and on a platform constructed in the tree canopy. The simultaneous collections were made during the day, usually between 9 A.M. and 3 P.M. one day a week at each tree station. The results of these collections, which were made during August, September and November are shown in Table 1.

To obtain some idea of the forest mosquito fauna in an area where sylvan yellow fever had been active the previous year on the Pacific slope, collections were first made for a short time (from June 1st to 12th), several weeks after the rainy

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TABLE 1

Diurnal forest mosquito captures near Villa Somoza, Nicaragua, during August, September and November 1953

Number of man hours collecting	468	[1]Per cent captured	
	No. taken	Ground	Canopy
Tribe Culicini			
Haemagogus equinus	85	3.8	96.2
Haemagogus spegazzinii falco	41	7.7	92.7
Haemagogus iridicolor	243	20.6	79.4
Haemagogus mesodentatus	2	0.0	100.0
Total *Haemagogus*	371		
Aedes leucocelaenus clarki	6	0.0	100.0
Aedes terrens	2	51.8	48.2
Aedes sexlineatus	1	100.0	0.0
Aedes angustivittatus	1	100.0	0.0
Aedes serratus group	3	100.0	0.0
Psorophora ferox	402	98.4	1.6
Psorophora lutzii	104	98.3	1.7
Total Culicini	890		
Tribe Sabethini			
Trichoprosopon magnus	487	9.5	90.5
Trichoprosopon espini	3	69.2	30.8
Trichoprosopon leucopus	1	100.0	0.0
Wyeomyia arborea	1	0.0	100.0
Wyeomyia (Dendromyia) sp.	23	54.1	45.9
Wyeomyia sp.	655	66.3	33.7
Limatus asulleptus	1	0.0	100.0
Sabethes cyaneus	7	0.0	100.0
Sabethes tarsopus	8	0.0	100.0
Sabethes chloropterus	195	5.5	94.5
Total Sabethini	1381		
Tribe Anophelini			
Anopheles eiseni	2	51.8	48.2
Anopheles fausti	4	0.0	100.0
Anopheles neivai	7	0.0	100.0
Chagasia bathanus	12	8.2	91.8
Total Anophelini	25		
Total all species	2296		

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

season had begun, at Valle Menier in Rivas Province, on the isthmus between Lake Nicaragua and the Pacific Ocean. This was an area where there had been heavy mortality of howling monkeys in 1952. During September and October of 1953, because of current reports of monkey mortality southwest of Managua on the Pacific slope of the continental divide, the work at Villa Somoza was interrupted to make collections at Guapinolar in Managua Province. The collections

TABLE 2

Abundance of certain diurnal mosquitoes at Pacific side localities in Nicaragua

Locality	Valle Menier			Guapinolar		
Inclusive collecting dates	June 1–12, 1953			Oct. 23–29, 1953		
No. of hours of collecting	105			84		
	Total no. taken	Per cent		Total no. taken	Per cent	
		Ground	Canopy		Ground	Canopy
Haemagogus equinus	2729	57	43	1609	38	62
Haemagogus anastasionis	25	56	44	42	69	31
Sabethes chloropterus	145	79	21	286	19	81

were carried on there somewhat irregularly at first, but we have seven full days of data gotten between the 23rd and the 29th of October when routine ground and canopy catches were made. For these two stations we had summarized in Table 2 only the captures of species known or suspected as sylvan yellow fever vectors. The rainfall and vegetation cover of these Pacific slope stations differ from the conditions at Villa Somoza. As in Panama, the Pacific side had a severe dry season, approximately four months long, and the natural vegetation is in consequence the tropical deciduous forest type. That is, the canopy on the Pacific side is lower and the woods much more open than those near Villa Somoza.

RESULTS

Certain features of the population dynamics of the arboreal forest mosquito fauna were found to differ substantially from those previously worked out in Panama. In analyzing the Nicaragua data we have come to realize that a rational explanation of the findings can best be made by considering each of the species of interest in terms of its "center of origin" or "center of dispersal." The biological principle involved is that recently evolved species (we believe the entire genus *Haemagogus* to be of recent origin) are in best adjustment with the environment in the region where they arose. An important way in which this is expressed is that the center of origin supports maximum population densities of the particular species. It will be seen below how this concept, in combination with the principle that each species has an optimum ecological niche, explains the Nicaragua findings, and incidentally makes clearer the previous findings in other parts of Middle America.

