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ASPECTS OF THE ECOLOGY OF MOSQUITOES IN SURINAM

by

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I. BITING ACTIVITY PATTERNS

INTRODUCTION

For about two years (1967–1968) investigations were conducted on the ecology of mosquitoes in relation to the transmission of arboviruses in Surinam (DE KRUIJF 1970). Part of this study dealing with the daily activity of biting mosquitoes is presented here.

Daily activity of biting anopheline females has been widely studied because of their ability to transmit malaria (MATTINGLY 1949, SENIOR-WHITE 1953, GILLIES 1957, SLOOFF 1964, and many others). Intensive studies on culicine mosquitoes transmitting arboviruses and other pathogen agents have been carried out in Africa and elsewhere (among many others HADDOW 1945, 1954, 1956, 1961a and b, 1961, MCCLELLAND 1960, BOORMAN 1961, SAMARAWICKRAMA 1967, TAYLOR & JONES 1969). Data on the diel activity of culicine mosquitoes in South America are relatively scarce; species transmitting jungle yellow fever, *Haemagogus* species and *Sabethes chloropherus*, having been studied most completely (KUMM & NOVIS 1938, BATES 1944, 1949, CAUSEY & SANTOS 1949, GALINDO et al. 1951, TRAPIDO & GALINDO 1957, GALINDO 1957, FORATTINI 1966b). AITKEN et al. (1968) have published some data on other species whereas FORATTINI (1962, 1966a and b) reviewed the scattered data on the daily activity of biting mosquitoes belonging to as many species as possible. It appeared that in the northern region of South America knowledge on the subject is very scarce.

Many studies have been conducted dealing with the nature of circadian (24-hours, daily) rhythms. Also several attempts have been made to explain or to understand the nature of the daily activity patterns of mosquitoes (a.o. GILLETT et al. 1959, HADDOW 1961b, CORBET 1960, 1966, LUMSDEN 1968, and TAYLOR & JONES 1969). In the Discussion a short review on this interesting part of rhythms will follow the discussion of the results.

I wish to express my sincere gratitude to the technicians M. KROMOSOTO and R. NURMOHAMED for their invaluable assistance in the course of the investigations. Various catchers assisted me with the 24-hour catches; among others thanks are due to A. NAIPAL, D. LESPERANCE, P. CHINLOI, E. PLAYFAIR, E. ANIJS, E. BLANK, and students of the Medical School, Paramaribo.

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Dr. K. BAKKER also criticized the manuscript and Mr. C. ROESSLER the English style. Mr. A. van den BROEK prepared the figures.

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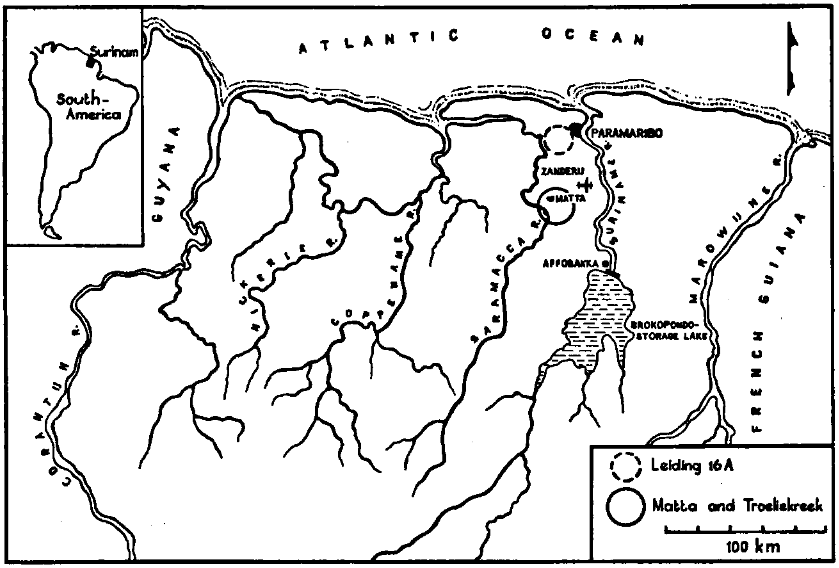


Fig. 1. Sketch map of the northern part of Surinam with localities.

AREA

All catches used for the determination of daily activity patterns were carried out in Troelikreek near Matta. The forest is situated in the savannah belt of Surinam which crosses this country from West-South-West to East-North-East in the Northern half of Surinam (Fig. 1). This forest belongs to the gallery forest, found along the creeks penetrating the savannahs. In fact it is an offset of the large marsh forest bordering the Saramacca river. These gallery forests tend to be marsh forest but do have some characteristics of a savannah forest according to the description of LINDEMAN & MOOLENAAR (1959). The average canopy in Troelikreek was 35–45 m with some trees reaching far above this level; the undergrowth was very dense. The catching station was located about 200 m into the forest near a small natural clearing in the undergrowth.

METHODS

All catches on human bait were carried out by handsucking with a transparent tube serving as a reservoir and a flexible tube through which the mosquitoes were sucked in. The reservoirs were easily exchangeable.

A label with time, place, and name of the catcher was always attached to the reservoirs. The aspirators used for emptying the traps were marked correspondingly. The use of this aspirator appeared to be very efficient (DE KRUIJF 1970, p. 18–19).

Normally the mosquitoes were caught when they tried to feed on the naked arms and legs of the catchers; also mosquitoes were caught that alighted on their clothes. The mosquitoes attacking the head were caught by the other catcher(s) as much as possible. Some catches above ground-level – some 24-hour sessions in Troelikreek and a few catches in 16A – were carried out by one man. All other catches were carried out at least by two persons. When the mosquitoes were so numerous that they became a real nuisance, the catchers did not uncover their arms and legs and caught the mosquitoes that landed on their clothes.

Differences in attractiveness between individual catchers might affect the results. However, careful examination of the results of the catches in 16A and Troelikreek revealed that variation could be dismissed completely in the long run.

Starting in February 1968, twelve 24-hours catches on human bait were carried out with intervals of two weeks in Troelikreek.

The present author decided to work with pairs of catchers to minimize differences in attractiveness and skill between the individual catchers (DE KRUIJF 1970). The composition of the pairs was changed every other 24-hour session. A team of 8 catchers – 4 pairs – worked at groundlevel during periods of two hours, so that they were "on" two hours and "off" six hours. This in contrast to the schedules of HADDOW (1954) and AITKEN et al. (1968). Collecting was done on a 15-minute base;

every 15-minute period a new tube was taken. Regardless of rain, collecting continued uninterruptedly; during heavy showers, however, the catchers were seated under a high plastic roof. At night the catchers used flashlights (two cell) which were the only lights permitted in the catching area. At the beginning of every nocturnal two-hour period the flashlights were provided with new cells.

HADDOW (1954) and AITKEN et al. (1968) noted the initial hour's catch as unusually high compared to the catches in the following hours. In imitation of these authors we decided to catch 25 hours and to exclude the results of the first hour from the evaluation of the data. The unusual high catch in the initial hour is ascribed to the disturbing effect of the catchers when entering the catching area for the first time and, possibly, the depletion of the mosquito population in the direct vicinity of the catchers (COLLESS 1957). Indeed, in Troelikreek a higher catch in the first hour of the 25 hour sessions compared to the following hours was also observed.

Time of the catch was marked as "catching-time" according to the method introduced by LUMSDEN (1952). This means that actual local time is converted, so that sunset is fixed at 18.00 h. Thus the catches in various parts of the year are adjusted to sunset and, hence, comparable.

RESULTS

The biting activity patterns in 24 hours are shown in the Figures 2–14 for 13 species, including 2 not further identified species of *Culex*. For the sake of clarity part of the graph has been repeated. Besides these species, numerous other species were caught during this part of the study. To decide whether data should be represented in a graph or not, a general rule was followed. A day of 24 hours can be divided in 24 classes of one hour, in 12 classes of two hours, and so on. Now the total number of specimens caught was to be not much less than the square number of the number of classes. Consequently the results (obtained in the twelve 24-hour sessions together) for 13 species and 1 genus could be represented in a graph.

Essentially diurnal species are: *Aedes scapularis*, *Psorophora ferox*, *Ps. albipes*. *Haemagogus capricornii*, *Culex* 2, *Limatus flavisetosus*, and *Wyeomyia* sp.

Essentially nocturnal species include *Culex portesi*, *C. spissipes*, and *C. virgultus*. *Aedes serratus* and *Culex* 1 are for about 80–85% diurnal, but maintain a small amount of activity during the nocturnal hours. *Ae. fulvus* is for about 75% nocturnal maintaining a small amount of activity during the diurnal hours. It should be observed that the three nocturnal species, and probably also *Ae.*

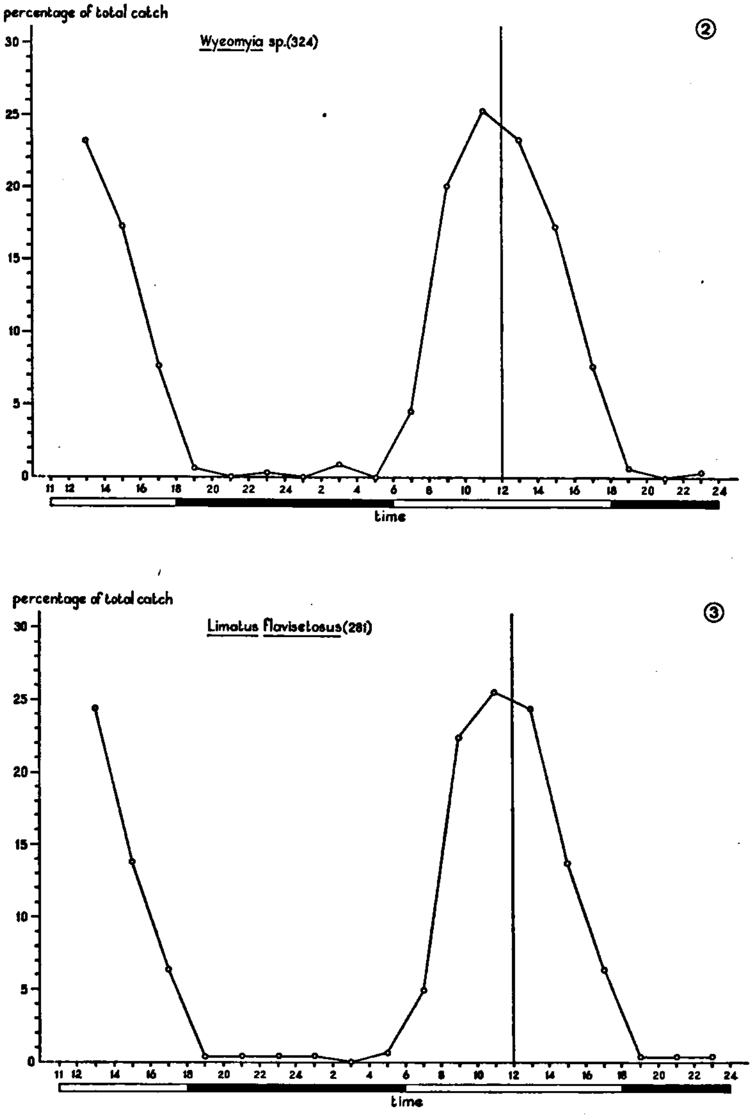


Fig. 2–3. Daily biting activity patterns for *Wyeomyia* sp. and *Limatus flavisetosus* in Troelikreek, Surinam. – Part of the graphs has been repeated, which is marked by a vertical line. Number of specimens per species between brackets.

fulvus have in fact a mixed nocturnal-crepuscular activity pattern.

