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OBSERVATIONS ON CLIMATE AND SEASONAL DISTRIBUTION OF MOSQUITOES IN EASTERN COLOMBIA*

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(With Plate 1 and 3 Figures in the Text)

1. INTRODUCTION

There is a considerable literature on variation in seasonal abundance of mosquitoes, particularly of anophelines, because of the importance of this subject in relation to malaria studies. Of much interest also, from the point of view of general biology, are studies of seasonal fluctuations in mosquito populations. Students of the statistical aspects of natural selection and of the distribution of genetic factors in populations have pointed out that the spread of variants through a population is bound to depend in great part on the nature of the fluctuations in population density, and the subject of seasonal and annual cycles has thus become of basic interest in relation to the processes of evolution. Such studies also form an integral part of any ecological work, since the environmental characteristics change in time as well as in space, and the adaptations of a particular species to factors in the physical environment may be as clearly shown by the seasonal distribution of the species as by its habitat distribution. A recent study at Villavicencio, Colombia, though fragmentary in itself, may have particular interest in these connexions because this locality is in the forested section of interior South America—a region of surpassing biological interest, on which there is almost no quantitative information available.

The work at Villavicencio is oriented primarily toward the study of the epidemiology of jungle yellow fever, hence attention has centered on the mosquito *Haemagogus capricornii*, which field work indicates to be the chief vector of the virus of yellow fever in the region (Bugher, Manrique, Garcia & Mesa, 1944). Attempt has been made, however, to keep the collection of data on a sufficiently broad basis to serve as part of a general study of the environmental relations of the mosquito fauna of this sample area of the American tropics, and the present article is written from the latter point of view. Some general notes on the methods of work were included in a previous article on the stratification of diurnal mosquitoes in the forest habitat (Bates, 1944*a*).

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2. CLIMATE

Routine climatic measurements made at the laboratory at Villavicencio are summarized in Tables 1–4. For our purposes it is most satisfactory to break the year at the first of March instead of the first of January. March is the zero month both for yellow fever and for the mosquito vectors; the events of January and February are essentially the closing phases of the preceding annual cycle, and the new cycle of rain, mosquitoes and yellow fever starts toward the end of March.

Perhaps the most striking characteristic of the Villavicencio climate is its uniformity through the year. There is a fairly regular annual cycle from the warm and dry months of January, February and March to the cold and wet months of May, June and July, but the annual oscillations occur within quite narrow limits. The maximum difference is in rainfall, and the least difference is in temperature. There is, however, a clear annual cycle in most biological phenomena which seems to be correlated with the rainfall. During the three years of observation the driest month has been February, and the months of December to March constitute a fairly well-defined dry season. The total amount of rain in these months may seem large, but the high evaporation rate and rapid run-off mean that this rainfall is below what might be called the 'threshold of effective precipitation'. Some streams and ground pools become continuously or intermittently dry, a few species of forest trees shed their leaves, the water table falls markedly, and so forth. This dry season is followed immediately by the period of heaviest rainfall (April and May), and these two conditions together seem to control the annual fluctuations in mosquito populations. Climatic differences in the period between June and November seem to be slight and irregular.

Villavicencio is situated 4 degrees north of the equator, at the base of the Eastern Andes. The streams here form part of the Orinoco system; but the drainage 200 km. south is Amazonian, and the foothill forests of the two drainages are continuous. The Eastern Andes rise very abruptly from the great plains of eastern Colombia, and the high precipitation measured at Villavicencio (4–5 m.) is dependent on this fact. The rainfall about 15 km. east of Villavicencio, away from the mountains, is only half as great (2·5 m. in 1943), though with a similar seasonal distribution.* Data, in part fragmentary, from various parts of the forested regions of the upper Orinoco and Amazonian drainages seem to indicate that the annual precipitation over most of this area is about 2·5–3·0 m. Temperature conditions over much of the area seem to be closely similar to those recorded at Villavicencio.

Some data on 'Colombian climatology' have been summarized by Chapman (1917, pp. 79–83). He describes the conditions that prevail in the Magdalena and Cauca valleys, where there are two annual rainy seasons and two dry seasons. In the lower portions of these valleys a heavy forest is supported by a precipitation that seems to be generally between 2 and 3 m. annually. It may be noted that the Villavicencio area has the highest rainfall of any part of Colombia for which records have been seen, with the exception of the Pacific coastal strip (Buenaventura), which has about 7 m. annually.

