

A CONTRIBUTION TO THE ECOLOGY AND BIOLOGY OF TREE HOLE  
BREEDING MOSQUITOES OF PANAMA

PEDRO GALINDO, STANLEY J. CARPENTER AND HAROLD TRAPIDO

# A CONTRIBUTION TO THE ECOLOGY AND BIOLOGY OF TREE HOLE BREEDING MOSQUITOES OF PANAMA<sup>1</sup>

PEDRO GALINDO, Gorgas Memorial Laboratory, Panamá, R. de P.  
STANLEY J. CARPENTER, Colonel, MSC, United States Army, and  
HAROLD TRAPIDO, Gorgas Memorial Laboratory, Panamá, R. de P.

This paper deals with certain aspects of the ecology and life history of tree hole breeding mosquitoes in Panama. The data on which the observations are based were gathered in the course of a study of the mosquito fauna related to the transmission of sylvan ("jungle") yellow fever in the area. Our primary interest has been the accumulation of basic information on the groups of mosquitoes either known or suspected as vectors of sylvan yellow fever, as an aid to the understanding of the epidemiology of the disease. The groups concerned are the genus *Haemagogus*, the subgenus *Finlaya* of *Aedes*, and the sabethine genus *Sabethes*. While various other mosquitoes which utilize the same tree hole breeding niche were taken in the course of the field work, and the information on them is included in the tables, the discussions concern in the main the groups mentioned above.

Data are summarized and discussed on the following points: (1) the geographical distribution and frequency of larvae appearing in simulated tree holes, (2) the comparison of the frequency with which mosquitoes utilize for breeding two different types of bamboo sections used to simulate tree holes, (3) the comparison of the frequency with which breeding sites near the ground are used as contrasted with sites in the forest canopy, (4) the characteristics of the delay in egg hatching, (5) the comparative egg productivity of the different species, (6) the time for development of the immature stages.

The locations and descriptions of the stations at which the field work was carried out are given in previous papers (Galindo, Carpenter and Trapido, 1951; and Trapido, Galindo and Carpenter, 1955). The field work was done during the rainy season of 1950, i.e., the period from May through December of that year, while the laboratory observations are in part based on field work done in 1949. In the discussion of the geographical distribution and frequency of larvae, reference is made to the concurrent adult collections reported in Trapido, Galindo and Carpenter, 1955. The classification scheme and the specific names used conform to the recent monograph of Lane (1953) on the neotropical Culicidae.

<sup>1</sup>Studies on the Forest Mosquitoes of Panamá. VIII. Costs of publication are paid by the Gorgas Memorial Laboratory.

## FIELD METHODS

The method of setting out sections of bamboo partially filled with water to simulate natural tree holes has been used by various investigators in the past, and is also described in a previous paper in this series (Galindo, Carpenter and Trapido, 1951). In brief, cut sections of bamboo, which we sometimes call "bamboo traps," were attached to trees, either within six feet of the ground, or else to the tree trunks at some height. The latter were located in trees which had incidentally been provided with semi-permanent ladders for the routine capture of mosquitoes approaching to bite human baits in the canopy, as part of the study of this specialized fauna. Bamboos of two sorts were used: one group with the tops open; and another with the tops covered, but with a hole about half inch in diameter drilled in the side near the top. The water in the bamboos was examined each week. Any larvae present were brought into the laboratory, and the water returned to the bamboo section with water added when necessary.

## DISTRIBUTION AND FREQUENCY OF THE SPECIES

Table I summarizes the data from the field collections, showing the species of which larvae were taken and their numbers and frequency at the various stations.

Of the *Haemagogus* present, *equinus* Theobald and *lucifer* (Howard, Dyar and Knab), common forest species, were most abundant. These were not taken as larvae, however, in the Chiriqui highlands, but their absence there is an accurate reflection of the very small numbers appearing as adults at elevations above 3,500 feet. Neither in the extensive work on *Haemagogus spegazzinii falco* Kumm *et al.*, in Colombia, where the species is very common, nor in Panamá, where it is less so, have breeding places been found with larvae present in numbers in any way commensurate with the adult populations. But the very small number of larvae taken in this study (four) is to some degree deceptive, for as will be shown later in this paper (see Tables III and IV), the eggs of this species hatch only after prolonged drying and repeated flooding.

