

PHYTOTELMATA AND MOSQUITO VECTORS OF SYLVATIC YELLOW FEVER IN AFRICA

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SUMMARY

(1) In tropical Africa, six species of *Aedes* are vectors of yellow fever, and further species of *Aedes* and *Eretmapodites* could be vectors.

(2) Immature stages of most of these mosquitoes occur in phytotelmata. Treeholes provide a habitat for *Aedes aegypti* (Linnaeus), *Aedes africanus* (Theobald), *Aedes luteocephalus* (Newstead), *Aedes metallicus* (Edwards), *Aedes simpsoni*^{1,2} (Theobald), *Aedes stokesi* Evans, *Aedes taylori*¹ (Edwards) and occasionally *Eretmapodites chrysogaster*¹ Graham, whereas plant leaf axils are the major habitat of *Aedes simpsoni*¹ and fruit husks are the habitat of several *Eretmapodites* and some *Aedes*.

(3) Availability of water-filled leaf axils is influenced greatly by agriculture, and those of banana and plantain as well as of cocoyam and pineapple are principal habitats of *A. simpsoni*. Rainfall frequency is a major determinant of water content in these axils, but dew contributes to the water in banana axils, and the structure of the leaf base in some varieties reduces evaporation.

(4) Eggs, larvae and pupae of *A. simpsoni* show an unusually high tolerance to limited periods of desiccation. In banana plantations at Botambi, in a forested area of the Central African Republic, total monthly rainfall was correlated significantly with monthly average number of water-containing axils, but not with monthly average number of *A. simpsoni* larvae per 100 banana plants. The latter is correlated significantly with landing/biting collections of adult females of *A. simpsoni*.

INTRODUCTION

A formidable disease whose epidemics can be deadly (100,000 cases and 30,000 dead during an epidemic in southwestern Ethiopia in 1960-62), yellow fever is rife in almost all of the tropical African countries.

¹ A species complex

²In Tanzania

TABLE 1. African yellow fever vectors found in phytotelm habitats

Mosquito genus and species	Treeholes	Leaf axils	Fallen plant parts	Citation
<i>Aedes</i>				
<i>A. stokesi</i> Evans	+	-	rare	Service 1965, Cordellier <u>et al.</u> 1974, Raymond <u>et al.</u> 1976, Cornet <u>et al.</u> 1978a,
<i>A. vittatus</i> (Bigot)	rare	-	-	Kerr 1933
<i>A. furcifer/taylori</i> (Edwards) ¹	+	-	rare	Cordellier <u>et al.</u> 1974, Raymond <u>et al.</u> 1976, Cornet <u>et al.</u> 1978b
<i>A. aegypti</i> (Linnaeus)	+	occasional	occasional	Doucet & Cachan 1962, Service 1965, McClelland 1968, Cordellier <u>et al.</u> 1974, Raymond <u>et al.</u> 1976
<i>A. africanus</i> (Theobald)	+	rare ³	rare	Laarman 1958, Doucet & Cachan 1962, Germain <u>et al.</u> 1972, Cordellier <u>et al.</u> 1974
<i>A. luteocephalus</i> (Newstead)	+	-	rare	Service 1965, Cordellier <u>et al.</u> 1974, Raymond <u>et al.</u> 1976, Cornet <u>et al.</u> 1978b
<i>A. metallicus</i> (Edwards)	+	rare	-	Teesdale 1941, 1957; McClelland 1968, Cordellier <u>et al.</u> 1974
<i>A. pseudoafricanus</i> Chwatt	+ ²	-	-	Chwatt 1949; Mattingly & Bruce-Chwatt 1954
<i>A. simpsoni</i> (Theobald) ¹	occasional ⁴	+	occasional	Gillett 1941, 1951, 1969, 1972; Gibbins 1942, Haddow 1948, Lumsden & Buxton 1951, Muspratt 1956, Surtees 1958, Lumsden 1955, Néri 1965, Brooks <u>et al.</u> 1970, Briegel & Freyvogel 1971, Pajot 1975, Lounibos 1981, Mouchet 1972
<i>Eretmapodites</i>				
<i>E. chrysogaster</i> Graham ¹	occasional	occasional	+	Doucet 1960, Service 1965, Cordellier <u>et al.</u> 1974, Raymond <u>et al.</u> 1976, Pajot 1975, 1978; Cornet <u>et al.</u> 1978b, Lounibos 1978, 1980

Symbols: + (usual habitat), - (unrecorded), occasional (habitat used from time to time, but irregularly), rare (habitat used very little).

¹A species complex whose members are separated by slight structural differences or allopatry. ²Known only from *Avicennia* (mangrove).

³Common in *Raphia* axils in Cameroon. ⁴Frequent in Tanzania.

For all these species, see also Hopkins 1952

Epidemics of the disease occurred yet again in 1969 and 1970 in west Africa, and rarely does a year go by without cases being recorded. Sylvatic yellow fever, a disease maintained and circulated amongst animal populations and sporadically and isolatedly passed on to man, is transmitted in Africa by six species of mosquitoes. Eleven additional species are not yet proven vectors, in that either virus has not been isolated from them in nature or transmission capability has not been demonstrated.

Twelve out of 17 of these species belong to *Aedes* or *Eretmapodites* and all, except for the *Aedes dentatus* Theobald group, normally or occasionally occupy larval habitats of plant origin: treeholes, leaf axils, fruit husks and other phytotelmata. The relationship between mosquitoes and the phytotelmata where their preimaginal life is passed is of fundamental scientific interest in the study of a natural environment as specific as a treehole or leaf axil. It is also of obvious epidemiological interest because the abundance of these vector mosquitoes depends primarily on the number of suitable phytotelmata and the conditions under which larval development may be accomplished. Table 1 shows that 7 of the 10 phytotelmatous *Aedes* and *Eretmapodites* which may transmit yellow fever normally use treeholes, whereas only *Aedes simpsoni* uses leaf axils. *Eretmapodites chrysogaster* uses fallen plant parts (leaves, fruit husks, etc.). *Aedes vittatus* is included in Table 1 because its larvae are sometimes found in treeholes although normally occupying rock cavities.

YELLOW FEVER VECTORS AND TREEHOLES

Treeholes are formed where branches bifurcate, by folds or wounds in the bark, in buttresses or among roots of certain species (e.g. *Adansonia*, *Isobertia*). They may also be formed where trunks or branches have been cut or broken, and their occurrence in natural forest appears random. Each may be present for several years until decomposition of the hollow branch or trunk, or healing of the opening by new growth, eliminates it. The size of the cavity varies with tree species: mango (*Mangifera*), kapok (*Ceiba*), tamarind (*Tamarindus*) and palm (*Cocos* etc.) have holes seldom exceeding 5 liters, whereas baobabs (*Adansonia*) often have enormous ones of over 20 liters (Ravaonjanahary 1978).

In the forest, *A. aegypti* oviposits in treeholes at all levels between the ground and canopy (Dunn 1927; Doucet & Cachan 1962), but in savanna woodland it prefers holes located near or at ground level (Service 1965; McClelland 1968). Observations in Zaire, Uganda, the Ivory Coast and Ethiopia (Laarman 1958; Corbet 1961; Doucet & Cachan 1962; Néri 1965) indicate that *A. africanus* oviposits near the ground and in the lower forest stories, but at Zika, Uganda, larvae were collected in cut bamboo placed at 33 m in the forest canopy (in Cordellier *et al.* 1974). *Aedes luteocephalus* oviposits near the ground (Cornet *et al.* 1978b: eastern Senegal) and rarely higher than 6 m (Service 1965: Nigeria; Cornet & Chateau 1974: western Senegal), and apparently the height above ground of the oviposition site varies inversely with latitude (Cordellier *et al.* 1974: Ivory Coast). *Aedes stokesi* oviposits at 0.75-1.50 m above ground in gallery forest derived from savanna (Cordellier *et al.* 1974: Ivory Coast) and at 2-6 m in Guinean woodland savanna (Service 1965: Nigeria). Although *Eretmapodites chrysogaster* larvae are generally found at ground level, they have been found at all