Table 1. *Rainfall at laboratory station, Villavicencio*

Month	1941		1942		1943		Mean	
	mm.	days	mm.	days	mm.	days	mm.	days
Mar.	211·0	14	304·0	18	116·0	12	210	15
Apr.	435·0	22	502·5	20	603·5	26	514	23
May	659·5	24	775·0	27	634·5	23	690	25
June	334·5	28	417·5	21	625·5	29	459	26
July	346·0	30	534·0	25	403·5	27	428	27
Aug.	502·0	27	508·0	21	618·5	24	543	24
Sept.	488·0	22	468·5	16	617·0	18	524	19
Oct.	505·0	27	395·0	21	594·5	24	498	24
Nov.	155·5	16	500·5	20	247·0	16	301	17
Dec.	136·0	12	313·0	18	296·0	13	248	15
Jan.	161·0	10	161·0	19	108·0	6	143	12
Feb.	30·5	7	108·5	13	123·5	7	87	9
Totals	3964·0	239	4987·5	239	4987·0	225	4645	236

Table 2. *Mean temperatures at laboratory station, Villavicencio* (° C.)

Month	1941	1942	1943	Mean
Mar.	28·2	27·8	26·5	27·5
Apr.	27·2	27·2	26·0	26·8
May	26·7	25·8	26·0	26·1
June	25·1	25·2	25·4	25·2
July	25·8	24·7	24·5	25·0
Aug.	26·4	26·3	25·7	26·1
Sept.	27·0	26·7	26·7	26·8
Oct.	27·1	26·7	26·8	26·8
Nov.	27·1	26·9	27·1	27·0
Dec.	27·0	25·9	26·9	26·6
Jan.	27·9	26·5	26·9	27·1
Feb.	28·2	26·8	28·4	27·8
Mean	27·0	26·4	26·4	26·6

Table 3. *Mean percentage relative humidity at noon in shade at laboratory station, Villavicencio (taken with sling psychrometer)*

Month	1941	1942	1943	Mean
Mar.	64·4	68·2	67·4	66·6
Apr.	71·3	61·9	73·4	68·9
May	77·0	76·2	72·7	75·3
June	76·6	75·9	74·6	75·7
July	70·9	73·5	78·3	74·2
Aug.	78·0	70·0	75·9	74·6
Sept.	70·2	70·2	72·4	70·9
Oct.	74·2	69·7	71·9	71·9
Nov.	71·0	70·1	72·5	71·2
Dec.	66·5	69·6	70·5	68·9
Jan.	62·6	66·3	65·3	64·7
Feb.	62·7	64·6	62·7	63·3

Table 4. *Total monthly evaporation in mm. from free water surface protected against sun and rain, laboratory station, Villavicencio*

Month ...	Mar.	Apr.	May	June	July	Aug.
1942	162	108	63	64	68	98
1943	130	68	64	58	54	72

Month ...	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
1942	100	92	90	94	100	108
1943	91	87	108	114	141	146

3. METHODS OF MOSQUITO CAPTURE

Two methods of checking on the abundance of mosquitoes have been used in gathering the material on which the present study is based: for diurnal mos-

* We are indebted to the Meteorological Department of the Aerovias Nacionales de Colombia for these data and for rainfall records from their airports in various parts of Colombia.

Photo 1. Capture stations in the Forzosa Area ('B–o' and 'B–6') with arrangements for making simultaneous captures at different levels. Although the platform in this tree is only 6 m. above ground level, the mosquito fauna sampled in the two stations is significantly different.

Photo 2. 'Egyptian type' of stable trap used for sampling the nocturnal mosquito fauna; a donkey is used as bait.

quitoes, the number coming to bite a man in an hour; for nocturnal species, the number caught per night in a stable trap baited with a donkey. The method of arriving at a man-hour rate has been described in some detail in a previous article (Bates, 1944*a*). For the purpose of checking on seasonal shifts in the fauna, man-hour rates are used from the following forest stations: Forzosa Area (foothill forest), two ground stations and the corresponding tree stations, collections being made twice weekly; Cuchilla Area (transition between foothill and piedmont forest), three ground and three tree stations, with collections once weekly; Ocoa Area (piedmont forest), two ground and two tree stations, with collections once weekly. The rate for a given week is thus the mean of 18 man-hours of capture in a selected series of forest environments; by balancing tree and ground stations, an effort is made to eliminate the possible effect of shifts in stratification on seasonal records. Pl. 1, photo 1 shows one of these forest capture stations (Forzosa, tree B).

The stable trap data are taken from captures made in an 'Egyptian type' trap (Pl. 1, photo 2) which has been kept continuously in a roadside clearing near the Ocoa forest for three years. Captures are made three times a week, using donkeys as bait. Notes on the construction and use of this type of trap have been given in a recent article (Bates, 1944*b*).