The difference in habitat predilection between the morphologically closely related *Haemagogus lucifer* (Howard, Dyar and Knab) and *argyromeris*



TABLE I

TOTAL NUMBER OF LARVAE OBTAINED IN BAMBOO TRAPS AT ALL STATIONS

LOCATION	LA VICTORIA		FORT SHERMAN		ARRAJAN		CAMPANA		CAMPANTA		CHIRIQUÍ LOWLANDS		CHIRIQUÍ HIGHLANDS		TOTALS	
	400-1,200		50		600-800		2,000-2,800		200-400		300-400		3,500-4,600		Times Taken	Number of Larvae
Elevation (In Feet)	Times Taken	Number of Larvae	Times Taken	Number of Larvae	Times Taken	Number of Larvae	Times Taken	Number of Larvae	Times Taken	Number of Larvae	Times Taken	Number of Larvae	Times Taken	Number of Larvae		
Tribe Culicini																
<i>Haemagogus spegazzinii</i>					1	1									3	4
<i>falso</i> Kumm et al.	2	3														
<i>Haemagogus equinus</i> Theobald	154	302	49	108	68	131	27	103	36	259	3	7			337	910
<i>Haemagogus lucifer</i> (H., D. and K.)	41	71	35	63	30	69	39	125	1	1	1	3			147	332
<i>Haemagogus argyromeris</i> Dyar and Ludlow	8	12	1	1					30	119					39	132
<i>Haemagogus</i> sp.									1	3					1	3
<i>Aedes leucoclaenus clarki</i> G., C. and T.	6	7			2	2					1	1			9	10
<i>Aedes leucoclaenus</i> Komp	13	26	1	3	8	10	16	48							38	87
<i>Aedes terreus</i> (Walker)	133	252	27	57	34	79	180	2,329	4	18	1	4	14	138	393	2,877
<i>Culex mollis</i> Dyar and Knab	44	251	38	207	25	151	9	119			20	586	1	2	137	1,326
<i>Culex corniger</i> Theobald					1	1					2	62			3	53
<i>Culex virgatus</i> Theobald			2	6	1	1									3	7
<i>Culex nigripalpus</i> Theobald	1	1	1	8							1	14			3	23
<i>Culex trichii</i> (Coquillett)	68	223	1	1											69	224
<i>Culex secundus</i> Bonnet-Wepster and Bonne	3	17			1	2									4	19
<i>Culex bitaenatus</i> Dyar and Nunez-Tovar	13	57					105	2,927			1	4	38	1,075	158	4,053
<i>Culex conservator</i> Dyar and Knab	105	382	77	273	98	408	1	1	8	80	6	53			295	1,197
<i>Culex corrigani</i> Dyar and Knab	29	69	12	49	11	45	2	14			5	26			39	203
<i>Culex restrictor</i> Dyar and Knab							17	84			1	36	1	2	19	122
<i>Culex browni</i> Komp	98	278	5	19							3	16			106	313
<i>Culex pinarocampo</i> Dyar and Knab													4	166	4	166
<i>Culex erythronifer</i> Galindo and Blanton													1	1	1	1
<i>Culex (Culex)</i> sp.													1	1	1	1
<i>Orthopodomyia fascipes</i> (Coq.)	56	132	24	92	68	271	26	450	2	2	4	57			180	1,004
<i>Toxorhynchites theobaldi</i> (Dyar and Knab)	60	64	18	18	38	39	10	10	12	13	22	24			150	168
<i>Toxorhynchites</i> sp.									1	1					1	1
Tribe Sabethini																
<i>Trichoprosopon digitatum</i> (Rondani)	4	4	11	80			1	29			1	6			17	119
<i>Wyeomyia paronoma</i> Dyar and Knab	6	11	5	6	1	2	1	2	1	1	4	25	1	5	19	52
<i>Limatus durhamii</i> Theobald	5	9	1	2	5	15									11	26
<i>Limatus assuleptus</i> Theobald	1	1			1	5									2	6
<i>Sabethes cyaneus</i> (Fabricius)	23	32	7	12	12	21	3	4			14	135			59	205
<i>Sabethes chloropterus</i> (Humboldt)	16	24	1	1	13	24	5	8	1	1					35	58
Tribe Anopheleini																
<i>Anopheles eiseni</i> Coquillett	49	58	29	32	18	26	4	6	3	4			1	1	104	127
<i>Anopheles neivai</i> H., D. and K.							1	1							1	1
Unidentified larvae		47		61		85										193
TOTAL		2,343		1,099		1,388		6,260		503		1,049		1,480		14,122