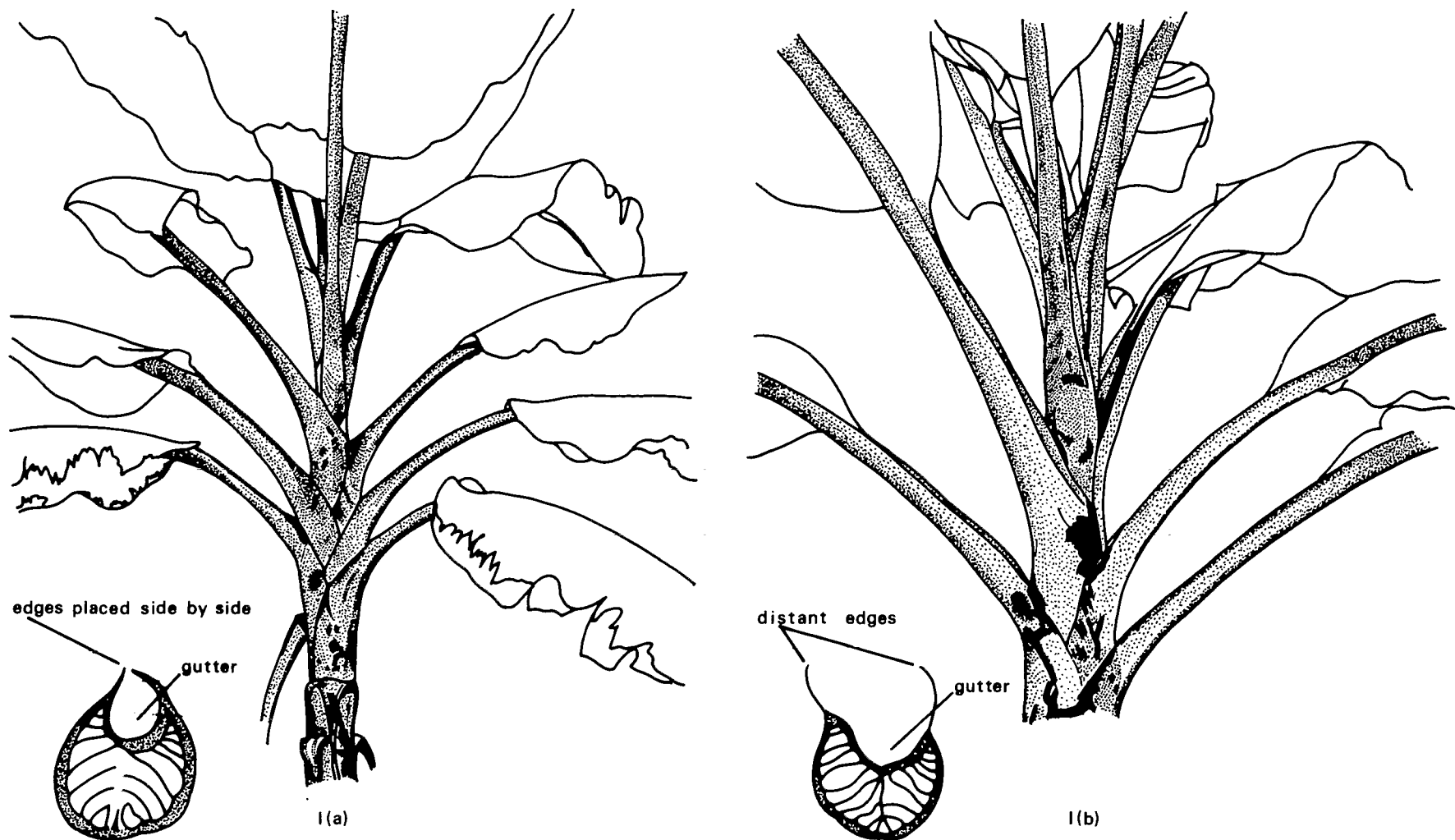


FIG. 1 Base of a crown of leaves of a banana plant, and cross-section of petiole.
 (a) Fondo variety in which petioles have juxtapsed margins and provide habitat for *Aedes simpsoni*. (b) Variety with widely separated petiolar margins.



FIG. 2 Photographs of banana plants. (a) Fondo variety, habitat of *Aedes simpsoni*.
(b) Variety which provides little or no habitat for *Aedes simpsoni*.

levels in tropical rain forest and gallery forest (Doucet 1960; Ivory Coast; Service 1965; Nigeria). These examples suggest that the ovipositional height range for each species is restrictive, but that the range may vary according to locality and its vegetation. The species occupying the greatest variety of vegetational types axiomatically are most likely to be widespread and are most likely to show a varying range in ovipositional height.

Information on the choice of treehole according to the volume of water contained is scarcer. *Aedes aegypti* and *A. metallicus* seem to prefer large treeholes, in particular baobabs, in Senegal, whereas *A. luteocephalus* and *A. furcifer/taylori* choose holes of smaller volumetric capacity (Cornet & Chateau 1974; Cornet et al. 1978b).

YELLOW FEVER VECTORS AND LEAF AXILS

Among yellow fever vectors, only *Aedes simpsoni* habitually uses water-filled plant leaf axils. The plants recorded as habitat include: bananas and plantains, pineapples, *Colocasia*, *Xanthosoma*, *Sansevieria*, *Pandanus*, *Dracaena*, *Canna*, *Strelitzia*, *Billbergia*, *Crinum* and *Heliconia* (Pajot 1975). The most important is the banana, cultivated all over tropical Africa, although other plants may be important locally due to their abundance, as for example, *Dracaena* in the Chaggaland, Tanzania, where it is cultivated intensively (Gillett 1969).

Bananas and plantains (Musa)

Numerous *Musa* species and varieties are cultivated in Africa, but the only ones which provide suitable habitats for *A. simpsoni* are those whose petiolar edges curve to form an almost closed gutter (Figs. 1 & 2) thus channelling water collected on the large surface of the lamina into the deep and almost watertight axils. These plants are of the Gonja group in Uganda (Haddow 1948) and comprise almost all those known as Fondo in the Central African Republic (CAR) (Pajot 1975).

The number of axils of a Fondo suitable for *A. simpsoni* varies considerably with the age of the plant. Thus, in the CAR, plantations of medium-aged plants contained more larvae than did plantations of young plants (pseudostem height 1-1.5 m) or old ones (pseudostem height 4 m) (Pajot 1975). This is because medium-aged plants possess on average more water-containing axils (3.9 per plant) than do young plants (1.4 axils per plant) or old plants (3.3 axils per plant). The minor difference between medium-aged plants and old plants is magnified by a much greater use by *A. simpsoni* of the medium-aged plants, so that a plantation of medium-aged plants contained 16X more larvae and pupae per plant than did a plantation of old plants (Pajot 1975).

Medium-aged plantations therefore favor development of *A. simpsoni*. In the CAR, such plants have an average of 5.8 well-formed axils but all axils are not filled with water even during abundant and frequent rains (Pajot 1975). Either the axil is not sufficiently watertight or the leaf catching and channelling the water is badly formed or positioned. The estimate of 3.9 water-containing axils per plant was based on observations during the wettest

months of 1968-1970, whereas the number of such phytotelmata fluctuated seasonally. During these same years, it was estimated that only 20% of the water-containing axils held larvae and pupae of *A. simpsoni* (Pajot 1975). Comparing the percentage of water-containing axils occupied by *A. simpsoni* larvae and pupae in three ecological zones in the CAR, it was found that in the urban area of Bangui less than 3% were occupied, whereas in derived savanna 18.4% were occupied, and in forest 19.6% were occupied (Pajot 1975). Differences like these hold obvious implications for epidemiological studies.

In the CAR, the water-containing axils of banana plants were situated between 0 and 300 cm above the ground, though most (84.5%) occurred between 100 and 200 cm (Fig. 3(a)). Axils containing *A. simpsoni* larvae were of comparable height (Fig. 3(b)), so it was concluded that ovipositing females did not show a preference for axils at a particular height (Pajot 1975).