The distinction between nocturnal and diurnal can be extended to a distinction of various activity patterns. There are, in general, two types of activity patterns, unimodal and bimodal. Several species show a unimodal pattern: *Limatus flavisetosus, Wyeomyia* sp. and *Haemagogus capricornii.* Other species show a bimodal activity pattern. These species are *Culex* 2, *C. portesi, C. spissipes, Culex* 1, *Ae. scapularis.*

Some species do not belong to either of both groups. It is possible that *Aedes fulvus* and *Culex virgultus* show a bimodal pattern but

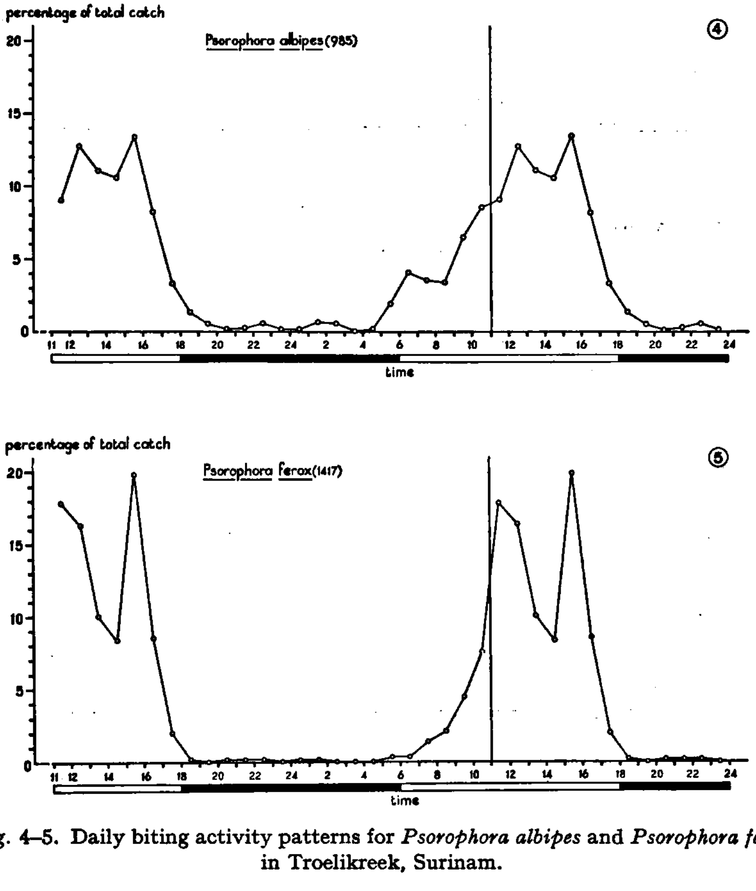
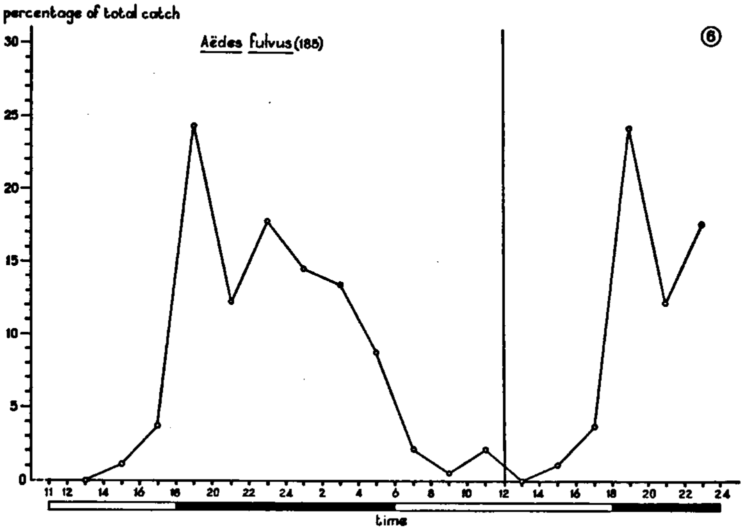


Fig. 4–5. Daily biting activity patterns for *Psorophora albipes* and *Psorophora ferox* in Troelikreek, Surinam.

this is not very distinct. *Ae. serratus* is active during the whole day, although biting activity tends to increase in the afternoon. This possibly points to a unimodal pattern. *Psorophora albipes* is most active in the afternoon. At that part of the day this species shows two slightly separate peaks; it is not clear if this is a unimodal or a bimodal pattern.



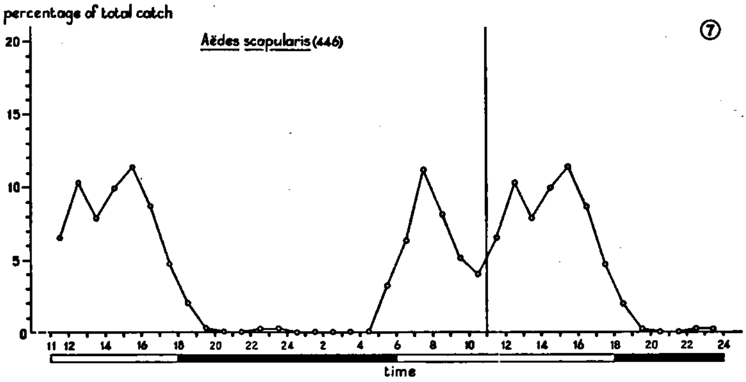


Fig. 6–7. Daily biting activity patterns for *Aedes fulvus* and *Aedes scapularis* in Troelikreek, Surinam.

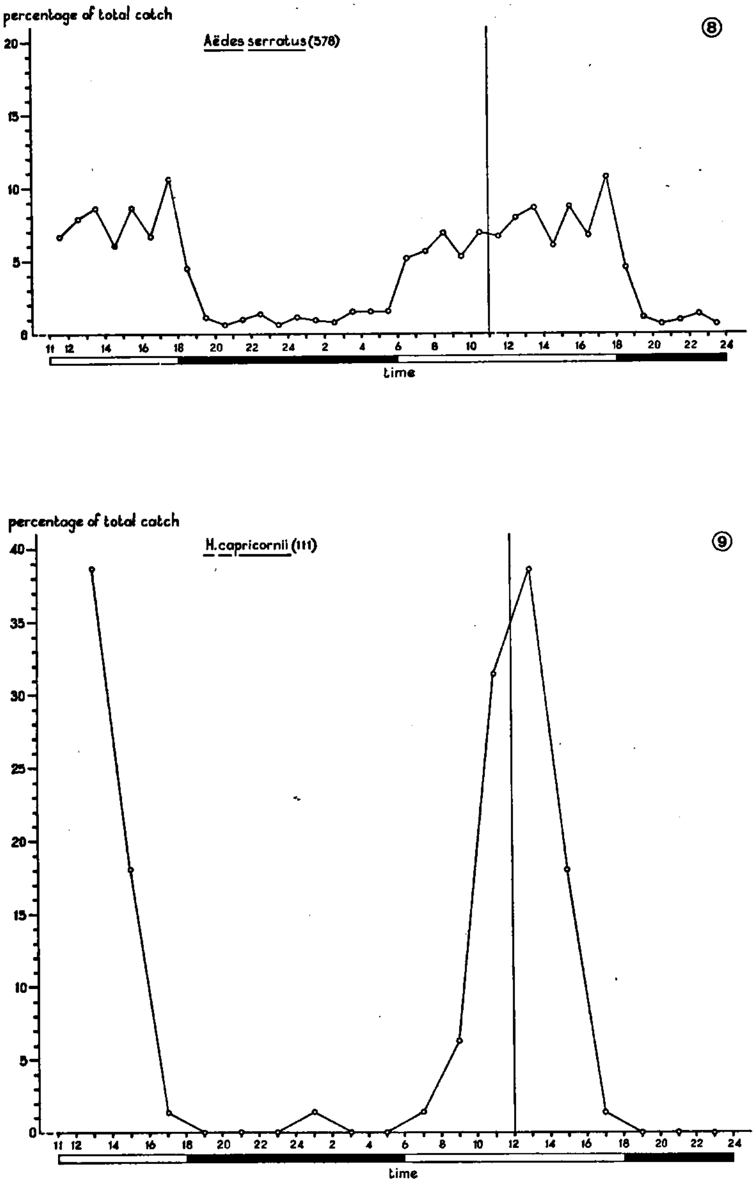
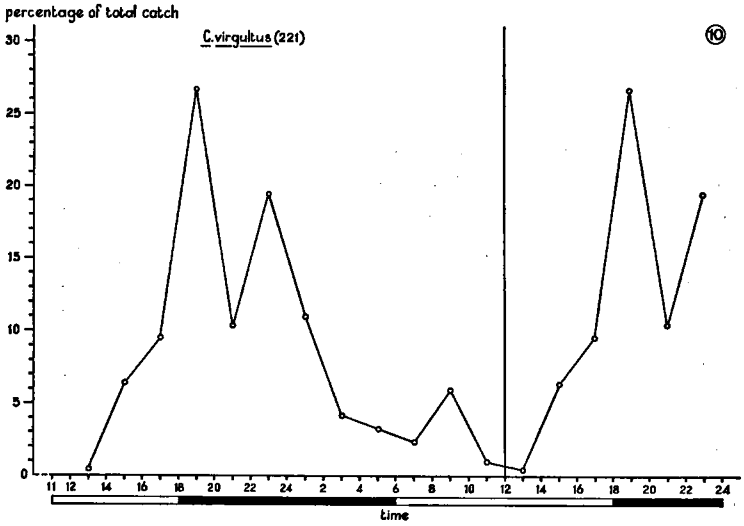


Fig. 8–9. Daily biting activity patterns for *Aedes serratus* and *Haemagogus capricornii* in Troelikreek, Surinam.



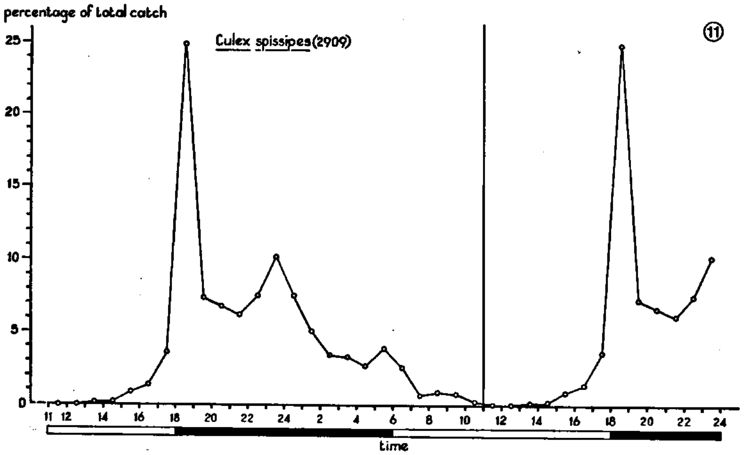


Fig. 10–11. Daily biting activity patterns for *Culex virgultus* and *Culex spissipes* in Troelikreek, Surinam.

Discussion

Comparison with data from literature

Few publications deal with the biting activity pattern of South-American mosquitoes. Activity patterns were found in the papers of Kumm & Novis (1938), Bates (1944), Forattini (1962–1966) and Aitken et al. (1968). Other papers present only tables or mention incidental observations (Bates 1944, 1945, 1949; Shannon 1931a, Trapido & Galindo 1957, Nielsen 1964, Forattini 1962, 1966).