4. SEASONAL INCIDENCE OF *HAEMAGOGUS CAPRICORNII*

Since most attention was given to the presumed yellow fever vector, *Haemagogus capricornii*, it may be well to consider the behaviour of this species first and in some detail. This mosquito is common in all types of forest in the Villavicencio area, and the larvae have been found in various arboreal container habitats, particularly tree holes. The eggs are able to resist desiccation for long periods of time, thus providing a mechanism for carrying the population through periods of drought. Larval development is moderately rapid. Under laboratory conditions the mean larval life in one experiment was 11·1 days at 30° C., with some larvae completing development in 7 days. This is a higher temperature than would be encountered in nature; and it is in any event hazardous to generalize from growth experiments under laboratory conditions without checks in natural breeding places. It seems likely, however, that development normally requires 2–3 weeks and that the minimum time requirements for a generation would be on the order of magnitude of a month. It is probable that the adults are relatively long lived under forest conditions, though there is no direct evidence on this point. They are very difficult to maintain under normal laboratory conditions, but with special techniques it has been possible to keep significant numbers of adults alive in the laboratory for periods of over 30 days at moderate temperatures (25 and 27° C.); it would seem necessary to postulate a relatively long adult life in nature in order to account for virus transmission.

The diagram for the *Haemagogus* population shown in Fig. 2 seems to be typical for the Villavicencio area: the populations in all three forests studied showed very similar distributions both in 1942 and 1943. The adult population is maintained at a low level during January, February and March, increases rapidly through April and May to reach a peak in June, then declines through July and August to a moderate level, which is maintained through December. The controlling factor in adult abundance thus seems to be the January–March dry season and the following heavy rains.

Weekly data on dry season conditions in relation to *Haemagogus* abundance in the Forzosa study area during 1943 are charted in Fig. 1. 'Level of water in test containers' represents the mean depth of water in six tin cans attached to the trunk of a tree: two 1 m. above ground, two at 14 m., and two at 24 m.

Table 5. *Contrast between maximum and minimum monthly catches of* Haemagogus capricornii *in the three forest areas during* 1943

(Mosquitoes per man-hour.)

Area	Maximum catch	Minimum catch	Proportion max./min.	Month of Max.	Month of Min.
Ocoa	5·9	0·2	29	May	Feb.
Forzosa	19·4	0·1	194	June	Feb.
Cuchilla	17·8	1·1	16	June	Mar.
General mean	15·5	0·6	26	June	Mar.

Checks were also kept on the amount of water present in ten tree holes, and fluctuations in the tree holes were found to be roughly comparable with those recorded in the tin cans, though more variable because of the differences in rate of water loss through seepage, etc. The tin cans seem to be a good index of the relation between water loss through evaporation and water gain through rainfall in forest container habitats. It seems clear that *Haemagogus* abundance is related to water available in the breeding places and that the rainy season increase in adult population is due to the hatching of eggs placed at a relatively high level in the breeding places.

One of the basic questions of yellow fever epidemiology is: can the virus be maintained through the dry season in the mosquito? If mosquitoes become too rare during the dry season to maintain the normal mosquito-mammal cycles, some virus 'reservoir' must be postulated and searched for. Table 5 was prepared with this question in mind. The data in Tables 8 and 9 show the general trend of fluctuations in the populations of *Haemagogus capricornii* (charted in Fig. 1); and this trend seems to be similar in each of the three forests on which the data are based. But, as is shown in Table 5, there are very significant differences between the forests. The population is relatively small in the Ocoa area; Forzosa and Cuchilla show generally similar densities, but in the dry season adult mosquitoes become much rarer in Forzosa than in Cuchilla. Absolute contrasts in abundance would probably be greater than shown by these monthly means, but the means are probably a better index than absolute maximum and minimum captures would be, since individual captures may reflect meteorological or other transient conditions.

5. SEASONAL INCIDENCE OF OTHER MOSQUITOES

The data on the more abundant mosquitoes of the region have been summarized in Tables 6–9, and the figures for 1943 have been charted in Figs. 2 and 3.

(a) *Mosquitoes that breed in permanent or semipermanent pools*

Anopheles rangeli. This is the common 'tarsimaculatus' anopheline of the Villavicencio area. The adults are difficult to distinguish from some of the other species of the group; but the eggs are very distinct,