At the peak of the rainy season, more than 58% of the axils contained less than 2 ml of water (Fig. 4(a)), but less than 4% of these contained *A. simpsoni* larvae and pupae. Almost 90% of the larvae and pupae collected were in axils containing more than 2 ml of water (Fig. 4(b)). Oviposition in axils with more than 2 ml appeared to be random with respect to volume of water contained (Pajot 1975).

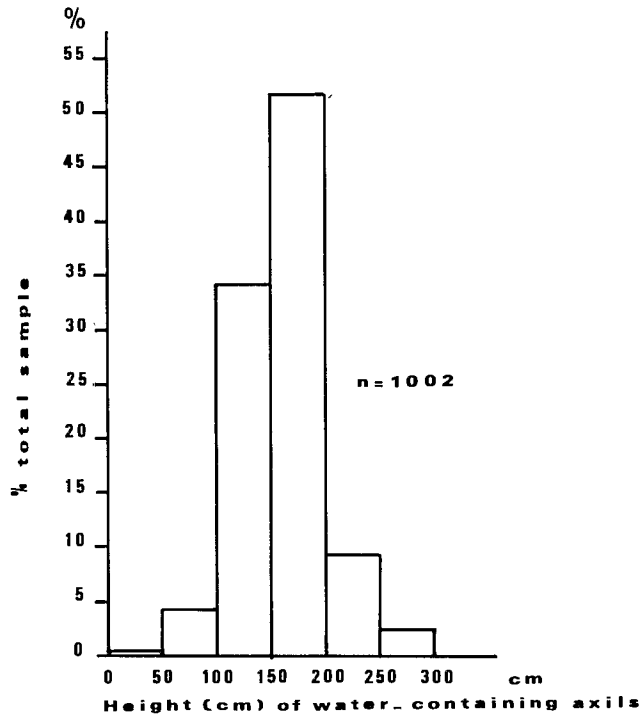
Importantly to mosquitoes, each plant has a terminal axil, a sub-terminal axil, and lower axils. The terminal axils are the youngest, tightly sheathing the pseudostem and usually with undamaged leaves, well positioned for collecting rain, whereas the lower axils are the oldest and least watertight. The highest axils are regularly supplied with water, even during periods of low rainfall, and they afford the best mosquito habitats. In the CAR, 55% of collections of *A. simpsoni* larvae and pupae from banana plants were from terminal axils, 24% from subterminal axils, and 21% from the lower axils combined (Pajot 1975).

Axillary position influences larval development in *A. simpsoni*. Lack of food seems to be the main factor in retarding larval growth in nature (Pajot 1975). Terminal and subterminal axils of bananas contain water which nearly always is clear and poor in debris and micro-organisms because it is frequently renewed, unlike that of the lower axils. Each rainfall completely or partially flushes the water in the highest (terminal) axils, washing out debris or micro-organisms in suspension and diluting whatever remains. When it rains daily, the terminal axils are poor in food. Larval development requires about one month in nature but only 10.7 days in the laboratory when food is abundant (Pajot 1976).

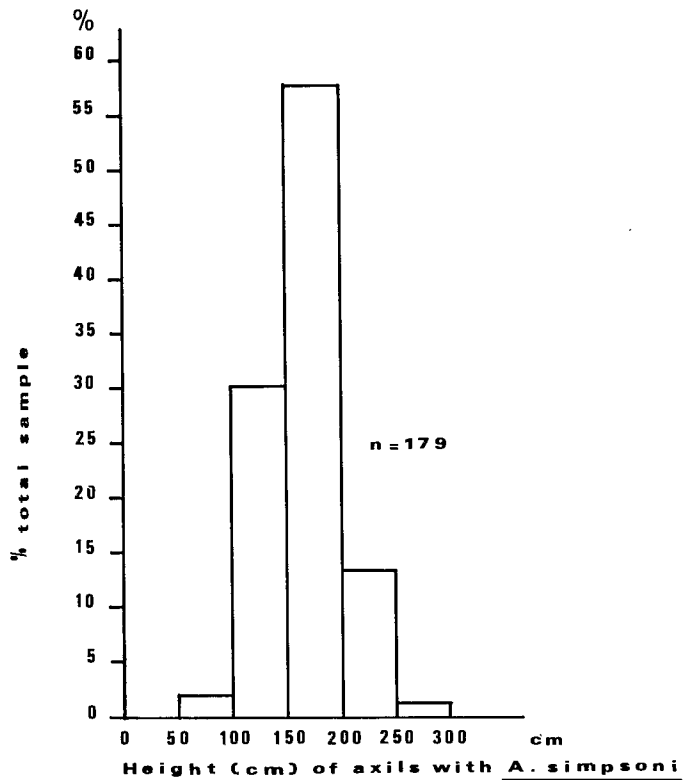
Besides *A. simpsoni*, the following mosquitoes occur in banana axils in the CAR (Pajot 1975):

Uranotaenia ornata var. *musarum* Edwards
Eretmapodites dracaenae Edwards
Malaya taeniarostris (Theobald)

The first of these was found in 3.2% of banana axils examined, and the last in 0.1%. In forested areas of the CAR, 0.8% of the water-containing axils of Fondo bananas contained larvae of *E. dracaenae*, and 0.24% larvae of both

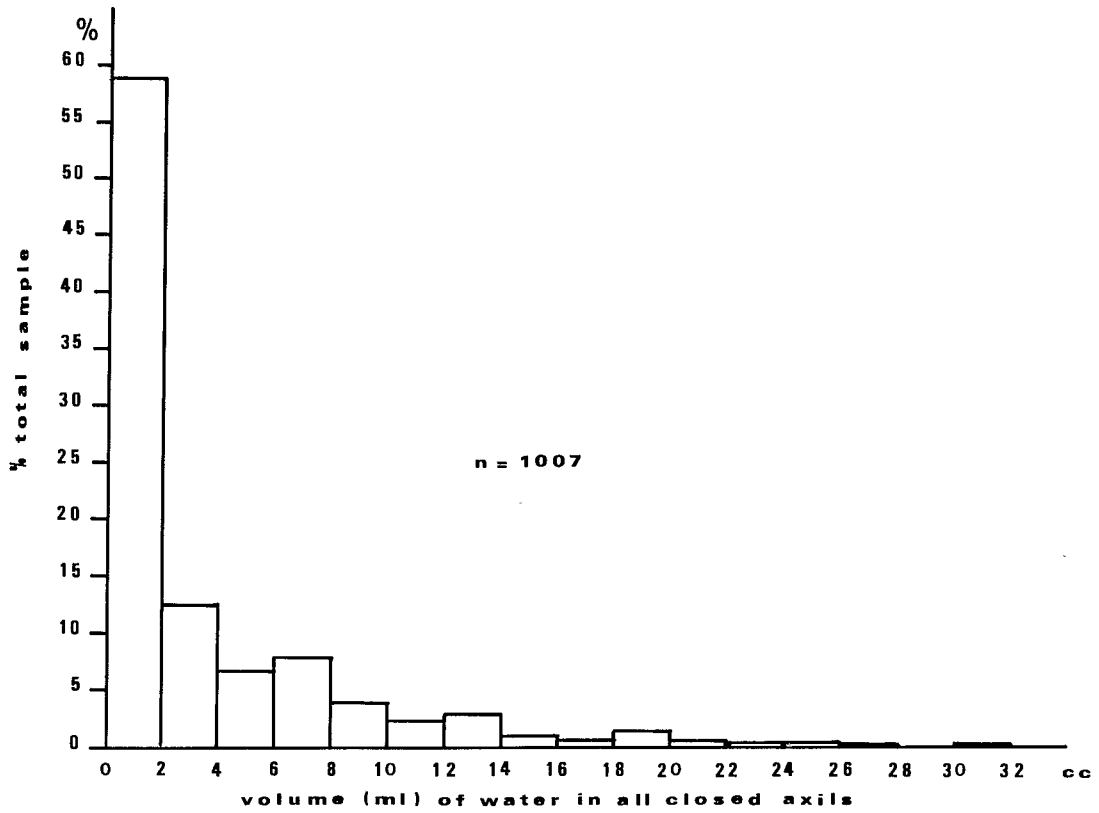


(a)