At the stations near Villa Somoza four species of *Haemagogus* were taken. Most abundant was *Haemagogus iridicolor*. It was about three times as common as *Haemagogus equinus*, which in turn was about twice as prevalent as *Haemagogus spegazzinii falco*. The fourth species, *Haemagogus m. mesodentatus*, was rare, only two specimens being taken during the three months of collecting. The composition of the *Haemagogus* catch at the Pacific side localities, Valle Menier and Guapinolar, was very different. *H. equinus* was the one species present in both areas, and was far more abundant at the Pacific side localities than at Villa

Somoza. The second species on the Pacific slope was *Haemagogus anastasionis*. (We have also taken a few *H. iridicolor* on the Pacific versant of Nicaragua, on incidental collecting trips, but not at the established stations.)

The very great difference in the densities of *H. equinus* in the two regions is a matter of much interest. We know from our studies in Panama (Trapido and Galindo, 1957 b) that there are substantial fluctuations in the densities of these tree-hole breeding mosquitoes at different times of the year, and it is therefore only with caution that short-term catches at different localities may be compared. But the magnitude of the differences in densities observed in Nicaragua are so great that it is evident that they are significant, particularly since all the collections were made during the rainy season, and since high densities at the Pacific slope stations were recorded both early and late in the rainy season. Based on an average collecting day of six hours, the density of *equinus* at Guapinolar was 196 per ten man-hours of collecting, at Valle Menier 260 per ten man-hours, but at Villa Somoza only 1.8 per ten man-hours. The difference in abundance in the two areas confirms a finding made in Panama; namely, that while *equinus* occurs in a number of different habitats, it reaches its maximum development in tropical deciduous forest and is relatively less common in tropical rain-forest. As mentioned above, the Caribbean side stations near Villa Somoza were located on an eastern facing slope where the vegetation has the aspect of rain-forest, while the Pacific side localities were in an area of much more open deciduous forest. The densities of *equinus* found at the Pacific side stations exceeded by far those found at any of the numerous collecting stations operated in Panama (Trapido *et al.*, 1955). We know deciduous forest to be the optimim habitat of *equinus*, and we also know that since this species ranges from Venezuela and Colombia to southernmost Texas (Galindo and Trapido, in preparation), the Pacific side Nicaraguan stations must be near the center of dispersal. Thus, in terms of both favored ecological niche and center of dispersal, the high *equinus* populations of the Pacific side Nicaraguan deciduous forest are understandable.

The failure of *H. spegazzinii falco* to appear in the Pacific side collections is probably due to two factors. First is the fact that Nicaragua is at the periphery of the range of the species, which, with its typical race *spegazzinii*, extends south to northern Argentine and has the center of its distribution far off in the basin of the Amazon. Second is the fact that the work in Panama has shown that this is a species whose optimum habitat is rain-forest (Trapido and Galindo, 1957 c). It persists in the Caribbean slope rain-forest in small numbers as far north as Honduras, but in the unfavorable deciduous forest environment of the Pacific side it extends no farther into Central America than the southern portion of the Rivas Isthmus, a short distance south of the location of the Valle Menier and Guapinolar stations.

H. m. mesodentatus in our experience is an Atlantic side form with the exception of a break through to the Pacific side in the San Jose valley of Costa Rica. It is associated with rain-forest, but is nowhere common south of Guatemala and Mexico. The finding of only two specimens at Villa Somoza is consistent with this distributional picture.

H. anastasionis, on the other hand, is primarily a species of the Pacific side and is characteristic of scrubby second growth or open deciduous forest. Thus its appearance only at the Valle Menier and Guapinolar stations is understandable.