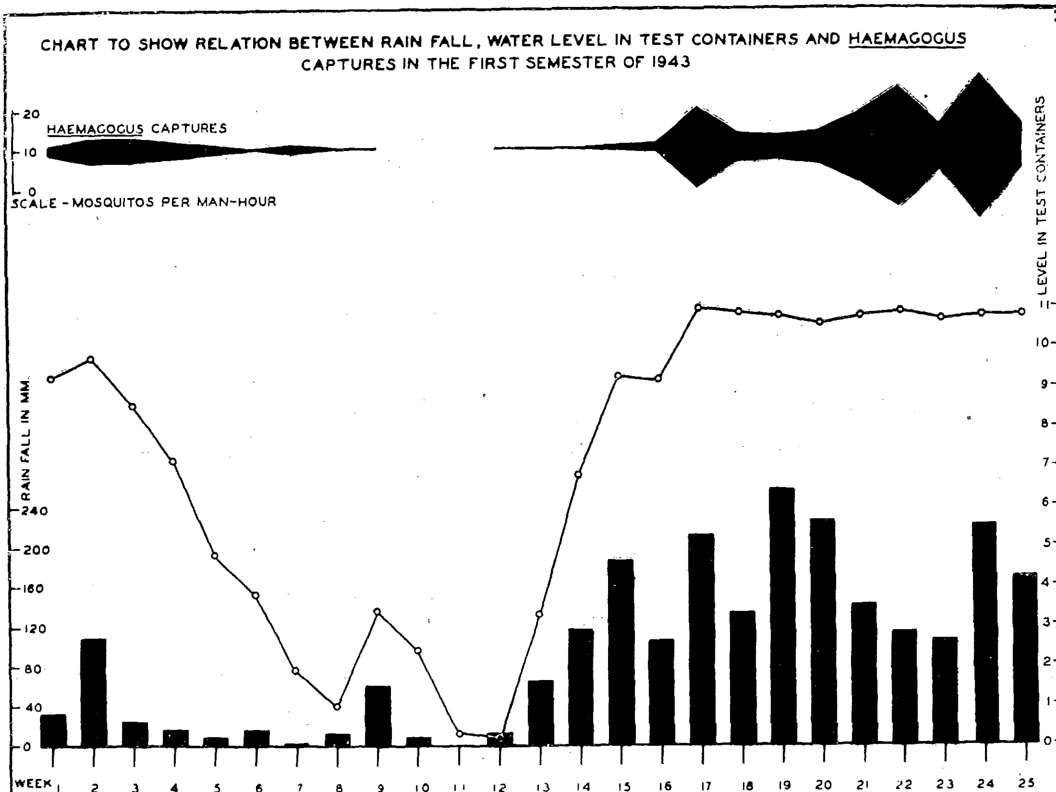

Fig. 1.

From this table it would seem rather unlikely that a series of virus cycles could be maintained throughout the year under Forzosa conditions (variation of 1 : 194 in density of *Haemagogus*), but perfectly possible that it should be maintained under Cuchilla conditions (variation 1 : 16). These two areas are only about 2 km. apart, but they may indicate, in miniature, differences between the larger geographical areas in which yellow fever is endemic and in which it is epidemic. Forzosa is on the brow of a hill, Cuchilla in a ravine; and one's first thought is that the ravine onditions may result in greater dry season humidity, permitting greater continuity of breeding places.

and series of females have been kept at different times of year for oviposition so that the species could be determined exactly. Adult identifications, with this check, have always been over 90 % correct, so that our figures are sufficiently reliable for the study of seasonal trends of this species. It is notable that the species was about ten times as abundant in the 1942 captures as in those of 1943; this probably represents extreme conditions, as the partial data available for 1941 and 1944 indicate intermediate populations. Such differences might also, however, reflect the technical limitations of the trapping method: inevitable changes in vegetation in the vicinity of the trap

Table 6. *Captures in the Ocoa stable trap, 1942**

Month	No. trials	*Anopheles rangeli*	*Culex* spp.	*Mansonia* sp.	*Psorophora cingulata*	*Psorophora ferox*	*Aedes serratus*	Total
Mar.	14	122	3·4	5·4	2·5	0	0·1	135
Apr.	13	192	9·2	26	50	0·1	9·2	284
May	12	553	19	18	142	2·0	21	766
June	14	326	37	47	82	0·6	28	528
July	13	260	50	42	89	0·6	29	484
Aug.	13	98	26	55	126	0·8	42	351
Sept.	13	25	16	37	28	0·2	9·1	118
Oct.	12	26	12	46	23	0	1·3	110
Nov.	13	26	24	52	14	0·3	2·6	122
Dec.	13	49	40	25	7·3	0·3	2·2	125
Jan.	12	58	32	17	5·7	0·2	1·2	127
Feb.	12	32	15	4·3	1·4	0·1	0·8	54
Total no. specimens		22,750	3662	4824	7333	67	1930	41,244

* Mean number of mosquitoes per trap night; 'totals' include all mosquitoes caught and are thus larger than the sum of the species specifically identified. Means are given as whole numbers except where the mean is less than 10, in which case the result is carried to the first decimal place.