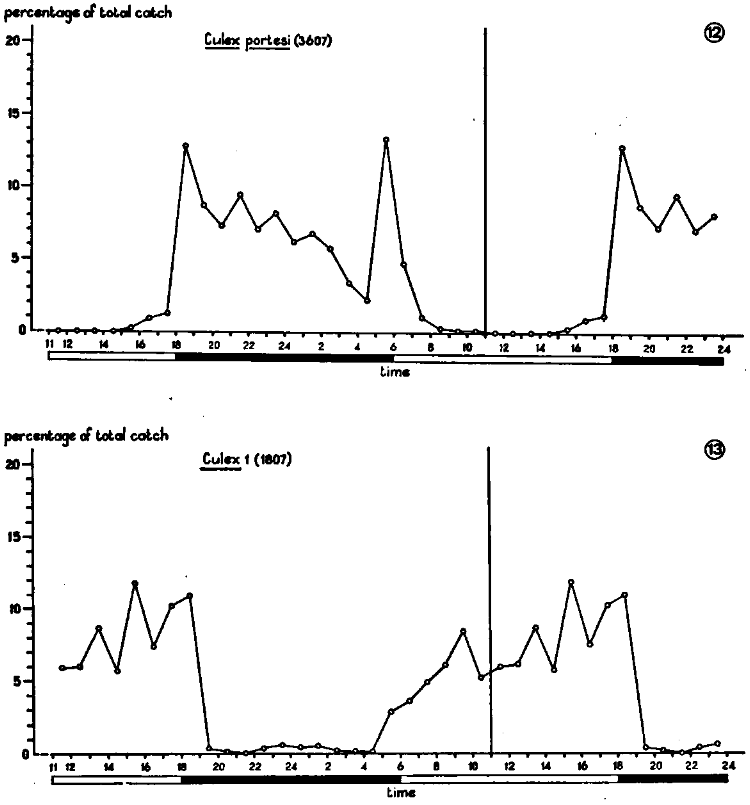


Fig. 12–13. Daily biting activity patterns for *Culex portesi* and *Culex* 1 in Troelikreek, Surinam.

Much more data are available for African and Asian mosquito species, especially the anophelines (several papers by HADDOW et al., BOORMAN 1960, SLOOFF 1964, etc). The data of TRAPIDO & GALINDO (1957) do not cover full day observations, but only observations during the midday hours from 9.00 h to 15.00 h; some other data are not reliable because the time intervals are too large, being mostly 3 or 4 hours.

Wyeomyia sp. (Fig. 2)

All *Wyeomyia* species seem to be essentially diurnal (FORATTINI 1966b). The activity pattern found in Trinidad (AITKEN et al. 1968) seems to be slightly bimodal. The pattern found in Surinam is unimodal. This may be due to the mixture of species in Surinam all slightly differing in main activity peak, while the pattern found in Trinidad concerns only one species (*W. medioalbipes*).

Limatus flavisetosus (Fig. 3)

As far as is known all *Limatus* species are diurnal (FORATTINI 1966b) which agrees with our data.

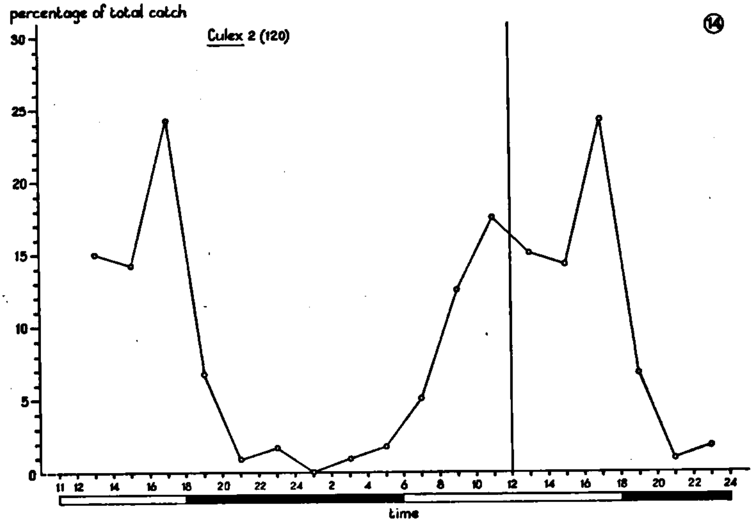


Fig. 14. Daily activity pattern for *Culex* 2 in Troelikreek, Surinam.

Psorophora ferox (Fig. 5)

Nearly all observations show that *Ps. ferox* is a typical diurnal species. However, two observations – FORATTINI (1966a) and NIELSEN (1944) – indicate that this species shows a crepuscular activity pattern and, besides, is active during nearly 24 hours except for a few hours around midnight. The other data, from Brazil (KUMM & NOVIS 1938; FORATTINI 1966), from Trinidad (AITKEN et al. 1968), from Panama (TRAPIDO & GALINDO 1957) and ours, show similar patterns for this species, although the hours with maximum activity vary slightly between the various observations. The morning peak occurs in Brazil from 9.00 h to 12.00 h, in Trinidad there is a slight peak from 8.00 h to 10.00 h and in Surinam at 11.30 h. In Panama no morning peak has been found. The afternoon peak occurs in Brazil at 16.00–18.00 h, in Trinidad at 13.00–17.00 h, in Surinam at 16.00 h, and in Panama at 14.00–15.00 h. In the last case, it is very well possible that the afternoon peak is at a later moment, because the catches stopped at 15.00 h.

Both observations (FORATTINI 1966a and NIELSEN 1964) which showed that this species is at least partly crepuscular-nocturnal, have one important characteristic in common which differs from all other observations. NIELSEN's data were from Florida which lies between lat. 25 and 30 N, while FORATTINI's were from Florianopolis, Brazil, which lies between lat. 25 and 30 S. All other data were collected just around the equator. This should suggest that the discrepancy between the observations might be caused by differences in daylength and duration of the twilight. In fact, this does not explain the nocturnal activity.

Aedes fulvus (Fig. 6)

Except for a few general observations from Brazil which agree with our data, nothing was known about the diel activity pattern of this species.

Aedes scapularis (Fig. 7)

The data from Brazil (FORATTINI 1966a), as compared with those from Surinam, reveal great differences. This species is active during the night in Brazil with some activity during the diurnal hours. In

Surinam it is only active during the diurnal hours. The observations in Brazil were from Florianopolis as were the observations on *Psorophora ferox*. The discrepancy between the data far *Ae. scapularis* from Brazil and from Surinam is exactly similar to that of *Ps. ferox*, hence, it should be explained in the same way for both species.

Aedes serratus (Fig. 8)

Observations both in Trinidad and in Surinam show a similar activity pattern. *Ae. serratus* is a diurnal species which in Surinam shows a slight increase in activity towards the afternoon, as is also mentioned by KUMM & NOVIS (1938) in Brazil. In Panama the mosquitoes seem to display their maximum activity in the morning, but whole day observations are needed to determine the activity pattern of this species.

Haemagogus capricornii (Fig. 9)

Although the data of various authors apply to different species of this genus, all observations show exactly the same biting activity pattern (KUMM & NOVIS 1938, BATES 1944, 1949, CAUSEY & SANTOS 1949, TRAPIDO & GALINDO 1957, ALVAREDO et al. quoted from FORATTINI 1966b, AITKEN et al. 1968; our observations). The activity pattern of the *Haemagogus* species is unimodal with a peak activity at midday.

Culex spissipes (Fig. 11)

A burst of activity at sunset has been observed in Trinidad as well as in Surinam. The peak at sunrise in Trinidad is completely absent in Surinam, but there is a slight peak about midnight. The incidental observations from Brazil seem to be intermediate between those from Trinidad and Surinam.

Culex portesi (Fig. 12)

Although very active during the night, this species shows a remarkable burst of activity just after sunset. This is very distinct in Trinidad, a little less in Surinam. The dramatic morning activity in Surinam does not occur in Trinidad. Nevertheless, both observations and also some incidental observations from Brazil agree fairly well.

Culex 2 (Fig. 14)

The incidental observations from Brazil seem to agree with our observations. Both show a mostly diurnal activity pattern which is possibly bimodal in Surinam.

All findings of the authors mentioned above were obtained by catches on human bait. There are indications that other methods will show other activity patterns. For instance, in some studies unbaited traps are used which means that the pattern found is not a biting activity pattern, but a flight activity pattern. Both kinds of activity are not necessarily similar. No references could be found concerning *Psorophora albipes* (Fig. 4), *Culex virgultus* (Fig. 10), and *Culex* 1 (Fig. 13).

Factors contributing to the biting activity pattern

There is circumstantial evidence that the biting activity in mosquitoes is controlled by an endogenous mechanism (GILLET et al. 1959, HADDOW 1961b, GILLETT 1961, CORBET 1963, 1966, LUMSDEN 1968, TAYLOR & JONES 1969). However, the expression of the biting activity is largely determined by other factors (RUDOLFS 1923, HADDOW 1961a, CLEMENTS 1963, CORBET 1966, LUMSDEN 1968).

One endogenous factor which, so far, has drawn the attention is age. There is evidence that the biting activity pattern of some insects like *Simulium* depends on age (CORBET 1966). LUMSDEN (1952) suggested that the bimodality of those patterns in mosquitoes could be due to the age-composition. For instance, the younger females bite early in the night, whereas the older females bite at the end of the night. Most authors, however, found no evidence that the biting activity of mosquitoes varied with age (GILLET 1961, GILLIES 1957, CORBET 1961b, GILLIES & WILKES, 1963, 1965).

In contrast to these observations are those of SENIOR WHITE (1953) and SAMARAWICKRAMA (1967, 1968) on respectively *Anopheles aquasalis* and *Culex pipiens fatigans*. They found that the biting activity pattern did indeed vary with age. However, these variations appeared to be too small and too gradual to cause any bimodality.

Preliminary observations in Surinam on *C. spissipes* agreed with those from GILLIES and others. Initial observations on *Aedes scapularis* and *Psorophora albipes*, on the contrary, tended to agree slightly with those of SENIOR WHITE and SAMARAWICKRAMA.

The cyclical nature of the biting activity pattern may be endogenous, but, besides possible influence of age on the activity pattern, other important components, contributing to the biting curve, are all exogenous (CORBET 1966, LUMSDEN 1968). BATES (1944, 1949) and HADDOW (1945) showed a close relationship between the biting cycle of some diurnal mosquito species and the daily variations in temperature and relative humidity. These species, *Haemagogus* and *Eretmapodites*, are bright-coloured. One of BATES' main ideas is that the bright colours of these – specifically diurnal – mosquitoes are an adaptation to the drier, lighter, and warmer conditions during midday hours as compared to the nocturnal hours, particularly in the canopy. Indeed, the bright-coloured species *Limatus flavisetosus* and *Wyeomyia* sp. (both ground-dwelling) and *Sabethus chloropterus* (canopy-frequenting) show also an activity pattern similar to that of *Haemagogus*. Obviously, conclusive evidence for BATES' ideas is hard to obtain.

It is known that temperature affects the pattern by inhibiting or activating the biting activity (RUDOLFS 1923, MATTINGLY 1969).

The nocturnal species with a bimodal activity pattern show activity peaks just after sunset and just after sunrise. Studies by CORBET (1966), HADDOW (1961a & b), and others have shown that light intensity is the time-cue ("Zeitgeber," ASCHOFF 1960, 1966) for oviposition cycles as well as biting cycles (LUMSDEN 1968). This has also been demonstrated by GILLET (1961) who found the feeding behaviour to be cyclical with light as the time-cue. In comparison to the evening peak, the morning activity starts later than light intensity would lead to expect. HADDOW (1964) suggests that the sunrise peak is somewhat delayed, if the light intensity is indeed the time-cue for the onset of biting activity. This may be due to the temperature which is lowest in the early morning hours.

The only species in Surinam with a biting activity pattern like the one HADDOW (1964) tries to explain, is *Culex portesi*. The morning peak of *C. portesi* is, indeed, delayed for about half an hour compared to the evening peak (DE KRUIJF, in press). This is clearly not the case for the other species with a bimodal activity pattern found in Surinam.