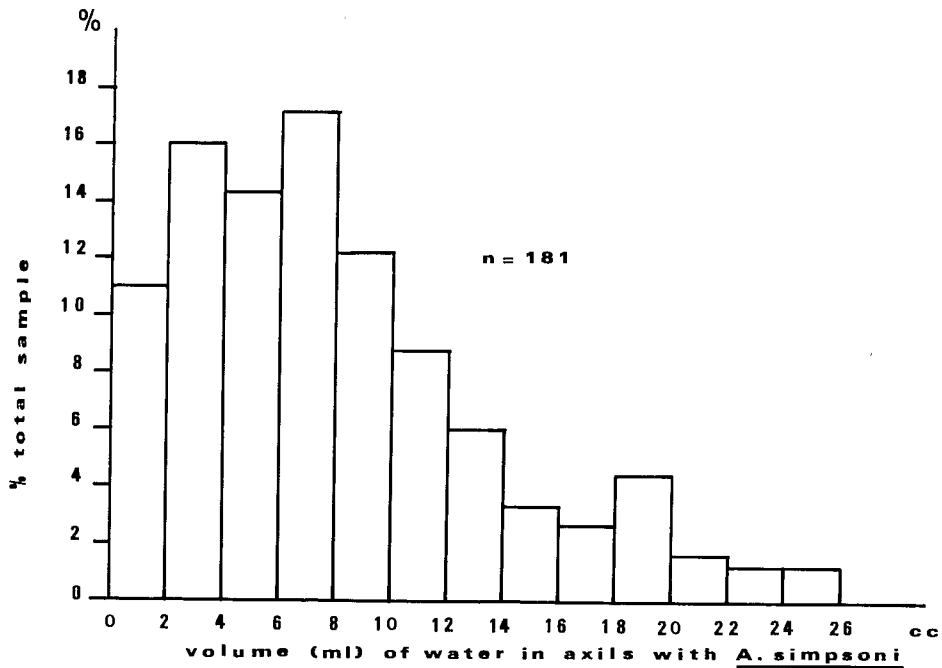


(b)

FIG. 3 Histograms showing (a) heights of banana plant axils with juxtaposed margins in forest at Botambi, Central African Republic, and (b) heights of axils occupied by larvae or pupae of *A. simpsoni*.



4 (a)



4 (b)

FIG. 4 Histograms showing (a) distribution of banana plant axils with juxtaposed margins in forest at Botambi, Central African Republic, according to water volume contained, and (b) distribution of axils containing larvae or pupae of *Aedes simpsoni*.

E. dracaenae and *A. simpsoni*. Haddow (1946) showed that *E. dracaenae* (= *E. ferox* Haddow) larvae are voracious predators. In the laboratory, they may each consume an average of nine *A. simpsoni* larvae in 24 hours. In view of the predatory nature of *E. dracaenae* larvae, these may have co-occurred, briefly, with *A. simpsoni* in more axils than the samples revealed.

Cocoyams (Colocasia and Xanthosoma)

Like bananas, cocoyams are cultivated throughout tropical Africa, often near houses. In Uganda, they are grown in banana plantations (Haddow 1948). In the CAR, cocoyam plantations are characterized by a restricted but dense cultivated area of short duration and annual variation. In the CAR forests, *Xanthosoma* (Fig. 5(a)) has 1.4 water-containing axils per plant on average, whereas *Colocasia* has 2.5. Unlike leaves of banana, those of cocoyams do not supply water to their axils because they are inclined towards the ground in a different plane from the petiole. *Aedes simpsoni* larvae were collected from 5.2% of water-containing axils of *Xanthosoma* and 7.6% of those of *Colocasia*, compared with 19.6% of those of bananas in the same region (Pajot 1975). Since cocoyams are cultivated on only a few hundred m² per banana plantation in the CAR, and never permanently, their importance for *A. simpsoni* is much less than that of banana plants. However, Néri (1965) observed that in Manera, Ethiopia, nearly 76% of suitable cocoyam axils contained *A. simpsoni* larvae. In Uganda, cocoyam axils often contain *A. simpsoni* larvae (Gibbins 1942; Haddow 1948), and in southeastern Nigeria, cocoyams harbor more larvae than do banana plants (Bown & Bang 1980).

Pineapples (Ananas)

In Bwamba County, Uganda, pineapple plants are well-suited for mosquito larval development, as 65% of axils examined contained water and 49% of these had *A. simpsoni* larvae (Haddow 1948). In contrast, in the CAR, pineapples (Fig. 5(b)) are unimportant in the production of *A. simpsoni*, because only 0.06 axils per plant examined contained larvae of this mosquito (Pajot 1975). In Nigeria, pineapples are also considerably less important for *A. simpsoni* than are bananas and cocoyams (Bown & Bang 1980).

Leaf axils of other plants

Except for *Dracaena* in the Chaggaland, Tanzania, other plants with water-containing leaf axils (*Sansevieria*, *Canna*, *Strelitzia*, *Billbergia*, *Crimum* and *Heliconia*) are generally of very minor importance in providing larval habitats for *A. simpsoni*.

FRUIT HUSKS AND OTHER FALLEN PLANT PARTS

This category contains fallen leaves, especially those of banana, fruits, especially cacao pods and coconuts, floral bracts and rotting, fallen tree trunks. *Eretmapodites* larvae are common in such habitats. In the CAR, larvae of eight *Eretmapodites* species were found in fallen leaves and bracts, and only once were *A. simpsoni* larvae found (Pajot 1975). Apparent scarcity of *A. simpsoni* larvae could have resulted from the presence of predatory *Eretmapodites* larvae. In Senegalese forests, fruit husks of the liana *Saba*, discarded by monkeys, contained larvae of 12 mosquito species, mainly those



FIG. 5 Photographs of cultivated plants whose leaf axils provide minor habitat for larvae and pupae of *Aedes simpsoni* in the Central African Republic. (a) *Xanthosoma* (cocoyam). (b) *Ananas* (pineapple).

of *Eretmapodites* which are specialized to this habitat (Raymond et al. 1976). *Aedes aegypti* larvae inhabit clearer water with less organic matter, such as occurs in fruit husks of the previous year, and other larvae found in these husks were those of the potential yellow fever vectors *A. africanus* and *A. furcifer/taylori* groups (Raymond et al. 1976). In coastal Kenyan forests the most productive habitats of *E. subsimplicipes* are rain-filled fruits of the Apocynaceae and Loganiaceae cast off by monkeys (Lounibos 1978).

ADAPTATION OF YELLOW FEVER VECTORS TO PHYTOTELMATA

Preimaginal stages of most mosquito vectors of yellow fever possess physiological characteristics which may be adaptive to existence in phytotelmata. All *Aedes* have drought-resistant eggs. Those of *A. aegypti* from Sierra Leone survived more than 13 months under laboratory conditions (Bacot 1918). Cooling (1924) noted hatching of *A. aegypti* eggs from treeholes which had been dry for 12-14 weeks. Drought resistance varies according to ecogeographical origin, and eggs from regions with a long dry season resist desiccation much longer than do those from wet regions with a short dry season (Mouchet in Ravaonjanahary 1978). In the CAR, drought resistance by eggs of *A. simpsoni* collected in the forest may last six weeks, a period sufficiently long to survive the dry period in this region (Pajot 1976). In Senegal, where the dry season is particularly long (approximately 5 months without rain), eggs of *A. simpsoni* remain viable for six months from oviposition (Cornet et al. 1978a).

Eggs of *A. metallicus*, *A. vittatus* and *A. furcifer/taylori* also are extremely drought resistant as viable ones have been found in regions where it had not rained for 14, 12 and 7-8 consecutive months respectively (Muspratt 1956; Cordellier et al. 1974; Hamon et al. 1971). In Senegal, *A. luteocephalus* eggs remained viable nine months after oviposition, yet in the same region *A. aegypti* and *A. vittatus* eggs have little drought resistance (Cornet et al. 1978a). Eggs of *A. luteocephalus* from eastern Senegal are not drought resistant if laid at the beginning of the rainy season, whereas those laid at the end of this season are very resistant (Cornet et al. 1978a, b).