Table 7. *Captures in the Ocoa stable trap, 1943**

Month	No. trials	*Anopheles rangeli*	*Culex* spp.	*Mansonia* sp.	*Psorophora cingulata*	*Psorophora ferox*	*Aedes serratus*	Total
Mar.	9	30	3·3	5·7	1·4	0	0	37
Apr.	12	29	12	2·0	7·7	5·0	0·9	52
May	13	45	24	37	89	3·0	6·7	210
June	14	47	46	58	58	2·7	3·9	219
July	15	21	30	11	28	0·6	1·5	91
Aug.	13	13	30	10	9·1	0·1	0·5	66
Sept.	15	7·1	27	5·2	16	0·1	0·6	56
Oct.	12	9·6	26	13	15	0·1	0·8	65
Nov.	13	3·8	28	2·7	32	0	0·7	69
Dec.	14	6·4	29	4·0	15	0·1	2·4	56
Jan.	12	8·7	23	3·0	12	0·2	1·1	49
Feb.	13	12	13	1·3	3·4	0·1	0·2	32
Total no. specimens		2993	3866	2047	3851	102	258	13,319

* See footnote to Table 6.

Table 8. *Standard captures of diurnal forest mosquitoes, 1942*

(Mosquitoes per man-hour.)

Month	*Haemagogus capricornii*	*Psorophora ferox**	*Aedes serratus**	*Aedes dominici*†	*Aedes leucocelaenus*†	*Anopheles boliviensis*†	*Sabethes cyaneus*	*Sabethes belisarioi*	*Sabethoides imperfectus*
Forzosa only:									
Mar.‡	3·0	—	—	0	0	0	—	—	—
Apr.	6·9	—	—	0·2	0·1	0	—	—	—
May	19·1	—	—	0·3	0·5	0·2	—	—	—
June	39·0	—	—	0·6	0·7	0·3	—	—	—
July	17·5	—	—	0·9	0·8	1·3	—	—	—
Aug.	13·0	—	—	0·6	0·5	1·2	—	—	—
All stations: comparable with 1943:									
Sept.	7·9	4·8	2·8	0·5	0·2	0·8	1·0	0·3	0·8
Oct.	5·6	1·3	1·5	0·3	0·2	1·0	0·2	0·5	1·0
Nov.	7·6	4·2	4·4	0·3	0·3	0·7	0·2	0·8	1·0
Dec.	4·5	2·3	7·7	0·3	0·1	0·4	0·03	0·8	0·5
Jan.	3·8	2·6	7·6	0·2	0·1	0·1	0·1	0·9	0·3
Feb.	1·0	0·9	2·1	0·1	0·1	0·1	0·2	0·4	0·5
Total no. specimens	6847	252	445	234	191	353	153	304	349

* Based on Ocoa captures only. † Based on Forsoza and Cuchilla captures only.

‡ 2 hours of capture only in March 1942.

Table 9. *Standard captures of diurnal forest mosquitoes*, 1943

(Mosquitoes per man-hour.)

Month	*Haemagogus capricornii*	*Psorophora ferox**	*Aedes serratus**	*Aedes dominici†*	*Anopheles boliviensis†*	*Sabethes cyaneus*	*Sabethes belisarioi*	*Sabethoides imperfectus*
Mar.	0·6	0	0·4	0·1	0·1	0·2	0·3	0·6
Apr.	5·9	2·2	5·4	0·3	0·6	0·2	0·2	0·4
May	11·5	9·7	8·3	0·5	0·8	0·2	0·2	0·7
June	15·5	10·3	9·5	0·3	1·9	0·3	0·4	0·9
July	9·4	3·7	2·0	0·2	0·8	0·3	0·2	1·1
Aug.	9·2	0·9	3·3	0·3	1·0	0·4	0·2	0·8
Sept.	3·7	1·0	2·5	0·2	0·6	0·4	0·2	0·8
Oct.	4·5	2·9	2·4	0·1	0·4	0·3	0·2	1·1
Nov.	4·9	1·6	6·5	0·1	0·3	0·1	0·3	0·9
Dec.	3·9	3·0	10·3	0·1	0·2	0·1	0·4	0·8
Jan.	0·8	1·3	4·7	0	0·1	0·1	0·2	0·8
Feb.	0·7	0·1	0·6	0	0	0·1	0·1	0·4
Total no. specimens	5578	651	993	129	410	217	227	749

* Based on Ocoa captures only. † Based on Forzosa and Cuchilla captures only.

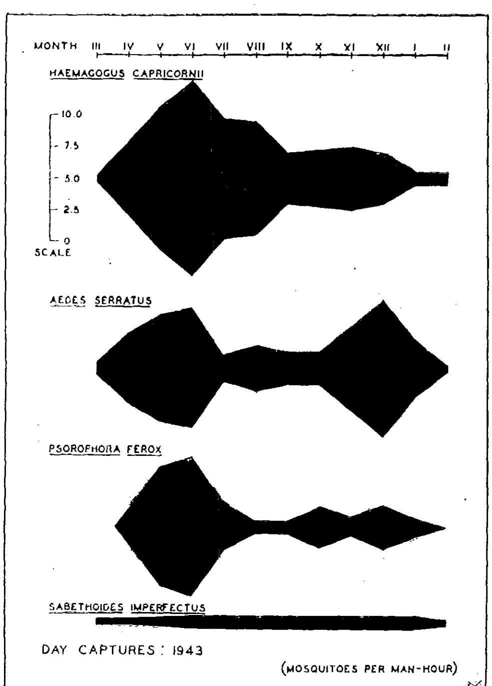

Fig. 2.