Dyar and Ludlow is brought out by the collections from the bamboo traps; *lucifer* was abundant in primary rain forest and less common in deciduous forest or second growth, while the converse is true of *argyromeris*. Thus while *argyromeris* was taken most abundantly in the relatively open deciduous forest at Campanita which lies in the rain shadow of Cerro Campana, *lucifer* was taken there only once. Contrariwise, at La Victoria and Ft. Sherman, where the conditions of true tropical rain forest are approached, *lucifer* was common while *argyromeris* was rare.

The commonest of the tree hole breeding *Aedes* of the subgenus *Finlaya* was the species *terrens* (Walker). This was true of individuals taken as adults attacking man as well for the larvae from the bamboo collections. Both adults and larvae became more abundant at elevations of 2,000 feet or more, as appears on comparison of the collections from Campanita (200' to 400') and Campana (2,000'), as well as the Chiriqui lowland and highland collections. The correspondence between adult and larval collections of *Aedes leucocelaenus clarki* Galindo, Carpenter and Trapido and *Aedes leucotaeniatu* Komp was not good. In the adult captures *leucocelaenus clarki* was about twice as common as was *leucotaeniatu*, while in the larval collections almost nine times as many *leucotaeniatu* were taken as were *leucocelaenus clarki*. In the western Panama province of Chiriqui neither of these was present in the larval collections, although small numbers of both species were captured here as adults.

Of all the larvae taken (14,122), slightly more than half were representatives of the genus *Culex* (7,807). The numbers of larvae of this genus were in no way reflected in the concurrent diurnal collections of adults of which less than 60 *Culex* were taken among the 72,211 mosquitoes collected (Trapido, Galindo and Carpenter, 1955). This disparity is due to the fact that with the exception of the subgenus *Carollia* the species are night flyers, and with the exception of *Culex mollis* Dyar and Knab they do not attack man. *Culex pinarocampa* Dyar and Knab and *restrictor* Dyar and Knab are here reported from Panamá for the first time, both having been described from Mexico. The first mentioned, of which only one specimen was taken, is accidental in the collections as the species normally breeds in the water accumulations in the leaves of the agave-like plant *Furcraea* where we have taken it in some numbers. The recently described *Culex erethyssonfer* Galindo and Blanton (1954) which ordinarily breeds in epiphytic bromeliads is also accidental in these collections.

As we had observed in our previous study (Galindo, Carpenter and Trapido, 1951), the numbers of larvae of *Sabethes* appearing in bamboo traps were not well correlated with the concurrent captures of adults attacking man. *Sabethes chloropterus* (Humboldt) appeared a little more

than nine times as frequently as *Sabethes cyaneus* (Fabricius) in the adult captures, while conversely *cyaneus* was three and a half times as abundant as *chloropterus* in the larval collections. Bamboo traps of the sort used by us appear not to be particularly favored as oviposition sites for *chloropterus*, at least when there is a choice of natural tree holes available. A third species of this genus, *Sabethes tarsopus* Dyar and Knab, which was twice as common as *cyaneus* in the adult captures did not appear at all in the larval collections. In our previous study only a single larva of this species had been taken.