When habitats fill with water, the eggs hatch, but generally not all at the same immersion. The staggering of hatching over a period of time is an important adaptive phenomenon for *Aedes* in phytotelmata. The first rains after the dry season are often inadequate to provide an aquatic medium which will persist for the duration of larval development. Eggs present during these first rains will not therefore be lost completely with the first immersion as some of them will hatch later. This staggering of hatching is also of importance in understanding the epidemiology of sylvatic yellow fever, as it is now known that transovarian transmission of the virus occurs (Aitken et al. 1979). The virus comes back progressively into circulation at the beginning of the rainy season following hatching of infected eggs. Staggering of hatching is common among *A. aegypti* eggs (Dunn 1928; Taylor 1934; Philip 1962). Eggs of *A. luteocephalus* from Senegal hatched on their first immersion if laid at the beginning of the rainy season, but hatching was staggered among eggs laid at the end of this season (Cornet et al. 1978a). Three immersions sufficed for 100% hatch of eggs of *A. aegypti*, *A. africanus*, *A. luteocephalus* and *A. simpsoni* collected at the beginning of the rainy

season in Nigeria, but nine immersions were necessary for 100% hatch of eggs laid at the end of this season (Bang et al. 1979). Egg clutches of *A. furcifer/taylori* hatched gradually during successive immersions or after a prolonged immersion, and simultaneous hatching occurred only when eggs had been kept dry for a long time (Jupp 1971).

Staggering of hatching plays an important role in *A. simpsoni* throughout the rainy season. Banana axils insufficiently supplied with water due to the condition or orientation of leaves, may only be filled by heavy rains. Staggering of hatching promotes the continued presence of some portion of egg clutches to be available for hatching at the incidence of such heavy rains which can provide sufficient aquatic medium for the development of the resultant larvae to the adult stage (Pajot 1976).

In general, mosquito larvae have little resistance to desiccation and die if left a few hours out of water. However, larvae of *A. luteocephalus* (Cornet & Chateau 1974) and *A. vittatus* (Service 1970) are able to live on a humid substrate for a few days. Over 85% of instar IV larvae of *A. simpsoni* pupated after 15 days out of water on wet mud, and an additional 2% after one month (Pajot 1976). Pupal survival was greater than 90%. In fact, pupation and adult emergence do not require free-standing water and can occur quite normally on a humid substrate. In nature, *A. simpsoni* larvae have been found living up to five weeks on wet mud or on a thin film of water at the base of axils (Haddow 1948; Rozeboom & Burgess 1962; Pajot 1976).

POPULATION DYNAMICS OF YELLOW FEVER VECTORS

In dense tropical African forests, the activity of adult mosquito vectors of yellow fever is never interrupted. In forest galleries and savannas, this activity stops for a period which varies according to the length of the dry season, from two months in the derived savanna of the Ivory Coast to more than six months in the sudano-sahelian zone (Cordellier 1978). Adult mosquitoes cannot survive in the low humidities of a long dry season unless favorable microclimates are maintained by dense vegetation (Cordellier 1978; Gayral 1970).

Monthly abundances of mosquitoes seem to depend on frequency rather than volume of rains. For example, a dry period of about two weeks dries up certain larval habitats, and consequently the adult population diminishes. Population expansion is encouraged by rainfall evenly distributed in time. In west Africa, risk of infection with yellow fever is high during the second half of the rainy season when vectors from treeholes are abundant. At the beginning of the dry season, the proportion of parous females increases and rapidly reaches 100% while larval habitats decrease in number. The most favorable period for transmission of yellow fever virus by *A. africanus* is at the end of the rainy season and beginning of the dry season in the CAR (Germain et al. 1977).

Population dynamics of A. simpsoni

Seasonal fluctuations in abundance of *A. simpsoni* adults appear different from one region to the next. In certain areas, abundances correspond more or less to rainfall variations, whereas elsewhere there seems to be no

correlation between the two. Thus, in Yaoundé, Cameroon, seasonal variations in numbers seemed to be linked to the intensity of rains, with a lag of about one month (Rickenbach *et al.* 1971). Yet, Teesdale (1957) showed at Kwale, Kenya, a lack of correspondence between the number of banana axils containing larvae of *A. simpsoni* and rainfall fluctuations. Haddow (1948) also pointed out that there was little connection between local rainfall and variations in the number of larvae of *A. simpsoni* inhabiting a batch of 100 cocoyams (*Xanthosoma*) in Uganda and Lounibos (1981) showed that *A. bromeliae*, a species of the *A. simpsoni* complex, differed from other *Aedes* found in tree-holes in that maximal larval numbers did not follow heavy rainfall.

In the CAR, larval and pupal populations of *A. simpsoni* in forest banana plantations were measured for over three years and compared with rainfall and adult populations (Pajot 1978). Figure 6 shows that between August 1968 and November 1971, rainfall variations were considerable, although not one month was without rain. Even at the driest of times, there were always some axils containing water (at least 2 ml) where larvae of *A. simpsoni* may develop. The minimum number of water-containing axils per banana plant was 0.43 in February 1970, still representing about 548 axils with water per ha of plantation. Although no month was rainless, possibly just a single rainfall may suffice to maintain water in the axils during months with low precipitation (November-March). During the dry season of 1969-70, the longest dry period was 34 days after a light rain of 0.1 mm preceded by 20 relatively dry days (only 6.8 mm of rain). The day before this 34-day period ended, a study showed there was an average of 2.5 phytotelmata per banana plant.

Axils receive water not only from rain but also from dew. The volume of water supplied by dew is generally negligible compared with that from rain, except during the dry season. The daily average dew collected during the dry seasons of 1968-69 and 1969-70 was 0.6 mm. Considering that the surface of an undamaged banana leaf is often one m², such an area will collect 60 ml of water (Pajot 1975). It is therefore not surprising that even axils which receive only some of this water will remain filled during the dry season. One must also consider morning mists which are frequent in forests, even in the dry season, creating considerable condensation on the vegetation. The persistence of water in axils during the dry season has also been noted in Ethiopia (Sérié *et al.* 1964) and in Kenya (Teesdale 1941) where banana axils still contained water after 43 days of drought.

Monthly rainfall totals and monthly average number of water-containing axils are shown in Fig. 6 for 1968-71 at Botambi, CAR. Despite considerable monthly variations during the rainy seasons, the values are significantly correlated (non-parametric test, $r_s = 0.46$, $t = 3.14$, $P < 0.01$). Analysis of monthly data shows general trends, but is too coarse a technique to show that at any given moment, the number of water-containing axils depends on the frequency and strength of rains which have fallen on the preceding day. Well-sealed axils supplied by undamaged, well-positioned leaves are filled rapidly by a few light showers. Heavy rains supply axils whose leaves are damaged, poorly positioned or non-existent. In the last case, axils catch water which falls directly in, and thus only intense rains or a series of frequent showers may fill them. The highest number of water-containing axils per plant was recorded in July 1970 (Fig. 6), when rainfall was heavy and evenly