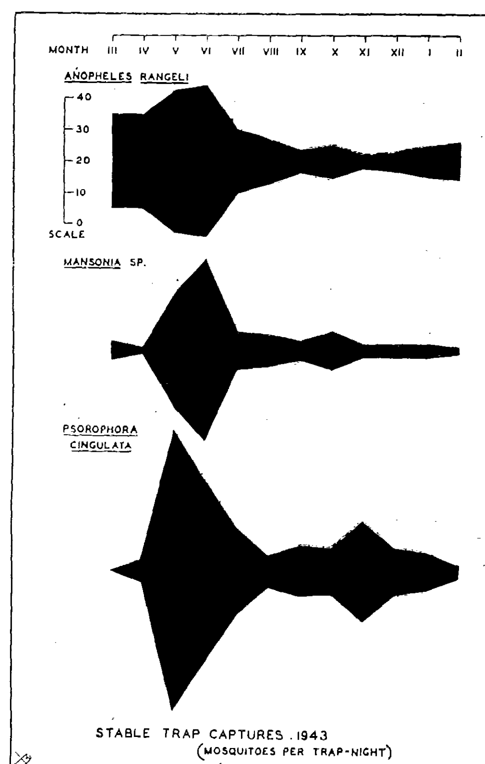

Fig. 3.

(standardization is difficult with tropical growth), differences between donkeys used as bait during the two years, or even slight changes in the trap in the course of wear and repair. The trend of the curves during the two years, aside from this difference in magnitude, is very similar, the population rising to a peak in May and June and falling off during the rest of the year.

Anophelines, like *rangeli*, have no known mechanism for aestivating, or passing an unfavourable season, so that variations in the adult population represent actual fluctuations in the total species population. With *Haemagogus capricornii* and similar mosquitoes a rise in adult population may represent merely the hatching of eggs that have lain dormant. The known breeding places of *rangeli* (sunny ponds, roadside ditches) increase in number and extent with the onset of the rains in April; but from May to December they show very little fluctuation, so that the decrease in population is probably not reflecting any contraction of the area available for breeding. Since the physical environment remains quite constant during this period, the decrease would seem to represent some change in biological relationships (e.g. prey-predator balance). The method of making periodic checks on the relative abundance of all larval stages as well as adults, used in studies of *Anopheles maculipennis* in Albania (Bates, 1941), might give valuable results in studying such a situation.

Mansonia sp. The *Mansonias* caught in the trap seem always to be one species (*fasciolata*), but no careful check has been kept. The trend is similar to that shown by *Anopheles rangeli*; the maximum population level seems to have been similar in 1942 and 1943, but the population was maintained at a high level longer in 1942.

Culex spp. This is a miscellany of many species lumped together, and there is no way of determining whether any particular species would show characteristic seasonal changes. The only interest in the figures is that they show *Culex* species always to be fairly numerous in the trap catches. Most of these species would be pond breeders; a few would be container breeders. But none, so far as we know, has a mechanism for aestivation.

(*b*) *Mosquitoes that breed in temporary pools*

Aedes serratus, *Psorophora ferox* and *P. cingulata* belong to this group. The capture data are from the Ocoa study area only, since these species are common only in level forest where they breed in the transient forest floor pools. All of them may show very abrupt variations in abundance, depending on the degree of inundation of these pools, variations that are somewhat masked by the monthly means that are used in the tables. During the dry season they may disappear completely for weeks at a time, though a very heavy mid-dry season rain will always be followed by the appearance of a few of these mosquitoes about a week later. *Aedes serratus* and *Psorophora ferox*, both diurnal species and usually found breeding in the same pools, as a rule show parallel fluctuations in abundance. It is curious that the December peak of *serratus* in 1943 (Fig. 2) has no *ferox* counterpart. Both species are occasionally caught in the stable trap (probably during the late afternoon and early morning hours), and it is interesting that the stable trap catch of *serratus* in 1943 showed the same bimodal distribution (Table 7) as the day captures (Table 9). This serves as a rough check on the two methods of sampling. The two types of capture were made in the same forest, but in very different situations and perhaps half a kilometer apart.