In addition to the factors mentioned above, the biting activity cycles of some species vary with the season as well as with the vertical distribution in forests (HADDOW 1961b, MATTINGLY 1969).

COLLESS (1957) gives some remarkable data concerning biting curves. He demonstrated that the catching curve of *Culex annulus* has a peak activity at sunset, then the biting activity gradually decreases till sunrise, after which it ceases. This curve could be explained as a depletion curve. This means that the biting population in the vicinity of the bait decreases as more mosquitoes become fed. As for the mosquito species in Surinam only the first part of the biting activity curve of *C. portesi* and the curve for *C. spissipes* answer to the description above. To what extent this explanation could contribute to a better understanding of the biting activity curves described in this chapter, is not known yet.

SUMMARY

From February 1968 – July 1968 a number of 24-hour catches on human bait in Troelikreek, Surinam, have been carried out in order to determine the daily activity patterns of several mosquito species. The results of thirteen species (Figs. 2–14) are given and compared with the patterns known from literature. The patterns of most mosquito species appeared to be essentially similar to those found in Brazil, Colombia, Panama, and Trinidad. Two species, *Aedes scapularis* and *Psorophora ferox*, showed a distinctly different pattern in the tropics from that in more temperate zones. Factors contributing to the biting activity are briefly discussed.

II. THE VERTICAL DISTRIBUTION IN FORESTS

INTRODUCTION

Studies on yellow fever in forests showed that vectors of this virus are typical canopy-dwelling mosquitoes (BUGHER et al. 1944; BATES & ROCA-GARCIA 1946, and many others). Further research in various parts of the world revealed that many canopy-dwelling mosquitoes play an important rôle in the transmission of viruses (LUMSDEN 1955, JONKERS et al. 1968a and b). Although most yellow fever vectors have been thoroughly studied as to their vertical distribution in forests in South America, data on other mosquito species appeared to be scarce. Nearly all known data of mosquito species on this subject are reviewed by FORATTINI (1962, 1966a and b). AITKEN (1967) and AITKEN et al. (1968) added new facts for many species in Trinidad.

Besides *Haemagogus*, *Sabethes* and a few *Anopheles* species, the vectors of yellow fever or malaria, only few other species are discussed regularly in papers on the vertical distribution in forests in South America. Moreover, the data on the commonly occurring species in the literature were rather controversial. For example CAUSEY & SANTOS (1944) caught 99.5% of the total catch of *Mansonia venezuelensis* at groundlevel but DEANE et al. (quoted in FORATTINI 1966b) caught only 52.4% of this species at groundlevel.

As yet no data on the vertical distribution of Surinam mosquitoes are known except some incidental ones on *Anopheles darlingi* (BRUIJNING 1952).

AREAS

Catches on human bait and with animal baited traps were carried out in three areas one of which was described previously: Troelikreek (DE KRUIJF 1970; see also p. 5). A description of both the others – Forest Leiding 16A and Matta – will follow below.

Forest Leiding 16A (Fig. 1)
This forest is situated in the coastal area of Surinam, about 20 km West-South-West of Paramaribo. The area is provided with drainage canals which are in contact with the Saramacca river. A large part of this area is cultivated – many rice fields – but there are still many residual forests. One of these forests, located along one of the drainage canals – Leiding 16A – was chosen as a study area. Hereafter this forest will be referred to as 16A.

According to the description of LINDEMAN & MOOLENAAR (1959), 16A belongs to swamp forest type A, although some characteristics correspond with type B. The classification depends mainly on the species distribution of the trees. Another important characteristic of swamp forest type A is that large parts are inundated during the wet seasons. Despite the drainage canals this applied to 16A. The length of the forest – along the canal – was about 500 m, the width about 250 m. The entrance was halfway the drainage canal. We penetrated approximately 100 m into the forest. The catching station was located at a shaded place intermediate between a glade and the dense parts of the undergrowth. In the vicinity of this location all traps were hung on trees or large branches.

The average height of the canopy was about 30–35 m. Most trees did not exceed 35 m. A platform was constructed in a small tree near the catching area at a height of about 6 m in the understory. In August 1968, the owner of the forest decided to cut it down which forced us to stop our observations in this area.

Matta (Fig. 1)
The essential characteristics of this forest are similar to those of Troelikreek. In the Arowak village of Matta, the catches were carried out along the creek at a wash-place of the inhabitants. There the creek formed a small pool, with a glade at one bank. During the catches on human bait the catchers were sitting in the bush near the edge of the open place and near the creek. A platform was constructed in a small tree, a few meters from the creek at a height of 7 m. The average canopy of this forest was about 25–35 m. The traps were hung in the bush adjacent to this glade.

For relevant information on the climate in forests in Surinam the reader is referred to SCHULZ' (1960) extensive work.

METHODS

A few observations were carried out on human bait, but most observations were done with animal-baited traps. The technique of catching on human bait is described on p. 5; some additional notes and a description of the animal-baited traps follow below.

Simple platforms were constructed to carry out stratification observations on human bait. The height of the platforms varied: in 16A the height of the platform was 6.4 m in Matta 7.0 m and in Troelikreek 15.0 m. During the series of morning catches – in 16A – we simultaneously carried out several catches on the platform with one catcher. These were compared with those of one catcher seated just at the foot of the tree with the platform. Part of the two 24-hour sessions in this area too could be used for data on the vertical distribution. These observations on stratification were made during the dry season.

In Troelikreek, only during three 24-hour sessions (DE KRUIJF 1970), were enough catchers available to carry out catches on the platform simultaneously with those at groundlevel. One catcher was seated on the platform, and two catchers at groundlevel at a distance of at least 50 m from the tree with the platform. These catches were carried out during a wet season.

In Matta most morning and evening catches were carried out simultaneously with two catchers at groundlevel and two catchers on the platform. Most catches were carried out during a dry season, only a few during a wet season. The catchers on groundlevel were seated within a distance of 10 m from the platform.

The evening catches in Matta were carried out in the same way as the morning catches; they lasted from 17.00 h till 20.00 h.

Catches with animal baited traps were all carried out with the Trinidad no. 10 traps. For a detailed description of this trap, see WORTH & JONKERS (1962).

The no. 10 traps were always baited with either mice or rats. After the bait had been placed, the traps were closed by cotton mosquito netting and emptied every 24 hours with an aspirator.

In 16A all traps were baited with the same bait. In Matta, on the contrary, the bait was moved each day to another trap, preferably to a trap which had been baited with another kind of animal. With these changes, possible differences between the locations of the traps were excluded as far as possible. The traps were operated for about 24 hours, from about 10.00 a.m. to the next morning about the same time. Hereafter such a period will be referred to as a TRAPRUN.

Because of the shortage of rats we were sometimes forced to use only mice in 16A and in Matta, or to use only one ratbaited trap. This partly explains the rather great differences between the numbers of trapruns for various heights, especially in 16A (see Table 1).

The heights of the traps were classified into three groups:

1. groundlevel: below 1.50 m;
2. middle level: between 6.00 and 10.00 m;
3. upperlevel: above 14.00 m.

In 16A the heights of the traps were 1.0 m, 6.0 m and 9.4 m for mouse-baited traps and 1.0 m and 14.0 m for rat-baited traps. In Matta the heights were 1.0 m, 6.6 m, 7.0 m, 9.4 m, 14.7 m and 14.8 m. The number of trapruns at middle level is larger than at the other levels, because most traps were hung between 6.0 m and 10.0 m. The differences in numbers of trapruns are thus partly explained by the shortage of rats and partly by the varying numbers of traps at different heights.

The observations in Matta and 16A with the animal-baited traps were carried out partly during a wet season and partly during a dry season.

Table 1 shows the number of trapruns by place and by bait, whereas the catches on human bait are represented by the number of man-hours.

TABLE 1

NUMBERS OF TRAPRUNS AND MANHOURS IN 16A, TROELIKREEK AND MATTA

Place	Bait	ground-level	middle level	upper level	total number of trapruns	total number of manhours
16A	human	48	48			96
	rats	52		20	72	
	mice	122	119		241	
Matta	human	32	32			64
	rats	56	42	31	129	
	mice	71	107	56	234	
Troelikreek	human	144		72		216
Totals					676	376

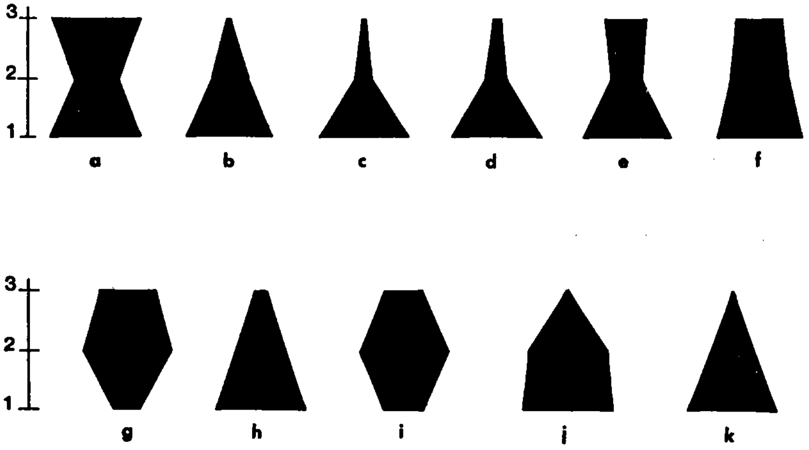


Fig. 15. The vertical distribution in forests at three levels of various mosquito species as indicated by several series of observations. – The graphs are qualitative. 1 = groundlevel (± 1 m); 2 = middle level (5–10 m); 3 = upper level (± 15 m).

RESULTS

In total five series of catches have been made, the results of which are compiled in Table 2. At least 35 species were represented once in these five series (DE KRUIJF 1970). However, the species of which less than 10 individuals were caught in each of two series, were not included in the table. An exception has been made, however, for *Haemagogus capricornii* and *Sabethes chloropterus* because of their importance to the transmission of the jungle yellow fever virus in South America. Samples containing less than 10 individuals have been omitted too. The vertical distribution suggested by such a small sample is not feasible especially when compared with a vertical distribution including many specimens. The data are tabulated in such a way that all results for one species can be compared. Although various differences, such as differences in daytime, length of the catching period, season, method and area have to be taken into account, it is possible to get a general impression of the vertical distribution of a species by comparing the suggested distribution in each series.

A short commentary will be given for each species represented in Table 2. In Fig. 15 the results are converted into a simple graph showing the distribution for three levels in forests. It is impossible to calculate exactly the proportions between the three levels based on various series. Therefore the graphs represent only the most probable vertical distribution of the various species. For some species the data are too controversial to suggest any kind of distribution. The species are listed alphabetically.

Aedes fulvus

In Troelikreek this species is equally distributed between upperlevel and groundlevel, whereas it is more ground-dwelling in 16A. Therefore the vertical distribution seems best represented by Fig. 15a.

Aedes scapularis

All series show that *Ae. scapularis* is ground-dwelling, although a

TABLE 2

FIVE SERIES OF OBSERVATIONS ON THE VERTICAL DISTRIBUTION OF 15 MOSQUITO SPECIES

Troelikreek h.b. = human bait catches in Troelikreek
16A tr. = catches with animal-baited traps in 16A
16A h.b. = human bait catches in 16A
Matta tr. = catches with animal-baited traps in Matta
Matta h.b. = human bait catches in Matta

If no specimens of a species have been caught during one or more series, then these series have been omitted.