average number of
Aedes simpsoni larvae
on 100 banana trees

average number of
phytotelmata per
banana tree

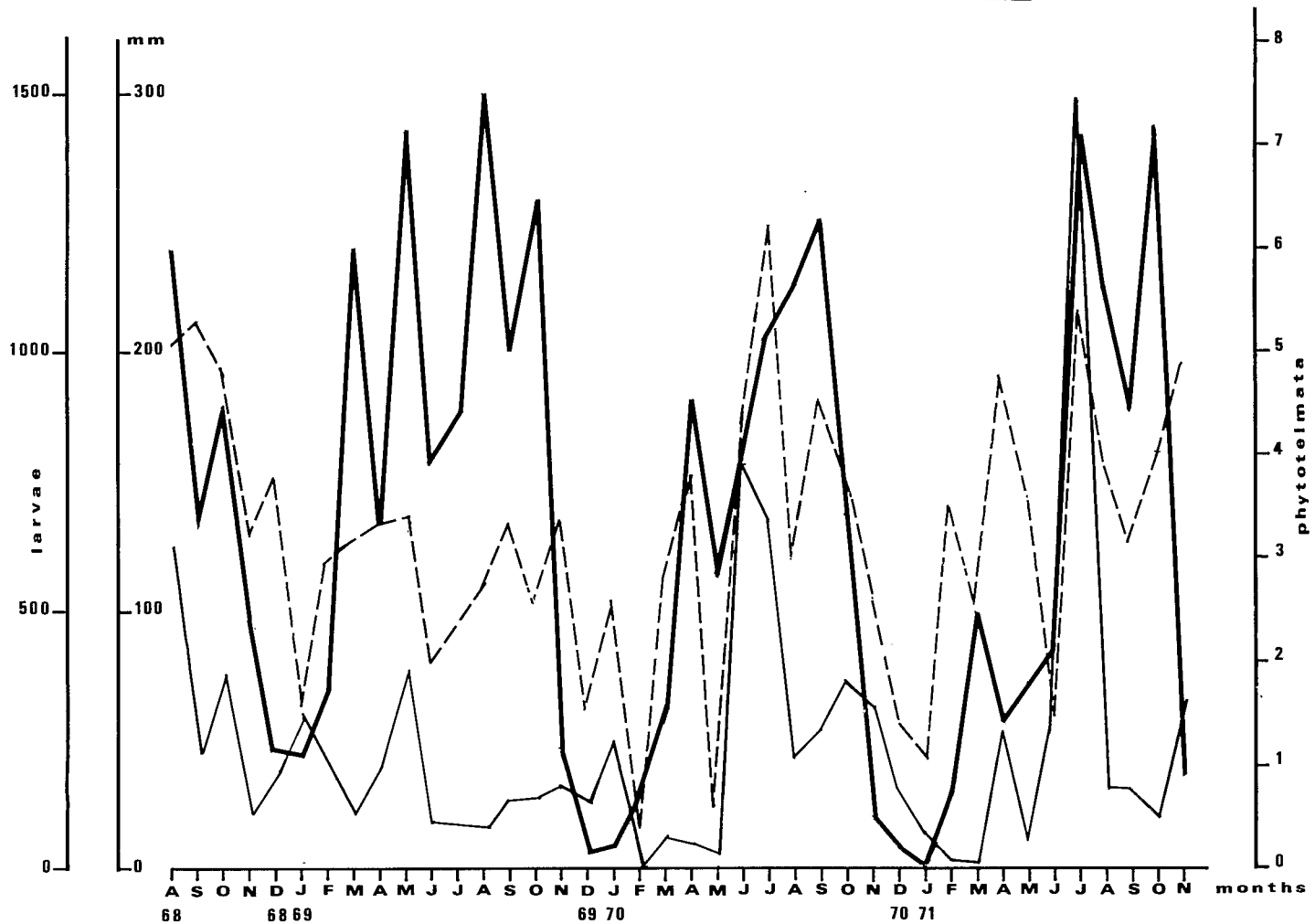


FIG. 6 Graph showing the relationship of monthly measurements in a banana plantation at Botambi, Central African Republic, from August 1968 to November 1971: (broad line) total monthly rainfall in mm; (narrow line) *Aedes simpsoni* larvae per 100 banana plants; (broken line) number of phytotelmata per banana plant.

distributed (16 days with rain), preceded by similar conditions in June (14 days with rain).

Among banana plantations in CAR forests, the monthly average percentage of water-containing axils occupied by *A. simpsoni* varied from 1.6 to 81% (broken line, Fig. 7). Similar variation was found on examination of the monthly average number of larvae per water-containing axil, exclusive of the axils without larvae (solid line, Fig. 7). This variability was determined by the number of ovipositing females, the number of available phytotelmata and their attractiveness, the proportion of eggs hatching, the importance of predators, and the duration of larval life. Due to lack of space in this brief chapter, only the role of predators is discussed.

As mentioned already, banana axils may contain *E. dracaenae* larvae which feed on *A. simpsoni* larvae. However, the effect of predation by *Eretmapodites* varies. From August 1968 to November 1971, a period of 40 months, *E. dracaenae* was found in the CAR banana plantations only in 14 months (Fig. 7) (Pajot 1978). It was not found in axils for nine consecutive months in 1970. Its presence and abundance seemed independent of rainfall. This predator was relatively abundant only from August to November 1969, a period of only four months. It occupied a maximum of 8.8% of available banana axils during this short period. Predation therefore seems to have only an intermittent influence on population dynamics of preimaginal *A. simpsoni*, any noticeable action occurring during limited periods. Among banana plantations in CAR forests, monthly average numbers of *A. simpsoni* larvae per 100 banana plants (narrow line, Fig. 6) were not correlated with total monthly rainfall ($r_s = 0.195$, $t = 1.20$, $P > 0.20$). In 1969, during the rains, the peak of the larval population was unique and of little importance whereas rainfall was particularly high with 4 peaks. In 1970, the peak for the larval population did not correspond at all with the rainfall one, whereas in 1971 it coincided with the first of the two peaks of the rainy season (Fig. 6) (Pajot 1978).

Adult populations were measured from late 1968 to late 1971. Landing/biting collections and insect net collections provided counts of adult females, and were significantly correlated with each other (non-parametric test, $r_s = 0.641$, $t = 3.50$, $P < 0.001$). The landing/biting collections were also correlated significantly with the number of larvae per 100 banana plants (non-parametric test, $r_s = 0.45$, $t = 2.13$, $P < 0.01$) (Pajot 1978).

CONCLUSION

The study of the relationship of yellow fever vectors in Africa and their phytotelmata is of particular interest to both biologist and epidemiologist. Treeholes and leaf axils are particularly favorable habitats for ecological studies of animal populations whose complete preimaginal life passes in natural surroundings of limited size whose parameters are easier to measure than those of biotopes of larger dimensions. Thorough knowledge of the dynamics of larval populations is particularly important for the epidemiologist, especially since discovery of transovarial transmission of yellow fever virus.