(*c*) *Mosquitoes that breed in natural containers*

The term 'natural container' was introduced by Shannon (1931) to cover a great class of breeding places of tropical forest mosquitoes: tree holes, water-containing plants, water in fallen leaves, flower parts and fruits. Shannon's classification of these habitats has been adopted and expanded by Hopkins (1936) in his study of African mosquito larvae. Container habitats are all very 'specialized', requiring peculiar modifications of behaviour and physiology on the part of the inhabitants, and a particular species of mosquito is usually sharply restricted to a particular kind of container habitat. The majority of the diurnal forest mosquitoes of South America breed in such habitats, and in mountain forests these are the only habitats available except the limited situations associated with mountain streams. Where container habitats show a seasonal cycle of availability, some mechanism for the carry-over of the mosquito population would seem necessary, and most species (particularly the sabethines and aedines) have eggs that are able to resist long periods of desiccation. The complications of life in a container habitat are well shown by the life history of the only Nearctic sabethine, *Wyeomyia smithii*, which lives in pitcher plants (*Sarracenia*) (Howard, Dyar & Knab, 1915, pp. 94–101).

Aedes dominici. This is perhaps a mixed category, as some of the related species can only be distinguished by the male genitalia (for comment on these identifications, see Bates, 1944*a*). The larvae live in water in bromeliads, which are not common in the particular forests where our studies were made, so the data are hardly extensive enough to be significant. It is notable that a few specimens were caught in all months except March 1942 and January and February 1943, and that there was a slight peak in July 1942 and May 1943.

Aedes leucocelaenus. Only 82 specimens were caught in 1943, and these show no clear distribution pattern, a few being caught every month in the year, with an apparent peak (17 specimens in 60 hours) in September; the apparent peak in 1942 (Table 8) was earlier. This species has very similar habits, both as larva and adult, to *Haemagogus capricornii*, and its apparent failure to show correspondingly great differences in seasonal incidence is curious.

Anopheles boliviensis. This species, like *Aedes dominici*, breeds in bromeliads. The capture data must be viewed with some suspicion because the species has predominantly late diurnal and crepuscular habits, and the captures were made at midday. The captures would seem to indicate a fairly uniform distribution between April and October, with a slight peak in June.

Sabethes cyaneus, *S. belisarioi*, *Sabethoides imperfectus*. The uniform level of capture of these three species through the year is striking and surely significant. *Imperfectus* is the most abundant, and its continued appearance in dry-season catches is very notable; in January and February it may outnumber *Haemagogus capricornii* in the captures. The chart (Fig. 2) shows this uniform distribution of the adult population. *Sabethes belisarioi* seems at times to show a definite increase under dry season conditions. All three species presumably breed in arboreal containers, though our knowledge of their larval habitats is inadequate. We have found that the eggs of *Sabethoides imperfectus* can withstand desiccation under laboratory conditions.

6. DISCUSSION

Mosquito life histories fall into two broad classes: the one in which development and reproduction is a continuous and regular process, and the other in which development may be interrupted at some stage of growth. The latter type of life history is illustrated by the various hibernation mechanisms of temperate zone mosquitoes, perhaps best summarized in Marshall's book (1938) on the British mosquitoes. Three types of hibernation mechanism are known, depending on whether the egg, larva or adult is involved. It is possible that corresponding mechanisms for aestivation exist in tropical mosquitoes, though the only well-known type of developmental interruption involves the egg stage. Most aedine mosquitoes (a broad grouping, including *Aedes*, *Haemagogus* and *Psorophora* in our fauna) have eggs which may lie dormant for long periods of time, hatching only after receiving an appropriate stimulus. This phenomenon seems to be similar in the temperate and tropical species of the group, though the precise type of stimulus necessary for hatching seems to be characteristic of the species, or perhaps even of the strain, of mosquito. There is an extensive literature on egg-hatching stimuli, and the results obtained by various workers are in part contradictory, perhaps because of failure to realize that a stimulus effective for one species may not be adequate for another. The mechanism in *Aedes aegypti* has been studied at length by Buxton & Hopkins (1927) and Shannon & Putnam 1934) and in certain North American *Aedes* by Gjullin, Hegarty & Bollen (1941). It seems very likely that the sabethine mosquitoes (e.g. *Sabethes*, *Sabethoides*, *Wyeomyia*) may show a similar phenomenon; but this has been described for only a few species. There is some difference of opinion as to whether embryonic development is ever suspended in the anopheline mosquitoes, though it seems clear that no such mechanism is present in the great majority of species.

This factor of possible suspension of development at some stage of growth must be taken into account in evaluating the significance of fluctuations in populations of adult mosquitoes. In *Anopheles rangeli* and similar mosquitoes, for instance, development seems to be purely a function of time and temperature; in a uniform climate such as that of Villavicencio the fluctuations of adult population would then be an accurate index of fluctuations in the total species population. In the case of a mosquito like *Haemagogus capricornii* or *Aedes serratus*, however, a large and unknown fraction of the total species population may be lying dormant at any one time. The species is thus buffered against temporary adversity, and the extent of seasonal and annual fluctuation in the total population would be very difficult to calculate.