Species series	total number of mos-quitoes	number of mosquitoes per man per 10 hours or per 12 trapruns			percentages		
		0– 1 m	5– 10 m	14– 15 m	0– 1 m	5– 10 m	14– 15 m
Ae. fulvus							
Troelikreek h.b.	27	1.4	—	1.7	45	—	55
16A tr.	55	5.2	3.8	—	58	42	—
16A h.b.	91	15.0	7.7	—	70	30	—
Ae. scapularis							
Troelikreek h.b.	30	2.5	—	0	120	—	0
16A tr.	45	3.9	2.4	—	62	38	—
16A h.b.	27	5.5	1.2	—	82	18	—
Ae. serratus							
Troelikreek	87	6.9	—	0.7	91	—	9
16A tr.	273	21.5	11.7	—	65	35	—
16A h.b.	59	13.7	1.0	—	93	7	—
Matta h.b.	79	28.5	11	—	96	4	—
An. aquasalis							
16A tr.	100	4.4	27.3	—	14	86	—
16A h.b.	1.554	206.0	182.5	—	53	47	—
Culex x (crybda)							
Troelikreek h.b.	456	35.2	—	5.7	87	—	13
16A tr.	177	22.4	2.8	—	89	11	—
Matta tr.	127	5.9	11.5	0.0	34	66	0
Matta h.b.	120	41.2	3.7	—	92	8	—
C. portesi							
Troelikreek h.b.	869	48.8	—	47.2	51	—	49

Table 2 (*continued*)

Species series	total number of mos- quitoes	number of mosquitoes per man per 10 hours or per 12 trapruns			percentages		
		0– 1 m	5– 10 m	14– 15 m	0– 1 m	5– 10 m	14– 15 m
Matta tr.	12.828	1678.5	209.6	334.8	76	9	15
Matta h.b.	4.255	984.0	6476	–	60	40	–
C. spissipes							
Troelikreek h.b.	812	57.5	–	20.3	74	–	26
Matta tr.	491	28.5	26.0	27.5	35	32	33
Matta h.b.	807	175.9	126.7	–	58	42	–
C. virgultus							
Troelikreek h.b.	151	5.2	–	14.9	26	–	74
Matta tr.	46	1.0	5.0	2.0	12	63	25
Matta h.b.	27	3.0	7.1	–	30	70	–
H. capricornii							
Troelikreek h.b.	65	1.4	–	8.0	15	–	85
M. titillans							
16A tr.	872	74.9	71.8	–	51	49	–
16A h.b.	1.172	193.7	99.2	–	66	34	–
M. venezuelensis							
16A tr.	199	18.0	–	15.0	55	–	45
16A h.b.	282	45.5	25.0	–	64	36	–
Matta tr.	195	20.4	8.5	4.9	60	25	15
Matta h.b.	1.324	311.7	184.9	–	63	37	–
Ps. albipes							
Troelikreek h.b.	250	13.8	–	14.0	50	–	50
16A tr.	119	7.3	21.5	–	25	75	–
16A h.b.	44	4.0	7.0	–	36	64	–
Ps. ferox							
Troelikreek h.b.	162	12.7	–	1.5	89	–	11
16A tr.	61	5.3	4.7	–	53	47	–
S. chloropterus							
Troelikreek h.b.	58	1.9	–	5.9	24	–	76
Wyeomyia sp.							
Troelikreek h.b.	150	10.6	–	3.9	73	–	27
16A tr.	36	3.8	1.8	–	68	32	–

few mosquitoes prefer a higher level. Fig. 15b shows the most probable vertical distribution.

Aedes serratus

Three series out of four indicate that *Ae. serratus* is a ground-dwelling species. In the fourth series this preference is less striking. Fig. 15c is the proposed vertical distribution.

Anopheles aquasalis

The vertical distribution as shown by two series of observations in 16A varies too much to indicate a general pattern. No figures adequately represent both results.

Culex 1

Three series of observations show that *Culex* 1 is ground-dwelling; the fourth series indicates that *Culex* 1 is quite scarce in the upper strata of the forest. Therefore the graphical representation in Fig. 15d seems most appropriate.

Culex portesi

The first series shows an equal distribution between upperlevel and groundlevel; the second series shows a slight preference for groundlevel compared with middle level; the third series shows an equal vertical distribution between middle level and upperlevel, but the preference for groundlevel is quite strong. The result of these figures would seem to be the graphical representation of Fig. 15e. In the middle level and upperlevel the mosquitoes are nearly equally distributed, but the number at groundlevel is higher than on either level.

Culex spissipes

For this species the observations suggest a more equal distribution among the three levels than for *C. portesi*, although the first series indicates a preference for groundlevel. Fig. 15f seems to be the most probable vertical distribution.

Culex virgultus

All series indicate that this species prefers middle level or maybe even a higher level. The vertical distribution as represented in Fig. 15g seems most probable.

Haemagogus capricornii

According to the single series this species strongly prefers the higher strata of the forests.

Mansonia titillans

All series indicate that this species shows a slight preference for groundlevel above middle level.

Mansonia venezuelensis

A slight preference for the lower levels is indicated by all observations. The graphical Figure 15h seems best to represent the vertical distribution.

Psorophora albipes

The observations show an equal distribution between the upperlevel and lower level, but a stronger preference for middle level. Therefore Fig. 15i seems to be the most probable representation of the vertical distribution.

Psorophora ferox

An equal distribution between groundlevel and middle level can be observed and also a preference for groundlevel above upperlevel. Fig. 15j is the most probable vertical distribution.

Sabethes chloropterus

A species which inhabits the upperlevel according to the single observation.

Wyeomyia sp.

Both observations show a preference for groundlevel. Fig. 15k shows the most probable vertical distribution.

Comparison of the data obtained by catches on human bait and catches with animal-baited traps, shows the percentages on groundlevel to be generally lower for the traps than for the human bait catches. The catches with animal-baited traps suggest a more equal distribution among the three levels than the series with human bait.

DISCUSSION

The scattered data in the literature seem to be rather inconsistent. (FORATTINI 1962, 1966a & b; AITKEN 1967; AITKEN e.a. 1968).

Our results of the various series of observations too are rather variable. For example *Culex* 1 (*crybda*) has been caught twice as much on middle level than on ground level but in three other series this mosquito has been caught six to eleven times more often on groundlevel than on both other levels.

1. *Seasonal variations in vertical distribution*

This means that in the wet and dry seasons a mosquito species shows a different vertical distribution. (CAUSEY & SANTOS 1949; BATES 1944; FORATTINI et al. 1968). However, BATES (1944) reports that groundlevel catches of *Haemagogus spegazzini* are greater during the dry season, whereas CAUSEY & SANTOS 1949) found the same species preferring groundlevel in the forest during the wet season. Because our series were carried out during various seasons this might be one of the causes of difference between the results of some series.

2. *Daily vertical migrations*

This phenomenon has been clearly shown by HADDOW (1961) who found great differences between the vertical distribution by day and by night for an African mosquito species. These vertical movements are known to occur also in American species (NIELSEN & NIELSEN 1953; SNOW 1955; FORATTINI et al. 1968). Because most human bait catches are carried out during only a few hours of the day, while all trap catches lasted 24 hours, it is possible that this caused the discrepancies mentioned earlier for some species.

3. *Incidental vertical migrations*

Some authors (HADDOW 1954) observed that some mosquito species followed the catchers when they climbed to the platforms. In our observations this phenomenon was noticed too, but the number of such specimens seemed small compared with the total catch.

4. *Environmental factors*

The development of a certain vertical distribution will depend on several environmental factors like micro-climate, the presence of suitable hosts and the vegetation. Thus vertical distribution may vary strongly in different regions. For some mosquito species however, a general tendency in their vertical distribution can be observed. Species such as *Haemagogus capricornii* and *Sabethes chloropterus* are always canopy-dwelling, others such as the *Mansonia* and *Culex* species have a more equal distribution. *Aedes* and *Wyeomyia* species in most cases show a strong preference for the lower levels in the forests.

SUMMARY

To study the vertical distribution of mosquitoes in Surinam five series of catches on various heights – on human bait and with animal baited traps – were carried out. In total more than 35 species were caught at least once but only 15 species are represented here. For most species a graphical representation of the vertical distribution is given based on two or more series.

III. SEASONAL DISTRIBUTION AND ABUNDANCE OF SOME POPULATIONS

INTRODUCTION

The importance of studies on seasonal variations of mosquito populations has been clearly shown by KUMM (1950) and many others (e.g. MUIRHEAD-THOMSON 1968, MATTINGLY 1969). In his review KUMM emphasized that the incidence of sylvan yellow fever in Brasil and Colombia showed a similar seasonal distribution as *Haemagogus* species, the known vector of jungle yellow fever virus, with a delay of about a month. From the U.S. many studies are known dealing with arbovirus epidemiology and weather conditions or seasonal variations in mosquito populations. One of these (HAYES & HESS 1964) demonstrated the relationship between weather conditions and outbreak of Eastern Equine Encephalitis in Massachusetts.

Population density fluctuations of mosquitoes depend on many factors but the presence of water is essential. The immature stages of mosquitoes are aquatic and, hence, no mosquitoes can breed without water. The distribution of rains throughout the year is the main criterion to separate the seasons in the tropics.

In the course of a study on vectors of malaria in Surinam GEIJSKES (1946) determined the seasonal distribution of three important *Anophelinae*; data on other mosquito species, however, notably Culicini, in Surinam were not available.

The author will describe here the seasonal distribution of various culicine mosquitoes (see also DE KRUIJF 1970).

METHODS

From June 1967 till August 1968, 156 catches on human bait were made, all in the same area, 16A. The catches always started between 8.00 and 10.00 a.m. and lasted not longer than 11.00 a.m.

The mosquito species concerned were all diurnal (see Chapter I). Because of technical problems and the variation in activity pattern of the various species, no mosquitoes were caught in the peak hours of their biting activity as is advised for such studies (HADDOW 1954; SOUTHWOOD 1966). Therefore, the catches were strongly restricted to a few morning hours, thus in the same biting activity period. When possible we carried out three catches a week with three catchers – sometimes two. During the first months the duration of the catches was half an hour; from January it could be extended to one hour. The contents of the tubes were identified separately, and recorded per catcher. For every species the total number per catch was converted to the number of specimens per man hour. Then the mean number of specimens per man hour per month was calculated and used for the description of the seasonal distribution.

It should be noted that sampling by way of baited catches was selective: only biting females in search of a bloodmeal were captured. Though several authors (SOUTHWOOD 1966; MUIRHEAD-THOMSON 1968) indicate that selective sampling can give a false picture of the population fluctuations, it seems to me that the seasonal distribution found with the baited catches reflects similar phenomena in the entire population (DE KRUIJF 1970).

The daily rainfall was measured at a station less than 2 km from the areas studied. Thanks are due to the Meteorological Department of Surinam for kindly supplying me with the rainfall figures.

RESULTS

During the series of morning catches in 16A more than 60 species were captured at least once. However, few species were sufficiently abundant to get a clear picture of the seasonal distribution. For six species and one genus the results are shown in Figures 16–22. The rainfall is expressed as the total amount of rain per month in mm, the mosquito population as the average per man hour per month.

In addition to the rainfall figures, Table 3 shows the number of days with rain.

The rainfall distribution shows a dry period from August to October with the exception of September which yielded a relatively high

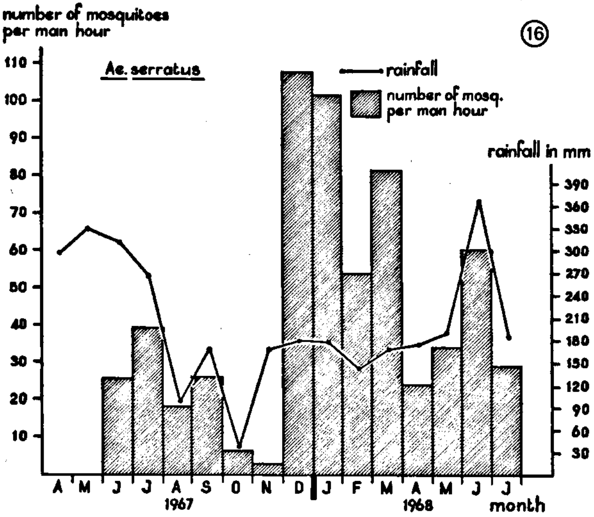


Fig. 16. The seasonal distribution of *Aedes serratus*. – Total number of specimens 14,719.