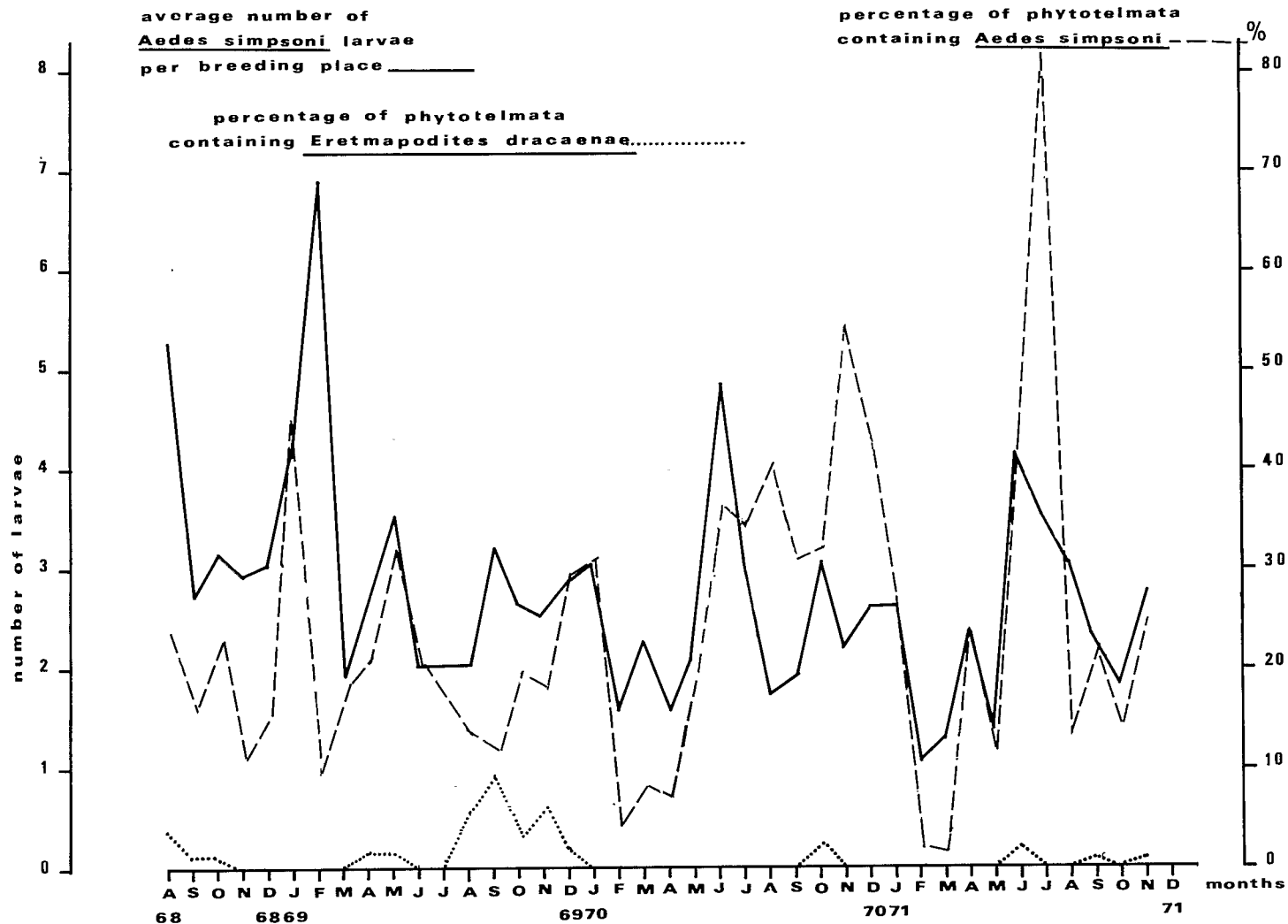


FIG. 7 Graph showing monthly measurements of abundances of mosquito larvae in banana leaf axils at Botambi, Central African Republic, from August 1968 to November 1971: (broken line) percentage of phytotelmata with *Aedes simpsoni*; (solid line) average number of *Aedes simpsoni* per axil with larvae; (dotted line) percentage of phytotelmata with *Eretmapodites dracaenae*.

Our knowledge is still fragmentary for mosquitoes inhabiting treeholes, particularly *Aedes* of the *africanus-luteocephalus* group which play a fundamental role in the epidemiology of yellow fever in vast regions of Africa (forest and forest fringes). It would be interesting to study the dynamics or preimaginal populations of treehole mosquitoes, hoping to reveal factors which have a significant role in the regulation of mosquito populations. This would perhaps enable one to predict changes in the abundance of vectors in regions where human populations are in danger.

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REFERENCES

- Aitken, T. H. G., Tesh, R. B., Beaty, B. J. & Rosen, L. (1979). Trans-ovarial transmission of yellow fever virus by mosquitoes (*Aedes aegypti*). *American Journal of Tropical Medicine and Hygiene*, 28, 119-121.
- Bacot, A. W. (1918). A note on the period during which the eggs of *Stegomyia fasciata* (*Aedes calopus*) from Sierra Leone stock retain their vitality in a humid temperature. *Parasitology*, 10, 280-283.
- Bang, Y. H., Bown, D. N., Omwubiko, A. O. & Lambrecht, F. L. (1979). Prevalence of potential vectors of yellow fever in the vicinity of Enugu, Nigeria. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 17, 139-147.
- Bown, D. N. & Bang, Y. H. (1980). Ecological studies on *Aedes simpsoni* (Diptera: Culicidae) in southeastern Nigeria. *Journal of Medical Entomology*, 17, 367-374.
- Briegel, H. & Freyvogel, T. A. (1971). Preliminary survey of *Aedes* (*Stegomyia*) mosquitos during the dry season of 1970 in the Tanzanian hinterland. WHO/VBC/71 274 (a W.H.O. duplicated, unpublished document).
- Brooks, G. D., Néri, P., Gratz, N. G. & Weathers, D. B. (1970). Preliminary studies on the use of ultra-low-volume applications of malathion for control of *Aedes simpsoni*. *Bulletin of the World Health Organization*, 42, 37-54.
- Chwatt, L. J. (1949). *Aedes* (*Stegomyia*) *pseudoffricanus* sp. nov.: a new species of *Aedes* from the Coast of Nigeria (British West Africa). *Nature* (Lond.), 163, 808.
- Cooling, L. E. (1924). On the protracted viability of eggs of *Aedes aegypti* and *A. notoscriptes* in a desiccated condition in a state of nature. *Health*, 2, 51-52.
- Corbet, P. S. (1961). Entomological studies from a high tower in Mpanga forest (Uganda). VIII. The age composition of biting mosquito populations according to time and level. *Transactions of the Royal Entomological Society of London*, 113, 335-345.
- Cordellier, R. (1978). Les vecteurs potentiels sauvages dans l'épidémiologie de la fièvre jaune en Afrique de l'Ouest. *Travaux et Documents de l'ORSTOM*, 81, 1-258.

- Cordellier, R., Germain, M. & Mouchet, J. (1974). Les vecteurs de fièvre jaune en Afrique. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 12, 57-75.
- Cornet, M. & Chateau, R. (1974). Quelques données biologiques sur *Aedes (Stegomyia) luteocephalus* (Newstead), 1907 en zone de savane soudanienne dans l'ouest du Sénégal. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 12, 97-110.
- Cornet, M., Dieng, P. L. & Valade, M. (1978a). Note sur l'utilisation des pondoirs-piège dans les enquêtes sur les vecteurs selvatiques de fièvre jaune. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 16, 309-314.
- Cornet, M., Chateau, R., Valade, M., Dieng, P. L., Raymond, H. & Lorand, A. (1978b). Données bio-écologiques sur les vecteurs potentiels du virus amaril au Sénégal oriental. Rôle des différentes espèces dans la transmission du virus. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 16, 315-341.
- Doucet, J. (1960). Moustiques forestiers de la République de Côte d'Ivoire. II. Note préliminaire sur l'échelonnement vertical de la faune culicidienne de la forêt du Banco (Abidjan). *Bulletin de la Société de Pathologie Exotique*, 53, 814-819.
- Doucet, J. & Cachan, P. (1962). Moustiques forestiers de la République de Côte d'Ivoire. VI. Observations sur les gîtes de ponte des moustiques du genre *Aedes* Meigen dans les arbres de la forêt du Banco (Abidjan). *Bulletin de la Société de Pathologie Exotique*, 55, 422-443.
- Dunn, L. H. (1927). Tree-holes and mosquito breeding in West Africa. *Bulletin of Entomological Research*, 18, 139-144.
- Dunn, L. H. (1928). Further observations on mosquito breeding in tree-holes and crab-holes. *Bulletin of Entomological Research*, 18, 247-250.
- Gayral, P. (1970). Contribution à l'épidémiologie du paludisme et des arboviroses en Afrique de l'Ouest. Résultats d'une étude entomologique sur les vecteurs d'une forêt relique en zone de savane. Thesis, Faculté de Pharmacie, Paris, 156 pp.
- Germain, M., Eouzan, J. P., Ferrara, L. & Button, J. P. (1972). Observations sur l'écologie et le comportement particuliers d'*Aedes africanus* (Theobald) dans le nord du Cameroun occidental. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 10, 119-126.
- Germain, M., Herve, J. P. & Geoffroy, B. (1977). Variation du taux de survie des femelles d'*Aedes africanus* (Theobald) dans une galerie forestière du sud de l'Empire Centrafricain. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 15, 291-299.
- Germain, M., Mouchet, J., Cordellier, R., Chippaux, A., Cornet, M., Herve, J. P., Sureau, P., Fabre, J. & Robin, Y. (1978). Epidémiologie de la fièvre jaune en Afrique. *Médecine et Maladies Infectieuses*, 2, 69-77.
- Gibbins, E. G. (1942). On the habits and breeding-places of *Aedes (Stegomyia) simpsoni* Theobald in Uganda. *Annals of Tropical Medicine and Parasitology*, 36, 151-160.
- Gillett, J. D. (1941). Report on small container breeding mosquitos made to the Government Entomologist, Kampala, Uganda (unpublished).
- Gillett, J. D. (1951). The habits of the mosquito *Aedes (Stegomyia) simpsoni* Theobald in relation to the epidemiology of yellow fever in Uganda. *Annals of Tropical Medicine and Parasitology*, 45, 110-121.