H. iridicolor is a species of restricted range and it is limited to Nicaragua, Costa Rica and western Panama. Its optimum habitat is the Caribbean side rain-forest. It was the commonest *Haemagogus* not only at the stations near Villa Somoza but also in the collections made in the Rio San Juan basin, about 120 miles to the south near San Gerardo, Alajuela Province, Costa Rica, where yellow fever appeared in 1951 (Galindo and Trapido, 1955). The fact that it was the most abundant species at both Villa Somoza and San Gerardo may be explained partly in ecological and partly in distributional terms. It was more abundant than *equinus* at these two localities because the optimum habitat of *equinus* is deciduous forest, while *iridicolor* is better adjusted to rain-forest. It outnumbered *spegazzinii falco* and *m. mesodentatus*, which like it are species reaching their best development in rain-forest, because the center of dispersal of the former is far to the south in the Amazon basin and the center of dispersal of the latter is to the north in Guatemala or Mexico. The San Gerardo and Villa Somoza localities are in a broad sense the center of distribution of *iridicolor*, and it is therefore presumably the best adjusted *Haemagogus* to the environment in this area.

The one other aedine mosquito of interest as a possible yellow fever vector is *Aedes leucocelaenus clarki*. This appeared at the Villa Somoza stations but was rare there, only six specimens being taken. It is a species with a distribution similar to that of *H. spegazzinii*; that is, it is widespread in South America, Central America being at the periphery of its range. Like *H. spegazzinii falco* its range ends in adjacent Honduras. It is even less common than that species in Nicaragua and Honduras.

Two sabethine mosquitoes are of interest as possible natural yellow fever vectors. We have been particularly interested in assessing the possible role of *Sabethes chloropterus* in Panama because adults are more in evidence in the dry season than are those of the aedines. In Panama it occurs in both rain-forest and deciduous forest, and it is similarly distributed in Nicaragua. At the Villa Somoza stations its numbers were only slightly lower than those of *iridicolor*, the most abundant *Haemagogus*, but it was far outnumbered by *equinus* at the Pacific side stations. The commonest sabethine of those identified to species at Villa Somoza was *Trichoprosopon magnus*. This species is of some interest as it was also the commonest arboreal mosquito in an area where yellow fever appeared in Honduras in 1954 (Trapido and Galindo, 1955).

The remainder of the catch made at Villa Somoza, shown in Table 1, is of interest for comparison with lists previously published for various forest localities in Panama, but as the other mosquitoes appear not to be involved in yellow fever transmission insofar as is known, they are not discussed individually here.

The vertical stratification of the catch between the ground level and the canopy at the Nicaraguan stations is shown in the tables. As had been mentioned above, the Villa Somoza stations were in an area where rain-forest conditions were closely approximated. The four species of *Haemagogus*, *Aedes leucocelaenus clarki*, and the two sabethines, *Trichoprosopon magnus* and *Sabethes chloropterus* appeared preponderantly there in the canopy. But in the open deciduous forest of the Pacific slope, at Valle Menier and Guapinolar, the catches of *Haemagogus* and *S. chloropterus* were much more evenly distributed between the ground and canopy. This confirms a similar finding in Panama (Trapido and Galindo, 1957 c); *i.e.*, that the degree to which essentially arboreal mosquitoes are confined to the tree tops is determined by the density of the covering canopy: in heavy rain-forest the stratification is extreme; in open deciduous forest substantial numbers of the arboreal species attack at ground level.

DISCUSSION IN RELATION TO YELLOW FEVER

H. spegazzinii falco is an established vector of yellow fever in South America (Whitman, 1951). The numbers taken at the Villa Somoza stations were so small that it is doubtful if the species played any important role in maintaining the disease there.

It has recently been demonstrated that *H. equinus* and *H. m. mesodentatus* of Guatemalan origin are capable of transmitting yellow fever by bite (Galindo *et al.*, 1957) and become infected in nature (Johnson and Farnsworth, 1956). The very high density of *equinus* at the Pacific side stations would seem to point to it as the principal vector there, if the heavy monkey mortality in the area is accepted as having been due to yellow fever. The failure of yellow fever to proceed further on the Pacific side of Nicaragua in the years since 1953 may also be explained in terms of *equinus* as the principal vector. The monkey mortality observed in that part of Nicaragua occurred during the rainy season (July 1952 in the southern part of the Rivas Isthmus, and August, September and October 1953 on the Pacific slopes south of Managua). Studies in Panama (Trapido and Galindo, 1957 b) have shown that *H. equinus*, while abundant during the rainy season, is very rare during the severe dry season in deciduous forest such as that in which the large numbers were taken in Nicaragua; and also that high humidity conditions are necessary for the average life span to exceed the extrinsic incubation period of the virus. While we made no dry season collections on the Pacific slope of Nicaragua we are confident that at that time of year *equinus* would be rare or absent, and that such individuals as might be present would be short lived as adults. If *equinus* were the principal species carrying on transmission during the rainy season, as seems likely, it would be difficult for it to maintain the virus cycle over the dry season, and apparently it did not.