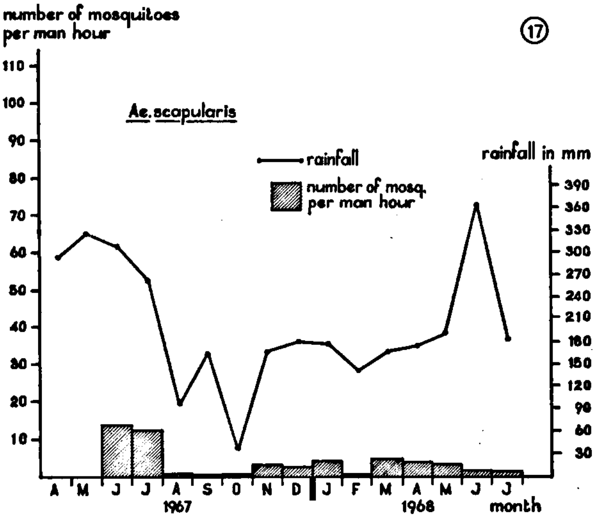


Fig. 17. The seasonal distribution of *Aedes scapularis*. – Total number of specimens 1,256.

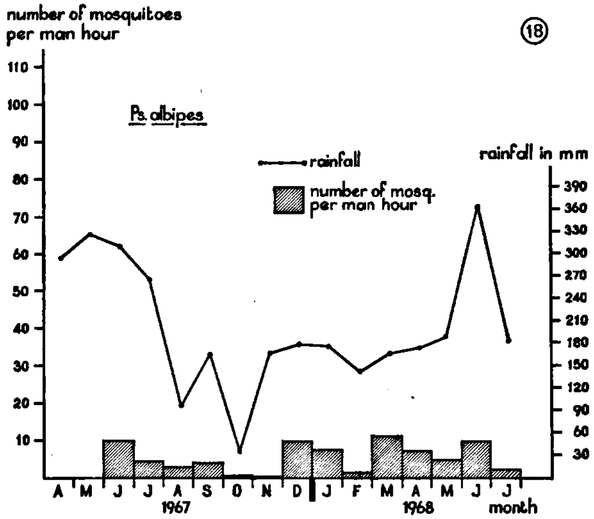


Fig. 18. The seasonal distribution of *Psorophora albipes*. – Total number of specimens 1,699.

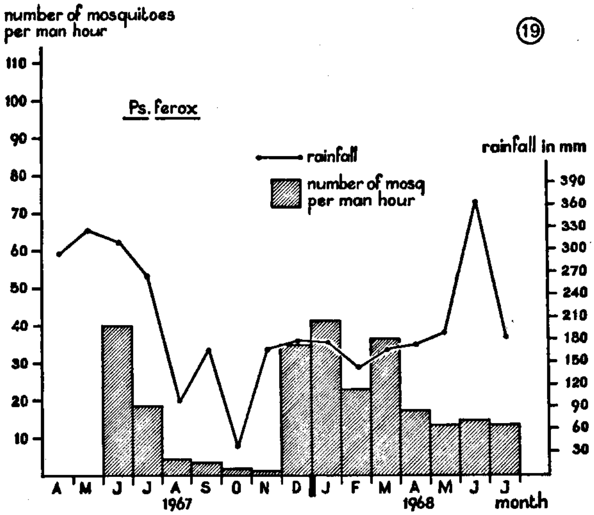


Fig. 19. The seasonal distribution of *Psorophora ferox*. – Total number of specimens 6,193.

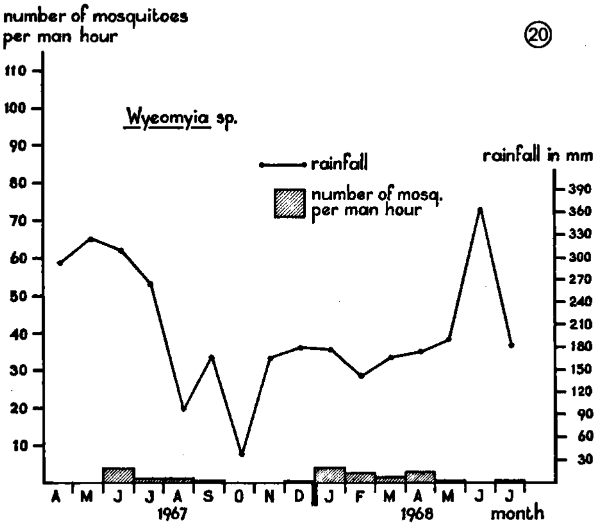


Fig. 20. The seasonal distribution of *Wyeomyia* sp. – Total number of specimens 468.

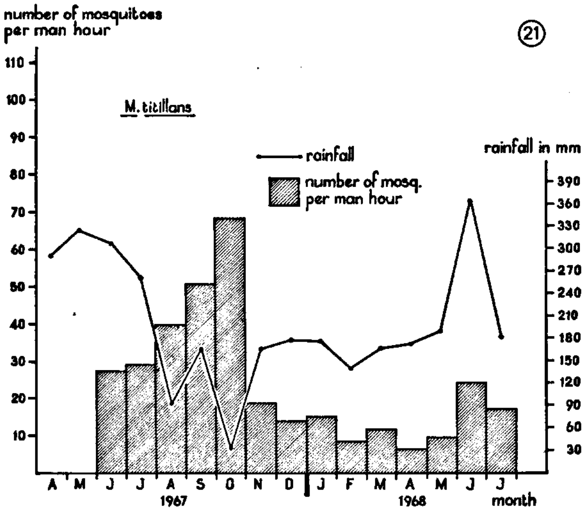


Fig. 21. The seasonal distribution of *Mansonia titillans*. – Total number of specimens 6 574.

rainfall peak. Although September, November and February show a moderate rainfall, this appeared to have been caused by heavy rainfall in a few days (see also Table 3). This rainfall was quite above normal according to the Meteorological Institute in Surinam. Both table and graph suggest three wet periods (May–July, December–

TABLE 3

NUMBERS AND PERCENTAGES OF RAINY DAYS PER MONTH IN 16A

Month	*rainy days*	%	*Month*	*rainy days*	%
April (1967)	14	47	December	18	58
May	25	81	January (1968)	21	68
June	23	77	February	11	38
July	17	55	March	15	49
August	12	39	April	13	43
September	7	33	May	16	52
October	7	22	June	25	83
November	8	27	July	16	52

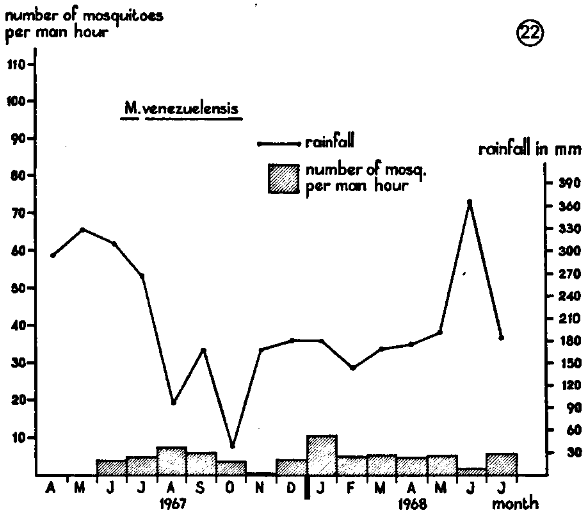


Fig. 22. The seasonal distribution of *Mansonia venezuelensis*. Total number of specimens 1,698.

January and May–July) and two dry periods (August–November and February–April) as was also found in another part of Surinam (GEIJSKES 1946). It seems that April 1967 and March 1968 are in fact just in between a wet and a dry month. Thus during the period of observation, although not clearly, dry and wet periods could be distinguished.

Aedes serratus

This species was by far the most abundant in 16A. *Aedes* species are mostly rainpool breeders. The fluctuations in the population agree exactly with the rainfall variation. A heavy rain in September is promptly followed by an increase of the *Aedes serratus* population. An increase of rain at the end of November and in December is followed by an explosion of this species. In February, with relatively few rainy days, a drop of the population is observed; this is also true in April. Thus the population density of this species appears to depend directly on rainfall.

Aedes scapularis

A rainpoolbreeder like *Ae. serratus,* this species also follows the rainfall pattern. The obvious increases or decreases shown for *Ae. serratus* cannot be accounted for in this species, probably because the low population density may obscure rises or falls in the same. Nevertheless the low densities in the dry season and in February are quite distinct.

Psorophora albipes

Though present in the beginning of the dry season *Ps. albipes* appeared to show the same characteristics as the two *Aedes* species. The population density is positively related to rainfall.

Psorophora ferox

Until April 1968 this species follows exactly the same pattern as the preceding species. However, instead of an increase in May–July (which might be expected compared with *Aedes serratus*), this species shows a stable density level. In spite of this *Ps. ferox* is positively related to rainfall.

Wyeomyia

Most *Wyeomyia* species are container breeders. The relation with rainfall shown in the graph was to be expected. Containers normally need a regular supply of rainwater. The low density did not permit more detailed examination.

Mansonia titillans

The increasing density towards and in the dry season, followed by a sharp drop in November, yields quite another pattern. Though hard to detect, this species follows the rainfall pattern from February till July. The population density in November–January is much lower than in the preceding months and is also quite steady. This pattern may suggest a change from a species related negatively to rainfall to a species positively related to rainfall. This is in no way confirmed by other observations.

Mansonia venezuelensis

A slight rise of the population density in August, a drop in November, and again a slight rise in January are the main characteristics of the distribution of this species. They indicate a relation between density and rainfall which, however, is weak.

DISCUSSION

The characteristics of the habitat of a species are reflected in the seasonal distribution.

Aedes serratus is a groundpool breeder (FORATTINI 1966b; AITKEN et al. 1968). With the onset of the rains innumerable temporary groundpools are created offering many breeding places. When the wet season progresses the forest floor will be partly inundated and many small groundpools will change into large pools. As is generally accepted the immature stages of many rainpool breeders are drowned when the rainpools become too large. The population density of *Ae. serratus* does not rise above the number in December but decreases after that month. Though there are many still unknown factors that may influence the population density, no doubt one of them is the decreasing number of suitable rainpools as the wet season progresses. DE KRUIJF, WOODALL & TANG demonstrated that rainpool-breeders were related to accumulated rainfall. After reaching a maximum, population densities decreased with increasing accumulated rainfall, thus indicating that prolonged rainfall did not offer more suitable ovipositing sites but instead less. This is also true for *Psorophora ferox*. It may be expected for *Ae. scapularis* and *Ps. albipes* but the low densities only suggest this explanation.

Wyeomyia's are mostly container breeders (FORATTINI 1966b, BRUYNING 1959). Populations of such species show a pattern similar to that of rainpool breeders. Because the container habitats generally dry up more slowly than rainpools, the population fluctuations will be more gradual than in rainpool breeders. However, this is not supported by other observations. Besides, the density is too low to permit a detailed examination.

The two *Mansonia* species are open swamp breeders (FORATTINI 1966b, AITKEN et al. 1968). *M. titillans* females glue their eggs in small masses to the underside of the leaves of floating plants (BATES 1949, FORATTINI 1966a, MATTINGLY 1969). Because of the acrobatic act involved in depositing their eggs, it seems reasonable to suppose a strong direct influence of rain on ovipositing: the mosquitoes will be washed off the leaves. This seems one of the main reasons that the *M. titillans* population is quite low during the wet seasons and may explain the increase in the first dry season. The population increase depends on the available swamps and these diminish towards the end of the dry season in November. Consequently a drop in the population density occurs. Thus population density of *M. titillans* depends on rain but apparently in a reverse way.