#### COMPARATIVE COLLECTIONS FROM TWO TYPES OF BAMBOO TRAPS

While bamboo traps with both open and closed tops were set out at various of the stations near the ground and in the forest canopy, only the collections made at Cerro La Victoria were under daily supervision, and thus only the data from these stations have been used in compiling the percentages recorded in Table II. At these stations there were more open top traps (42) than covered ones (18), and in calculating the percentages of each species taken in the open top traps a corresponding correction factor was applied to the data. Too few larvae of certain of the species were taken to give significant percentages, but the data are sufficient to show that most of the species used the open top bamboos in preference to those with closed tops. The marked exceptions appear in the cases of *Sabethes cyaneus* and *chloropterus*. Both of these appeared less than ten percent of the time in the open top traps, the bulk of the specimens coming from closed top traps. These results confirm those of our previous study (Galindo, Carpenter and Trapido, 1951). The closed top traps with a small side hole approximate the sort of tree cavity in which a small opening gives entrance to a relatively large flask-shaped rot hole. An important characteristic of cavities of this sort is the fact that the contained water is less subject to evaporation than is the case in cavities with large openings exposed to sun and wind. We have previously shown (Galindo, Trapido and Carpenter, 1950) that *Sabethes chloropterus* and *cyaneus*, whose eggs do not withstand desiccation as do those of *Haemagogus*, persisted as adults during the dry season months while the *Haemagogus* all but disappear. The strongly marked preference shown by *Sabethes* for utilizing water accumulations accessible only through small entrance holes may thus be the device by which these mosquitoes find the water necessary to maintain their breeding cycle during the unfavorable dry season.

#### COMPARATIVE COLLECTIONS FROM BAMBOO TRAPS AT GROUND AND CANOPY LEVELS

The comparisons of the collections of larvae



from bamboo traps located near the ground and in the canopy are shown as percentages in Table II.

As noted previously, the numbers of *Haemagogus spegazzinii falco* taken as larvae are never commensurate with the adult population. Only four larvae were taken in the present study, all in bamboos hung in the canopy. The adults also are predominantly taken in the canopy. At the opposite extreme for *Haemagogus* we find *argyromeris* which is not an inhabitant of the deep forest, and all the larvae of this species appeared in bamboos located near the ground. In concurrent collections of adults over 90 percent were taken at ground level. *Haemagogus equinus* and *lucifer* which are intermediate in vertical distribution as adults were also intermediate with regard to the sites from which larvae were taken. Of the *Aedes* (*Finlaya*) the most arboreal species was *leucocelaenus clarki* with slightly more than half the larvae being taken in traps in the canopy. *Aedes leucotaeniatius* utilized almost entirely the traps near the ground. These data are in ac-

cord with the adult stratification; *leucotaeniatius* being taken predominantly on the ground and *leucocelaenus clarki* being more arboreal. The correspondence between adult and larval collections in *Sabethes* was also positive; both *chloropterus* and *cyaneus* were predominantly arboreal as adults and also as larvae in bamboos.

#### DELAYED HATCHING

Tables III and IV summarize the data illustrating the delay in hatching of certain of the tree hole breeding mosquitoes with eggs which resist desiccation. In Table III are given the data on bamboo sections which had been exposed in the field during 1949 and which were brought into the laboratory in February 1950. These bamboos were stored without water in the laboratory and subsequently flooded at the one to two month intervals shown in the table. The bamboos exposed in the field during 1950 were brought into the laboratory in December of that year and similarly treated during 1951 (Table IV). During 1951 the bamboos were flooded at somewhat

TABLE II  
LARVAE OBTAINED IN BAMBOO TRAPS AT CERRO LA VICTORIA STATIONS  
(May through December, 1950)