H. m. mesodentatus does not occur on the Pacific side of Nicaragua, and was so rare at the Caribbean side stations that one cannot conceive it to have been an element in maintaining yellow fever, even though it is apparently an effective vector in Guatemala.

H. iridicolor, like its close relative *lucifer* of Panama and Colombia, has not been the subject of experiment. But as all *Haemagogus* thus far tested have been shown to be capable of transmitting yellow fever, it seems reasonable to suppose that under suitable conditions *iridicolor* would be a vector. The certain incrimination of *iridicolor* and *lucifer* as vectors, however, will have to await confirmation by laboratory experiments. But in the rain-forest of the Rio San Juan basin of Costa Rica, and in the Caribbean slope forests of Nicaragua, a region where *iridicolor* is at the center of its distribution and is the commonest *Haemagogus* present, circumstantial evidence would indicate that it did play some part in maintaining transmission.

The ability of *H. anastasionis* to transmit yellow fever has never been experimentally tested, but since it is a member of the same subgenus (*Stegoconops*) as such efficient vectors as *spegazzinii* and *mesodentatus*, it is probably capable of transmitting. The numbers taken, however, were so small in comparison with *equinus* that it is doubtful whether it was of significance in transmission where it was found at the Pacific slope stations.

Aedes leucocelaenus is an established vector of yellow fever in South America (Whitman, 1951) but its race *clarki* was so rare in the Nicaraguan collections that it could not have been an element of any importance in transmission.

In Panama *Sabethes chloropterus* was found to be the forest canopy species whose adult populations best withstand dry season for reasons associated with certain aspects of its life cycle (Trapido and Galindo, 1957 b). Very recently it has been shown to be capable of transmitting yellow fever by bite (Galindo *et al.*, 1957) and virus has been recovered from it in nature (Johnson and Farnsworth, 1956). The numbers taken at the Nicaraguan stations are perhaps sufficient to suppose it was involved in transmission there. We have no dry season data from Nicaragua to use in estimating its possible role at that difficult time of year.

There is little evidence on which to consider the possibility of *Trichoprosopon magnus* as a vector. It has been mentioned in the literature (Whitman, 1951) that a laboratory transmission was accomplished with the Brazilian *Trichoprosopon frontosus*, but the details of the experiments have not been published. As mentioned, above, we found *magnus* to be the commonest arboreal mosquito following an epizootic of yellow fever on the north coast of Honduras (Trapido and Galindo, 1955) but virus was not recovered from it (Rodaniche, 1956). Until it has been the subject of experimental study we can only note with interest that it was the commonest arboreal species in the epizootic area near Villa Somoza.

SUMMARY

The results are given of forest canopy mosquito surveys at three places in Nicaragua where there was evidence of sylvan yellow fever activity during 1952 and 1953. At these localities five species of *Haemagogus* were taken: *spegazzinii falco*, *iridicolor*, *m. mesodentatus*, *equinus* and *anastasionis*, the last named only on the Pacific slope, and the first three only on the Caribbean slope. *H. iridicolor* is also present on the Pacific slope in small numbers but was not in the collections made at the two fixed stations operated there. Also present and of interest as possible vectors were *Aedes leucocelaenus clarki* and *Trichoprosopon magnus* on the Caribbean side only, and *Sabethes chloropterus* on both the Caribbean and Pacific versants. On epidemiological grounds *H. equinus* appears to have been the vector on the Pacific side and *H. iridicolor* the principal vector on the Caribbean slope. The possible role of *S. chloropterus*, considered an important species in

carrying virus over the dry season in Panama, could not be assessed as the Nicaraguan collections were made only in the rainy season. Also in doubt is the possible part played by *Trichoprosopon magnus*, the commonest arboreal mosquito at the Caribbean side stations, since its ability to transmit has not yet been determined. It is thought that the numbers of three species known to be vectors elsewhere, *H. spegazzinii falco*, *H. m. mesodentatus* and *A. leucocelaenus clarki* were too small for them to have been significantly involved in transmission.

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