Anopheles rangeli, in both 1942 and 1943, was about ten times as abundant at its population peak as at its population minimum, and on the average it was about ten times as abundant in 1942 as in 1943. It would thus seem that a mosquito population, in the relatively constant environment of Villavicencio, can show a population fluctuation over a two-year period of the order of magnitude of 1:100. It may be that these two years represent extreme conditions, since the partial records available for 1941 and 1944 indicate an intermediate population level. An even greater order of magnitude of population fluctuation is indicated by the data obtained by Kumm & Zúniga (1944) for *Anopheles albimanus* and *A. pseudopunctipennis* in El Salvador, where climatic cycles are more marked than in Villavicencio.

The suspension of embryonic development for indefinite and varying lengths of time, shown by aedine and probably by sabethine mosquitoes, very likely results in a more stable total species population, though this is perhaps not so in species that hatch freely on the application of a comparatively slight stimulus to the eggs (e.g. *Psorophora cingulata*, the eggs of which hatch at once on immersion in plain rain water). An investigation of this subject, taking into account the oviposition habits of the adult, the type of stimulus required for egg hatching and the speed of larval development, would undoubtedly yield results of considerable interest. From the point of view of yellow fever epidemiology, however, the fluctuations of the adult population alone must be taken into account, since there is no evidence that the virus can pass from an infected mosquito to the next generation.

7. SUMMARY

1. Weekly captures of diurnal mosquitoes were made in three study areas of Villavicencio, in the forest region of Colombia, over a two-year period; and data on the abundance of nine of the more common types are given. Captures of nocturnal mosquitoes with a stable trap were made in one area at the same time, and data on six mosquito types from these captures are given.

2. Most species show well-marked trends in adult abundance, the peak for most types being in May and June, immediately following the dry season. A few species of diurnal forest mosquitoes, however, show a remarkably uniform level of abundance throughout the year.

3. It is pointed out that adult mosquito abundance has a quite different meaning, depending on whether the development of the mosquito is continuous or interrupted at some stage of growth. The ability of the eggs of aedine mosquitoes to lie dormant for long periods of time provides a buffer against adverse conditions, and modifies the significance of the adult population present at any given period.

4. Data are given on rainfall, temperature, noon humidity and evaporation over a three-year period at Villavicencio. The climate in this area is remarkably uniform. There is an annual dry season, well marked but not severe, usually extending from December through part of March, which seems to be the controlling factor in seasonal fluctuations in biological phenomena.

REFERENCES

Bates, M. (1941). 'Field studies of the anopheline mosquitoes of Albania.' Proc. Ent. Soc. Wash. 43: 37–58.

Bates, M. (1944*a*). 'Observations on the distribution of diurnal mosquitoes in a tropical forest.' Ecology, 25: 159–70.

Bates, M. (1944*b*). 'Notes on the construction and use of stable traps for mosquito studies.' J. Nat. Malaria Soc. 3: 135–45.

Bugher, J. C., Manrique, J. Boshell-, Garcia, M. Roca- & Mesa, E. Osorno- (1944). 'Epidemiology of jungle yellow fever in eastern Colombia.' Amer. J. Hyg. 39: 16–51.

Buxton, P. A. & Hopkins, G. H. E. (1927). 'Researches in Polynesia and Melanesia.' London School Hyg. and Trop. Med., Mem. No. 1, xi+260 pp.

Chapman, F. M. (1917). 'The distribution of bird life in Colombia.' Bull. Amer. Mus. Nat. Hist. 36: 729 pp.

Gjullin, C. M., Hegarty, C. P. & Bollen, W. B. (1941). 'The necessity of a low oxygen concentration for the hatching of *Aedes* mosquito eggs.' J. Cell. Comp. Physiol. 17: 193–202.

Hopkins, G. H. E. (1936). 'Mosquitoes of the Ethiopian Region. I. Larval bionomics of mosquitoes and taxonomy of culicine larvae.' London, British Museum (Natural History), viii+250 pp.

Howard, L. O., Dyar, H. G. & Knab, F. (1915). 'The mosquitoes of North and Central America and the West Indies.' Publ. Carneg. Instn, No. 159, Vol. III 523 pp.

Kumm, H. W. & Zúniga, H. (1944). 'Seasonal variations in the numbers of *Anopheles albimanus* and *A. pseudopunctipennis* caught in stable traps in Central America.' Amer. J. Hyg. 39: 8–15.

Marshall, J. F. (1938). 'The British mosquitoes.' London: British Museum (Natural History), xi+341 pp.

Shannon, R. C. (1931). 'The environment and behavior of some Brazilian mosquitoes.' Proc. Ent. Soc. Wash. 33: 1–27.

Shannon, R. C. & Putnam, P. (1934). 'The biology of *Stegomyia* under laboratory conditions. I. The analysis of factors which influence larval development.' Proc. Ent. Soc. Wash. 36: 185–216.