SPECIES	TOTAL		PERCENT IN OPEN TOP TRAPS		PERCENT IN CANOPY TRAPS	
	Times Taken	Number of Larvae	Times Taken	Number of Larvae	Times Taken	Number of Larvae
<b>Tribe Culicini</b>						
<i>Haemagogus spegazzinii falco</i> Kumin et al.	2	3	100.0	100.0	100.0	100.0
<i>Haemagogus equinus</i> Theobald	154	302	68.9	73.2	44.7	44.8
<i>Haemagogus lucifer</i> (H., D. and K.)	41	71	60.4	59.6	35.5	32.0
<i>Haemagogus argyromeris</i> Dyar and Ludlow	8	12	100.0	100.0	0.0	0.0
<i>Aedes leucocelaenus clarki</i> G., C. and T.	6	7	67.7	51.2	42.6	52.6
<i>Aedes leucotaeniatius</i> Komp.	13	26	100.0	100.0	11.1	5.6
<i>Aedes terreus</i> (Walker)	133	252	79.8	89.3	32.2	38.4
<i>Culex mollis</i> Dyar and Knab	44	261	73.0	69.7	43.7	44.9
<i>Culex nigripalpus</i> Theobald	1	1	100.0	100.0	0.0	0.0
<i>Culex irishii</i> (Coquillett)	68	223	54.3	59.0	64.1	71.3
<i>Culex secundus</i> B.—W. and B.	3	17	47.4	68.7	43.5	50.0
<i>Culex bitaeniolus</i> Dyar and Nunez-Tovar	13	57	49.4	61.7	30.9	32.6
<i>Culex conservator</i> Dyar and Knab	105	382	37.2	32.7	59.0	69.8
<i>Culex corriganii</i> Dyar and Knab	29	69	52.9	51.2	68.0	73.8
<i>Culex vexillifer</i> Komp.	98	278	59.7	57.0	46.9	49.2
<i>Orthopodomyia fascipes</i> (Coquillett)	56	132	63.7	60.3	43.5	38.5
<i>Toxorhynchites theobaldi</i> (D. and K.)	60	64	37.5	38.5	63.1	64.5
<b>Tribe Sabethini</b>						
<i>Trichoprosopon digitatum</i> (Roudani)	4	4	55.5	56.5	60.0	72.2
<i>Wyeomyia aporonoma</i> Dyar and Knab	6	11	45.9	53.1	0.0	0.0
<i>Limatus burhamii</i> Theobald	5	9	63.0	24.4	27.0	61.9
<i>Limatus assaleptus</i> Theobald	1	1	100.0	100.0	0.0	0.0
<i>Sabethes cyaneus</i> (Fabricius)	23	32	8.2	7.2	66.0	68.6
<i>Sabethes chloropterus</i> (Humboldt)	16	24	6.0	5.8	91.5	94.4
<b>Tribe Anophelini</b>						
<i>Anopheles eiseni</i> Coquillett	49	58	51.7	50.9	57.0	61.6
TOTAL	938	2,296	.....	.....	.....	.....



shorter intervals as will be seen on comparison of the two tables. In all cases water was permitted to stand in the reflooded bamboos for 24 to 48 hours.

It is well known (Bates, 1949) that substances added to the water which reduce the oxygen content enhance the hatching of aedine eggs. Thus had these bamboos been flooded with a yeast infusion more complete hatching on early flooding probably would have been obtained. In these experiments, however, we attempted to simulate natural events as they happen in the field. In these trials the organic matter which accumulated in the bamboo sections was the means by which the reduction of oxygen content was produced, as it is in the field. The data from the two sets of bamboos, exposed and flooded in succeeding years are in general agree-

TABLE III

DISTRIBUTION OF DELAYED HATCHING OF LARVAE IN 24 BAMBOO TRAPS EXPOSED IN THE FIELD DURING 1949, AND FLOODED AT INTERVALS IN THE LABORATORY DURING 1950

No. of FLOODING	DATES FLOODED	<i>Haemagogus equinus</i>	<i>Haemagogus spegazzinii falco</i>	<i>Haemagogus lucifer</i>	<i>Haemagogus arayanensis</i>	<i>Aedes leucocinctus clarkei</i>	<i>Aedes taenioscintatus</i>	<i>Aedes terreus</i>
1st.	Mar. 27	80	0	5	0	0	0	6
2nd.	May 22	39	0	9	6	0	1	0
3rd.	June 20	20	7	1	7	3	0	5
4th.	July 24	25	1	0	2	0	0	3
5th.	Aug. 28	0	0	1	0	0	0	0
6th.	Oct. 2	0	0	0	0	0	0	0
TOTAL.....		165	8	16	15	3	1	14

ment, though minor differences do appear. While it has been suggested that the variations in hatching rate may be due to any of several factors, including seasonal differences, strain differences, and even differences in the eggs of individual females (Hovanitz, 1946), the most obvious difference which might occur in the field and in this experiment would be the variation in the extent to which the oxygen content of the water had been reduced. Hovanitz (1946) also demonstrated species differences in egg hatching of *Haemagogus*, and it is this intrinsic difference between species which is clearly brought out by our data.