M. venezuelensis shows a similar pattern although not as clear as *M. titillans* probably because of the lower population density.

A comparison for *Ae. serratus* between results from Trinidad (AITKEN et al. 1968) and those of the present author shows an exactly similar pattern for this species.

The Trinidad results for *M. venezuelensis* show a slight difference. In Trinidad during the wet season the population density seems to decrease earlier than in Surinam. However, this may be caused by abnormally high rainfall in September so that the swamps contained more and longer lasting water than in other years. Comparison of

Wyeomyia medioalbipes with our mixture of *Wyeomyia* species shows an essential difference. In Trinidad it is most commonly encountered during the drier portions of the year while in Surinam the species is nearly absent in the same periods. No reasonable explanation for this discrepancy can be given.

In his discussion on the seasonal distribution of three *Anopheles* species GEIJSKES (1946) showed that *Anopheles aquasalis* and *A. pessoai* are most abundant during the wet season and that *A. oswaldoi* was most numerous during the dry season. In general, the seasonal distribution of *A. oswaldoi* agrees with the distribution of *M. titillans*, whereas the distributions of *A. aquasalis* and *A. pessoai* agree closely with those of *Aedes* and *Psorophora* species. Because the seasonal distribution is related to the breeding sites as argued above *A. oswaldoi* may be considered a swamp breeder, while both other species are rainpool breeders.

SUMMARY

In 16A a series of 156 morning catches were regularly carried out in 14 months (1967, 1968). These results permitted a description of seasonal distribution of the most common mosquito species: *Aedes serratus, Ae. scapularis, Psorophora albipes, Ps. ferox, Wyeomyia* sp., *Mansonia titillans* and *M. venezuelensis.* The seasonal fluctuations in population densities were associated with the breeding habits of the various species.

IV. AGE-STRUCTURE AND DAILY SURVIVAL RATES

INTRODUCTION

The age structure of mosquitoes and the corresponding daily survival rate are of the utmost importance for the population dynamics and for the transmission of pathogens. They are crucial factors in the epidemiology of mosquito-borne disease (DETINOVA 1962, MUIRHEAD-THOMSON 1968, MATTINGLY 1969, etc.). Literature concerning this subject, in relation to the arboviruses in South America, however, is practically wholly absent.

When the age-structure of a certain mosquito population is known, the daily survival rate of the mosquitoes may be calculated. This appeared to be a useful parameter in mathematical models for the epidemiology of vector-borne disease. The concept has been applied and described by various authors to malaria epidemiology (DRAPER & DAVIDSON 1953, DAVIDSON 1954, 1955, DETINOVA 1962, 1968, GILLIES & WILKES 1963, 1965, MUIRHEAD-THOMSON 1968).

In the following some observations on age structure and daily survival rate will be described.

MATERIALS AND METHODS

For the determination of the physiological age of mosquitoes several methods are known (DETINOVA 1962). In the present study a technique of DETINOVA (1945, cited from DETINOVA 1962) has been chosen, which is based on the changes of the tracheoles in the ovaries during the first gonotrophic cycle. In nulliparous mosquitoes the tracheoles are coiled and called skeins. During the development of the ovaries the skeins unroll, which is clearly visible after the IIIrd stage of the ovarian cycle (CHRISTOPHERS 1911, in: DETINOVA 1962). After the development of the ovaries is completed all or nearly all skeins are unrolled. This proces is irreversible. Mosquitoes that have ovaries with skeins, are thus nulliparous and those without skeins or with nearly all skeins unrolled, are parous. Obviously, this method can only be applied to determine the nulliparous/parous rates.

The differences as described above are shown in Fig. 23. This method cannot be used if the mosquitoes have ovaries in the IIIrd stage or beyond. In that case the skeins are partly unrolled and, therefore, the nulliparous mosquitoes cannot be separated with certainty from the parous ones. During our observations at most 1% of the examined mosquitoes had ovaries in the IIIrd stage or beyond. These mosquitoes were not used for the determination of the nulliparous/parous rates with the exception of those which still retained some eggs and, hence, were parous.

The mosquitoes used for these determinations were captured partly in 16A, partly in Troelikreek, and partly in Matta. In 16A samples of four species were dissected: *Aedes serratus*, *Ae. scapularis*, *Psorophora ferox* and *Ps. albipes*. From Troelikreek samples of the same species and of *Culex portesi* and *C. spissipes* were dissected.

The mosquitoes were dissected as soon as possible but never later than 18 hours after catching. If they had to be preserved longer than a few hours, they were stored in ice. This was necessary in Troelikreek; in 16A and Matta the time between the catches and the dissections was only a few hours. After arrival at the laboratory the mosquitoes were killed, identified, and immediately dissected in distilled water. The ovaries were then dried on slides and examined under low power. The dissections were mainly done by two technicians, whereas the examinations were carried out by the author.

As is pointed out by many authors (DRAPER & DAVIDSON 1953, DAVIDSON 1954, 1955, LAURENCE 1963, etc.) it is possible to calculate the daily survival-rate if the length of the gonotrophic cycle and the proportion parous mosquitoes are known.

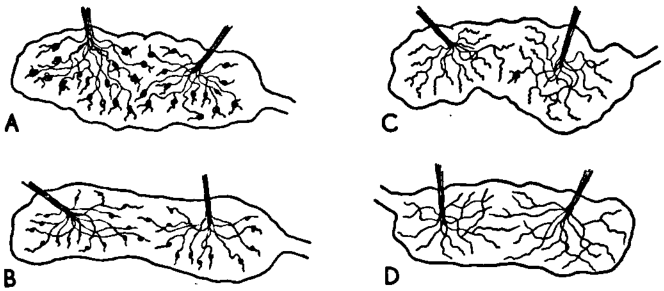


Fig. 23. Various aspects of the ovaries of an *Anopheles* when microscopically examined in dry mounts. – A = nulliparous specimen in stage I or II. B = nulliparous specimen in stage III. C = parous specimen with one ovariole not yet developed. D = parous specimen with all ovarioles developed at least once (after SLOOFF, 1964).

The formula used for these calculations, is $p^n = M$; where p = the daily survival-rate, n = the length of the gonotrophic cycle, M = the proportion parous mosquitoes (DAVIDSON 1954). The mathematical derivation of this formula can be found in MACDONALD (1952) and DAVIDSON (1954).

RESULTS

In 16A, during the last part of the wet season May–July 1968, the nulliparous/parous rates were determined for four species: *Aedes serratus, Ae. scapularis, Psorophora albipes* and *Ps. ferox*. Table 4 shows the number of specimens dissected, the number of batches, the mean proportion of parous mosquitoes, and the minimum and maximum proportions for each species. It must be noticed that the number of individuals per batch rather varied within the species. The number of specimens per batch for *Ae. scapularis* and *Ps. albipes* was mostly very low because of the low population density. This means that the estimated proportion should be considered with caution. On the other hand, the numbers of individuals per batch of *Ae. serratus* and *Ps. ferox* are large enough to consider the proportion to be reliable. The mean proportions of parous mosquitoes in 16A for all species are quite similar. However, the difference between minimum and maximum proportions varies distinctly for the various species. For *Ae. serratus* these figures are 0.27 and 0.74 and for *Ae. scapularis* 0.00 and 1.00, while both *Psorophora*'s are in between.

TABLE 4

DISSECTED MOSQUITOES FROM 16A

16.V.1968–29.VII.1969

Species	number of specimens (and batches)	mean proportion parous mosquitoes	minimum maximum proportion	
Ae. serratus	911 (9)	0.58	0.27	0.74
Ae. scapularis	57 (5)	0.54	0.00	1.00
Ps. albipes	124 (8)	0.59	0.09	0.80
Ps. ferox	337 (9)	0.55	0.40	0.91

In Fig. 24 the proportion for *Ae. serratus* and *Ps. ferox* are plotted against time. The rainfall figures per day are also plotted in this graph (solid bars).

An increase of the proportion in *Ae. serratus* is nicely shown; this is confirmed by the Spearman-test (P = 0.025). With regard to *Ps. ferox* there is no significant increase.

Table 5 shows similar figures as Table 4, but these are from Troelikreek and Matta. The batch of *Culex portesi* in Troelikreek, one batch of *C. spissipes* and two batches of *Ae. serratus* were obtained on February 17 and 18, 1969. The proportions of parous mosquitoes in these batches did not influence the mean proportions, determined during May–July 1968. As in 16A the mean proportions of all species – except *C. portesi* – are much in agreement with each other: the largest is 0.49 for *Ps. ferox*, the others are 0.41 and 0.42. The minimum and maximum proportions are less different than in 16A with the exception of *Ae. serratus*. Because the number of batches is

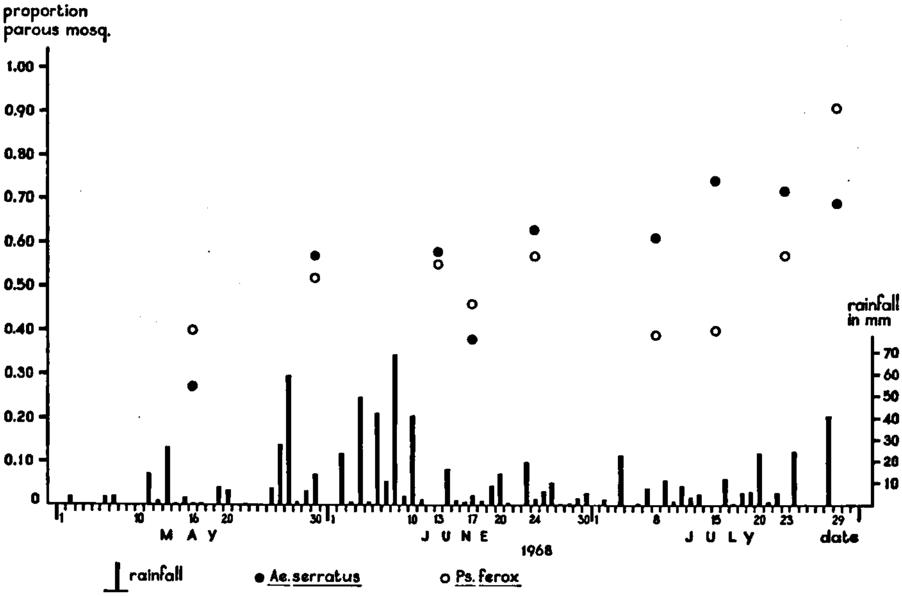


Fig. 24. The proportion parous mosquitoes of two species plotted against time, with rainfall data also represented.

TABLE 5

DISSECTED MOSQUITOES FROM TROELIKREEK AND MATTA

Troelikreek 21.V.1968–31.VII.1968, 17–18.II.1969; Matta 31.X.1968–17.III.1969.

Species	number of specimens (and batches)	mean proportion parous mosquitoes	minimum maximum proportion	
Troelikreek:				
Ae. serratus	223 (7)	0.41	0.10	0.57
Ae. scapularis	219 (4)	0.41	0.15	0.68
Ps. albipes	273 (5)	0.41	0.20	0.64
Ps. ferox	195 (4)	0.49	0.26	0.75
C. spissipes	675 (6)	0.42	0.23	0.65
C. portesi	100 (1)	0.53	—	—
Matta:				
C. portesi	1825 (22)	0.59	0.44	0.71

too small, nothing can be said about a possible increase or decrease. Comparison of the proportions in 16A and Troelikreek reveals quite a difference between the averages within the species, notwithstanding the fact that all proportions were obtained during the same period.