- Gillett, J. D. (1969). *Aedes simpsoni* in Chaggaland, Tanzania. *Annals of Tropical Medicine and Parasitology*, 63, 147-156.
- Gillett, J. D. (1972). *Aedes simpsoni* in Chaggaland II. Breeding in banana axils. *East African Medical Journal*, 49, 285-290.
- Haddow, A. J. (1946). The mosquitoes of Bwamba County, Uganda. IV. Studies on the genus *Eretmapodites* Theobald. *Bulletin of Entomological Research*, 37, 57-82.
- Haddow, A. J. (1948). The mosquitoes of Bwamba County, Uganda. VI. Mosquito breeding in plant axils. *Bulletin of Entomological Research*, 39, 185-212.
- Hamon, J., Pichon, G. & Cornet, M. (1971). La transmission du virus amaril en Afrique occidentale. Ecologie, répartition, fréquence et contrôle des vecteurs, et observations concernant l'épidémiologie de la fièvre jaune. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 9, 3-60.
- Hopkins, G. H. E. (1952). *Mosquitoes of the Ethiopian Region. I. Larval Bionomics of Mosquitoes and Taxonomy of Culicine Larvae* 2nd edn. British Museum, London.
- Jupp, P. G. (1971). The laboratory colonization of *Culex (Culex) theileri* Theobald and *Aedes (Diceromyia) furcifer* (Edwards) (Diptera: Culicidae). *Journal of the Entomological Society of Southern Africa*, 34, 191-193.
- Kerr, J. A. (1933). Studies on the abundance, distribution and feeding habits of some West African mosquitoes. *Bulletin of Entomological Research*, 24, 493-510.
- Laarman, J. J. (1958). Research on the ecology of culicine mosquitoes in a forest region of the Belgian Congo. *Acta Leidensia*, 28, 94-98.
- Lounibos, L. P. (1978). Mosquito breeding and oviposition stimulant in fruit husks. *Ecological Entomology*, 3, 299-304.
- Lounibos, L. P. (1980). The bionomics of three sympatric *Eretmapodites* (Diptera: Culicidae) at the Kenya coast. *Bulletin of Entomological Research*, 70, 309-320.
- Lounibos, L. P. (1981). Habitat segregation among African treehole mosquitoes. *Ecological Entomology*, 6, 129-154.
- Lumsden, W. H. R. (1955). Entomological studies, relating to yellow fever epidemiology, at Gede and Taveta, Kenya. *Bulletin of Entomological Research*, 46, 149-183.
- Lumsden, W. H. R. & Buxton, P. A. (1951). A study of the epidemiology of yellow fever in West Nile District, Uganda. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 45, 53-78.
- Mattingly, P. F. & Bruce-Chwatt, L. J. (1954). Morphology and bionomics of *Aedes (Stegomyia) pseudoafricanus* Chwatt (Diptera, Culicidae), with some notes on the distribution of the subgenus *Stegomyia* in Africa. *Annals of Tropical Medicine and Parasitology*, 48, 183-193.
- McClelland, G. A. H. (1968). Field observations on periodicity and site preference in oviposition by *Aedes aegypti* (L.) and related mosquitoes (Diptera: Culicidae) in Kenya. *Proceedings of the Royal Entomological Society of London (A)*, 43, 147-154.
- Mouchet, J. (1972). Prospections sur les vecteurs de fièvre jaune en Tanzanie. *Bulletin de l'Organisation Mondiale de la Santé*, 46, 675-684.
- Muspratt, J. (1956). The *Stegomyia* mosquitoes of South Africa and some neighbouring territories (including chapters on the mosquito-borne virus diseases of the Ethiopian zoo-geographical region of Africa). *Memoirs of the Entomological Society of Southern Africa*, 4, 1-138.

- Néri, P. (1965). Revue taxonomique, aspect écologique et biologique des diptères (Culicidae) présents dans la forêt de Manera (Province de Kaffa), Ethiopie. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 3, 47-56.
- Pajot, F.-X. (1975). Contribution à l'étude écologique d'*Aedes (Stegomyia) simpsoni* (Theobald, 1905) (Diptera, Culicidae). Etude des gîtes larvaires en République Centrafricaine. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 13, 135-164.
- Pajot, F.-X. (1976). Contribution à l'étude écologique d'*Aedes (Stegomyia) simpsoni* (Theobald, 1905) (Diptera, Culicidae). Observations concernant les stades préimaginaux. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 14, 31-48.
- Pajot, F.-X. (1978). Dynamique des populations d'*Aedes (Stegomyia) simpsoni* (Theobald), 1905 en Centrafrique. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 16, 129-150.
- Philip, C. B. (1962). Breeding of *Aedes aegypti* and other mosquitoes in West African rock-holes. *Annals of the Entomological Society of America*, 55, 706-708.
- Ravaonjanahary, C. (1978). Les *Aedes* de Madagascar (Diptera, Culicidae). 1 - Etude monographique du genre, 2 - Biologie d'*Aedes (Diceromyia) tiptoni*. *Travaux et Documents de l'ORSTOM*, 87, 1-210.
- Raymond, H. L., Cornet, M. & Dieng, P. Y. (1976). Etudes sur les vecteurs sylvatiques du virus amaril. Inventaire provisoire des habitats larvaires d'une forêt-galerie dans le foyer endémique du Sénégal oriental. *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 14, 301-306.
- Rickenbach, A., Ferrara, L., Germain, M., Eouzan, J. P. & Button, J. P. (1971). Quelques données sur la biologie de trois vecteurs potentiels de fièvre jaune *Aedes (Stegomyia) africanus* (Theo.), *A. (S.) simpsoni* (Theo.) et *A. (S.) aegypti* (L.) dans la région de Yaoundé (Cameroun). *Cahiers ORSTOM, Série Entomologie Médicale et Parasitologie*, 9, 285-299.
- Rozeboom, L. E. & Burgess, R. W. (1962). Dry-season survival of some plant-cavity breeding mosquitoes in Liberia. *Annals of the Entomological Society of America*, 55, 531-535.
- Sérié, C., Andral, L., Lindrec, A. & Néri, P. (1964). Epidémie de fièvre jaune en Ethiopie (1960-1962). Observations préliminaires. *Bulletin de l'Organisation Mondiale de la Santé*, 30, 299-319.
- Service, M. W. (1965). The ecology of the tree-hole breeding mosquitoes in the northern guinea savannah of Nigeria. *Journal of Applied Ecology*, 2, 1-16.
- Service, M. W. (1970). Studies on the biology and taxonomy of *Aedes (Stegomyia) vittatus* (Bigot) (Diptera: Culicidae) in Northern Nigeria. *Transactions of the Royal Entomological Society of London*, 122, 101-143.
- Surtees, G. (1958). Notes on the breeding habits of some culicine mosquitoes (Diptera: Culicidae) in Southern Ghana. *Proceedings of the Royal Entomological Society of London (A)*, 33, 88-92.
- Taylor, A. W. (1934). A note on the mosquitoes breeding in tree-holes in Northern Nigeria. *Bulletin of Entomological Research*, 25, 191-193.
- Teesdale, C. (1941). Pineapple and banana plants as a source of *Aedes* mosquitoes. *East African Medical Journal*, 18, 260-267.
- Teesdale, C. (1957). The genus *Musa* Linn. and its role in the breeding of *Aedes (Stegomyia) simpsoni* (Theo.) on the Kenya coast. *Bulletin of Entomological Research*, 48, 251-260.

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