We may first note that in all cases in which a substantial number of eggs was present, the hatching was distributed over more than one flooding. The second noteworthy point is that there were two consistent patterns of hatching,

but with certain of the species intermediate. One pattern is best illustrated by *Haemagogus equinus*, a species in which there is substantial hatching on the first and succeeding floodings until all the viable eggs have produced larvae. In 1950 larvae appeared after each of the first four floodings covering a period of five months, while in 1951 the hatching was consistent through the tenth flooding up to seven months after the bamboos had been brought into the laboratory. The second pattern is illustrated by *Haemagogus spegazzinii falco*. In the case of this species, there was no hatching on the first or second

TABLE IV

DISTRIBUTION OF DELAYED HATCHING OF LARVAE IN 62 BAMBOO TRAPS EXPOSED IN THE FIELD DURING 1950, AND FLOODED AT INTERVALS IN THE LABORATORY DURING 1951.

No. of FLOODING	DATES FLOODED	<i>Haemagogus equinus</i>	<i>Haemagogus spegazzinii falco</i>	<i>Haemagogus lucifer</i>	<i>Haemagogus arayanensis</i>	<i>Aedes leucocinctus clarkei</i>	<i>Aedes taenioscintatus</i>	<i>Aedes terreus</i>	<i>Aedes septentrionalis</i>
1st.	Jan. 15- Feb. 5	87	0	10	0	8	2	22	1
2nd.	Feb. 27- Mar. 13	99	0	7	1	1	1	13	2
3rd.	Apr. 2-5	83	11	8	0	0	5	8	0
4th.	Apr. 12	41	3	7	0	5	7	7	0
5th.	May 2	56	7	9	0	4	0	23	2
6th.	May 10	53	15	13	1	1	8	11	0
7th.	June 6	7	0	0	0	0	0	0	0
8th.	June 28	35	5	4	0	0	1	0	0
9th.	Aug. 2	12	1	1	0	0	0	1	0
10th.	Aug. 27	2	1	1	0	0	0	0	0
11th.	Sept. 7	0	0	0	0	0	0	0	0
TOTAL.....		475	44	60	2	19	24	145	5

flooding in either 1950 or 1951. The first hatching did not occur until the third flooding, and in 1951 larvae continued hatching through the tenth flooding. The consequences of these divergent hatching patterns are reflected in the annual abundance cycle of adults, for as we have previously shown (Galindo, Trapido and Carpenter, 1950) adults of *Haemagogus equinus* quickly reach a peak after the beginning of the rainy season, while the appearance of *spegazzinii falco* is delayed, and the peak is not reached until several months after the beginning of the rains in May. *Haemagogus lucifer* follows the



*equinus* pattern with hatching on the first flooding. *Haemagogus argyromeris* is intermediate between *equinus* and *falco* in that the first hatching occurred in both years on the second flooding. The results obtained in the case of *Aedes leucocelaenus clarki* and *Aedes leucotaeniatus* are less consistent, but this may well be due to the very small numbers of these species appearing in the 1950 floodings.

As the eggs of the various species were distributed at random through the various bamboos, it follows that the external stimuli for hatching were also at random. The distinctive hatching pattern of *Haemagogus spegazzinii falco* as contrasted with *equinus* and *lucifer* is thus clearly a

great in *equinus* (17.9) as in *spegazzinii falco* (9.7). *Haemagogus lucifer* and *argyromeris* oviposit less readily in the laboratory, while *chalcospilans* Dyar only rarely will deposit eggs in vials. The species of *Aedes* held in this manner varied in their egg production from an average of 10.5 for *leucotaeniatus* to 53.5 for *septemstriatus* Dyar and Knab. Among the sabethines, *Sabethes chloropterus* oviposited most readily in the laboratory, with an average of 23.3 eggs per oviposition. *Sabethes tarsopus* seldom laid eggs, and the number of eggs per oviposition was small (2.5 average). Approximately one quarter of the *Sabethes cyaneus* and *Trichoprosopon magnus* (Theobald) laid eggs, and the average numbers

TABLE V  
EGG PRODUCTIVITY OF FOREST MOSQUITOES UNDER LABORATORY CONDITIONS

SPECIES	NUMBER OF ENGORGED FEMALES	TOTAL NUMBER OF FEMALES THAT LAID	PERCENTAGE OF FEMALES THAT LAID	TOTAL NUMBER OF EGGS LAID	AVERAGE NUMBER OF EGGS PER LAYING
<i>Haemagogus equinus</i> Theobald.....	265	165	62.3	2,946	17.9
<i>Haemagogus spegazzinii falco</i> Kumm et al.....	63	45	71.4	435	9.7
<i>Haemagogus lucifer</i> (H., D. and K.).....	212	40	18.9	413	10.3
<i>Haemagogus argyromeris</i> D. and L.....	9	1	11.1	1	1.0
<i>Haemagogus chalcospilans</i> Dyar.....	150	2	1.3	8	4.0
<i>Aedes leucotaeniatus</i> Komp.....	51	11	21.6	116	10.5
<i>Aedes leucocelaenus clarki</i> G., C. and T.....	61	49	80.3	454	15.8
<i>Aedes terreus</i> (Walker).....	85	32	37.2	690	25.6
<i>Aedes septemstriatus</i> Dyar and Knab.....	4	2	50.0	107	53.5
<i>Aedes quadrivittatus</i> (Coquillett).....	147	24	16.3	294	12.3
<i>Sabethes chloropterus</i> (Humboldt).....	202	107	52.9	2,496	23.3
<i>Sabethes tarsopus</i> Dyar and Knab.....	44	4	9.1	10	2.5
<i>Sabethes cyaneus</i> (Fabricius).....	46	11	23.9	325	29.5
<i>Trichoprosopon magnus</i> (Theobald).....	58	15	25.9	436	29.1

reflection of intrinsic physiological differences between species in response to the external hatching stimulus.

#### EGG PRODUCTIVITY

Numbers of females which were taken in the field were permitted to feed on the collectors, and then confined in glass vials (25 x 80 mm.). The bottoms of the vials were provided with a moist cotton pad covered with a filter paper disk, and the vials were stoppered with gauze covered cotton plugs. The mosquitoes confined in this manner were given supplemental nutrition by moistening the cotton stopper with sugar solution. The vials were held until the mosquitoes died, when the numbers of eggs deposited on the moist filter paper disks were recorded. In Table V are summarized the data showing the number of eggs laid, and the average number of eggs per oviposition.

It will be seen from this table that *Haemagogus equinus* and *Haemagogus spegazzinii falco* oviposit readily under these conditions, but that the number of eggs per oviposition was almost twice as

of eggs produced was almost the same for the two species, *cyaneus*, 29.5 and *magnus*, 29.1.

#### DURATION OF IMMATURE STAGES

Records were kept on the time necessary for the development from egg to adult of nine species from which eggs had been obtained in the laboratory from wild caught females. In the case of the *Haemagogus* and *Aedes* (*Finlaya*), which undergo a dormant period in the egg stage, the eggs which had been deposited on moist filter paper disks in vials, were stored in covered petri dishes. While the eggs of these species resist desiccation, if they are permitted to dry out completely a substantial percentage collapse and do not hatch on subsequent flooding. The eggs were therefore kept slightly moist during the maturation period. After ripening for not less than two weeks, the filter papers with attached eggs were submerged in tap water to which yeast had been added. The yeast infusion favors hatching by lowering the oxygen content of the water (Bates, 1949). In the case of the sabethine eggs which do not undergo a dormant period, the filter



papers with eggs were submerged in the yeast infusion a day or two after they were laid. Larvae which hatched were permitted to develop in small (15 cm. diameter) enamel pans. They were fed yeast mixed into the water, and ground dog biscuit. The pans were sheltered from the sun on an open porch at the laboratory and were thus subject to out-door environment temperatures experienced in Panamá City. Temperature readings of water in pans under these conditions range from 23.5° to 28.5° C with an average of about 25.5° C.

The summary of the information obtained in this way is given in Table VI. The most rapidly developing species was *Haemagogus equinus* with a mean of 11.2 days and a minimum of nine days. This result confirms that of Hovanitz (1946) who also found *equinus* to be the most rapidly

The three *Aedes* (*Finlaya*) species, *leucocelaenus clarki*, *leucotaeniatus* and *terrens* all completed their mean development period within three days of one another (12.5 to 15.5 days). The three sabethines were much slower and more erratic in development, with mean development periods of from 25.9 to 30.6 days. *Sabethes chloropterus* and *cyaneus* demonstrated a particularly wide spread in the minimum and maximum time for the emergence of adults, from 18 to 50 days in the case of the former and 20 to 55 days in the case of the latter. The long period necessary for the development of *Sabethes chloropterus* together with the wide spread between minimum and maximum times may provide further explanation for the persistence of this species through the dry season previously discussed in this paper.

TABLE VI  
DURATION OF IMMATURE STAGES OF FOREST MOSQUITOES

SPECIES	NUMBER OF OBSERVATIONS	NUMBER OF DAYS FROM HATCHING TO ADULT EMERGENCE		
		Minimum	Mean	Maximum
<i>Haemagogus equinus</i> Theobald.....	2,536	9	11.2	15
<i>Haemagogus spegazzinii falco</i> Kumm <i>et al</i> .....	421	12	14.8	19
<i>Haemagogus lucifer</i> (H., D. and K.).....	373	12	13.4	19
<i>Aedes leucocelaenus clarki</i> G., C. and T.....	432	11	13.3	16
<i>Aedes leucotaeniatus</i> Komp.....	98	10	12.6	18
<i>Aedes terreus</i> (Walker).....	482	13	15.5	19
<i>Trichoprosopon magnus</i> (Theobald).....	227	24	27.5	34
<i>Sabethes chloropterus</i> (Humboldt).....	2,271	18	25.9	50
<i>Sabethes cyaneus</i> (Fabricius).....	281	20	30.6	55

developing species studied by him in Colombia, the species compared being *H. spegazzinii falco*, *H. splendens* Williston and *H. lucifer*. While Hovanitz reports development in as little as seven days at similar temperatures (25–27° C) we have also had emergence in as short a period as this in experiments other than those included in our table. The other two *Haemagogus* studied by us, *lucifer* and *spegazzinii falco*, had the same minimum (12 days) and maximum (19 days) but slightly different means (13.4 and 14.8 days respectively). The order of the development of these two species is the converse of that reported by Hovanitz who found *lucifer* to be the least rapidly developing species. Hovanitz had, however, relatively few observations on *lucifer*. Bates (1947), who made experiments with *H. spegazzinii falco* at several different temperatures, obtained average development times of from 12.5 days at 30° C to 26 days at 20° C. The average development time he reports for the immature stages at room temperature, with a mean of 25.5° C, which was almost exactly that experienced in our experiments, was 15.0 days, which is very close to that obtained by us, 14.8 days.

#### REFERENCES

- Bates, Marston. 1947. The development and longevity of *Haemagogus* mosquitoes under laboratory conditions. *Ann. Ent. Soc. Amer.* 40: 1–12.
- Bates, Marston. 1949. The natural history of mosquitoes. Macmillan Company, N. Y.: i-xv, 1–379.
- Galindo, Pedro and F. S. Blanton. 1954. Nine new species of neotropical *Culex*, eight from Panama and one from Honduras (Diptera, Culicidae). *Ann. Ent. Soc. Amer.* 47: 231–47.
- Galindo, Pedro, S. J. Carpenter and Harold Trapido. 1951. Ecological observations on forest mosquitoes of an endemic yellow fever area in Panama. *Amer. J. Trop. Med.* 31: 98–137.
- Galindo, Pedro, Harold Trapido and S. J. Carpenter. 1950. Observations on diurnal forest mosquitoes in relation to sylvan yellow fever in Panama. *Amer. J. Trop. Med.* 30: 533–74.
- Hovanitz, William. 1946. Comparisons of mating behavior, growth rate, and factors influencing egg-hatching in South American *Haemagogus* mosquitoes. *Physiol. Zool.* 19: 35–53.
- Lane, John. 1953. Neotropical Culicidae. Univ. Sao Paulo, Brazil. 2 vols.: 1–1112.
- Trapido, Harold, Pedro Galindo and S. J. Carpenter. 1955. A survey of forest mosquitoes in relation to sylvan yellow fever in the Panama Isthmian area. *Amer. J. Trop. Med. & Hyg.* In Press.