From the catches with animal-baited traps in Matta samples were taken to determine the nulliparous/parous rates during several months. Only *C. portesi* was sampled because other species were too scarce in number. The mean number per batch of dissected mosquitoes was about 83 (the smallest number 25, the highest 101). There appeared to be no increase nor decrease in the course of the time (see Table 6). The mean proportion is fairly high, compared to the figures for the other species in Troelikreek in the neighbourhood of Matta. However, the mean proportion for *C. portesi* is quite similar to that of the species of 16A.

The difference between minimum and maximum proportions parous mosquitoes is much smaller than in any other species, an assertion which is supported by the circumstance that the number of batches of *C. portesi* is much larger than that of any other species. Hence, the age composition of the population of *C. portesi* is rather stable over a long period. During the period the dissections were made, the population density was also stable: the mean number of specimens per traprun on groundlevel was 58 (the number of trapruns 139); the highest number in 14 days was 114, the lowest 24.

As stated above, the daily survival-rate (p) can be calculated from $p^n = M$, in which n is the duration of the gonotrophic cycle and M is the proportion of parous mosquitoes. The use of this formula is only permitted when several requirements are met (Davidson 1954). First, the mosquitoes must be all in the same ovarial stage. Secondly, derivation of the survival-rate from the proportion of parous mosquitoes and the gonotrophic cycle depends on the assumption that the population has a relatively stable age compo-

TABLE 6

PROPORTION PAROUS MOSQUITOES OF *C. portesi* IN MATTA ON VARIOUS DAYS AND SURVIVAL RATE PER MONTH

31.X.1968–17.III.1969

Date	proportion parous mosq.	daily survival-rate	Date	proportion parous mosq.	daily survival-rate
31.X	0.56		12.XII	0.52	
6.XI	0.68		18.XII	0.65	
7.XI	0.62		24.XII	0.66	
12.XI	0.68	0.94	10.I	0.68	
14.XI	0.65		16.I	0.64	0.94
21.XI	0.44		23.I	0.53	
22.XI	0.56		6.II	0.58	
29.XI	0.69		7.II	0.57	0.93
5.XII	0.51		18.II	0.53	
6.XII	0.51		14.III	0.53	0.94
11.XII	0.51	0.93	17.III	0.71	

mean proportion parous mosquitoes = 0.591 standard deviation = 0.077
mean daily survival-rate = 0.936 standard deviation = 0.019

sition. The first requirement could be met without any difficulty because all dissected mosquitoes were in the Ist to the IInd stage of the ovarian cycle. However, the second one is obviously not met by rainpool-breeders. Populations of those species receive an irregular new supply of nulliparous mosquitoes, depending on rainfall. In addition, the proportion of parous mosquitoes tends to increase gradually towards the end of the wet season. Thus no survival-rates for *Aedes*, *Psorophora* and *Culex spissipes* – all rainpool-breeders – have been calculated in this study.

The population of *Culex portesi* however, meets the requirements necessary for the calculation of the daily survival-rate. It has a stable age-composition as shown above. In Table 6 the proportion of parous mosquitoes on various days is shown and also the daily survival-rate per month. The duration of the gonotrophic cycle, used in these calculations, is 8 days according to the duration found by way of the "power-spectrum" (DE KRUIJF 1970). According to DAVIS & MARTINEZ (1970) the duration is even higher; they found a mean of 10 days. As can be seen in Table 6, the daily survival-rate remained equal during the whole period.

DISCUSSION

The new supply of nulliparous mosquitoes of rainpool-breeders decreases with the disappearance of the rainpools towards the end of a wet season. This will obviously result in an increase of the proportion of parous mosquitoes. Although the number of observations is rather small, *Aedes serratus* shows a significant increase at the end of a wet season (Fig. 24). The relatively low proportion on June 17, compared to that on June 13, should be mentioned. This may be explained as a result of the heavy rainfall about ten days earlier, on June 4–9. The duration from egg-hatching till first bloodmeal is found to be 9–10 days (DE KRUIJF 1970).

Psorophora ferox did not show any significant increase of the proportion of parous mosquitoes. The number of observations on the three remaining species, *Aedes scapularis*, *Psorophora albipes* and *Culex spissipes*, are too small to permit any conclusions as to a trend of the proportion of parous mosquitoes in time, although such a course might be expected because these species are all rainpool-breeders.

The mean proportions for the species in 16A were about equal which is not surprising in view of their similar breeding habitats. This is also true for the species in Troelikreek, with the exception of *Culex portesi.* The mean proportions in 16A are distinctly higher than in Troelikreek, although they were obtained in the same period. Also the variations between minimum and maximum proportions within the species are different in both areas. The difference between *C. portesi* in Matta and all other species is obvious. These observations indicate a fundamental distinction between *C. portesi* and the other species. There is a regular new supply of nulliparous mosquitoes throughout the various seasons in *C. portesi,* and an irregular – in the course of the wet season decreasing – supply of nulliparous mosquitoes in the other species. Of course, this should be associated with the larval habitats of the species. *C. portesi* is a semi-permanent groundpool-breeder (DAVIES & MARTINEZ 1970), the others are rain-pool-breeders.

The daily survival-rate could only be calculated for *C. portesi.* For species with an unstable population it should be calculated in other ways.

A high daily survival-rate favours the transmission of disease by arthropod vectors. Another factor contributing to transmission is a prolonged high and relatively stable level of the population size of the vectors. Observations described in this paper, have shown that these requirements are completely met with by *C. portesi.* The high daily survival-rate of *C. portesi* as shown in Table 6, is about equal to those known for the most important vectors of malaria, *Anopheles gambiae* and *A. funestus* (DAVIDSON 1954, GILLIES & WILKES 1965). Such a high survival-rate means that about 5% of the population will be older than 50 days. Hence, from an ecological standpoint *C. portesi* should be a suitable vector of disease, i.c. of arboviruses.

Of about 40 viruses isolated in the course of this study, about 20 were isolated from *C. portesi,* while most others came from sentinel baby mice in Matta (DE HAAS & DE KRUIJF 1971). In this area *C. portesi* is by far the most abundant species. In Trinidad, JONKERS et al. (1968) in 5 years isolated 357 viruses from mosquitoes: 250 from

C. portesi (one virus per 132 specimens), the remaining from a number of species (one virus per, at least, 1200 specimens). This shows clearly that, in Trinidad, *C. portesi* is the most important vector of arboviruses as it appears to be in Surinam. It also strongly supports MATTINGLY's (1969) suggestion that vector capacity is mainly determined by ecological conditions.

SUMMARY

From several catches samples of some mosquito species were taken to determine the nulliparous/parous rates. It appeared that the *Aedes serratus* population showed a significant increase in the proportion of older females towards the end of the wet season. For other species this could not be confirmed. The *Culex portesi* population in Matta had a stable age composition during several months.

Other data and the calculated daily survival rate of this species suggested that *C. portesi* is a suitable vector of arboviruses. A great number of viruses were actually isolated from *C. portesi* both in Trinidad and in Surinam.

V. CHECKLIST OF MOSQUITOES
CAPTURED IN 1967 AND 1968

INTRODUCTION

The last complete account of Surinam mosquitoes was published by BONNE & BONNE-WEPSTER (1925). A few incidental observations were recorded later, one of them on *Wyeomyia* of Surinam (BRUIJNING 1959). It seemed useful to give a checklist of all mosquito species captured during the present study in addition to the description of Anophelinae by VAN DER KUYP (1950).

For the identification the following references were used: AITKEN & GALINDO 1966, BONNE & BONNE-WEPSTER 1925, BRUIJNING 1959, FLOCH & KRAMER 1965, FORATTINI 1962, 1966 a and b, KOMP 1942, LANE 1953, LANE & WHITMAN 1951, MARTINEZ & CARCAVALLO 1965, ROZEBOOM & KOMP 1950, SENEVET & ABONNENC 1941, SHANNON 1931b.

For the nomenclature we followed the *"Synoptic Catalog of the Mosquitoes of the World"* by STONE, KNIGHT & STARCKE (1959), and the *Supplements I* and *II* by STONE (1962, 1963).

The species probably new for Surinam are marked with an asterisk. The collection in the Centraal Laboratorium in Paramaribo is damaged due to bad conditions in the storage room.

Some species can only be identified with certainty when males are captured. Apart from a few exceptions no males were captured. Therefore the identification of some species (*Haemagogus* sp., *Wyeomyia* sp. and most *Culex*) could not be done or should be considered with caution.

LIST OF SPECIES

captured and identified during 1967, 1968, and 1969

(Full name according to STONE, KNIGHT & STARCKE (1959) and STONE (1926, 1963).)

+Probably new for Surinam

ANOPHELINAE

Anopheles (*Stethomyia*) *nimbus* (Theobald)
Anopheles (*Anopheles*) *apicimacula* Dyar & Knab
Anopheles (*Anopheles*) *punctimacula* Dyar & Knab+
Anopheles (*Nyssorhynchus*) *aquasalis* Curry
Anopheles species

CULICINAE

Sabethini

Trichoprosopon (*Runchomyia*) *leucopus* (Dyar & Knab)+
Trichoprosopon (*Runchomyia*) *longipes* (Fabricius)
Trichoprosopon species
Wyeomyia species
Phoniomyia splendida (Bonne-Wepster & Bonne)
Limatus durhamii Theobald
Limatus flavisetosus Castro+
Limatus species
Sabethes (*Sabethes*) *cyaneus* (Fabricius)
Sabethes (*Sabethes*) *tarsopus* Dyar & Knab
Sabethes (*Sabethoides*) *chloropterus* (Humboldt)
Sabethes species

Culicini

Mansonia (*Mansonia*) *pseudotitillans* (Theobald)
Mansonia (*Mansonia*) *titillans* (Walker)
Mansonia (*Rhynchotaenia*) *nigricans* (Coquillett)+

Mansonia (*Rhynchotaenia*) *venezuelensis* (Theobald)
Mansonia species
Uranotaenia lowii Theobald
Orthopodomyia fascipes (Coquillett)
Aedeomyia squamipennis (Lynch Arribalzaga)
Psorophora (*Psorophora*) *ciliata* (Fabricius)+
Psorophora (*Psorophora*) *lineata* (Humboldt)
Psorophora (*Janthinosoma*) *albipes* (Theobald)
Psorophora (*Janthinosoma*) *ferox* (Humboldt)
Psorophora (*Grabhamia*) *cingulata* (Fabricius)
Psorophora species
Aedes (*Ochlerotatus*) *fulvus* (Wiedemann)
Aedes (*Ochlerotatus*) *hortator* Dyar & Knab
Aedes (*Ochlerotatus*) *scapularis* (Rondani)
Aedes (*Ochlerotatus*) *serratus* (Theobald)+
Aedes (*Ochlerotatus*) *taeniorhynchus* (Wiedemann)
Aedes (*Finlaya*) *terrens* (Walker)
Aedes (*Howardina*) *fulvithorax* (Lutz)
Aedes (*Stegomyia*) *aegypti* (Linnaeus)
Aedes species
Haemagogus (*Stegoconops*) *capricornii* Lutz ssp.
Haemagogus species
Culex (*Culex*) *mollis* Dyar & Knab
Culex (*Culex*) *nigripalpus* Theobald
Culex (*Culex*) *virgultus* Theobald+
Culex (*Melanoconion*) *crybda* Dyar [*Culex* 1]
Culex (*Melanoconion*) *taeniopus* Dyar & Knab [*Culex* 8]
Culex (*Melanoconion*) *spissipes* (Theobald)
Culex (*Melanoconion*) *portesi* Senevet & Abonnenc+
Culex (*Melanoconion*) *ybarmis* Dyar
Culex (*Mochlostyrax*) *caudelli* (Dyar & Knab) [*Culex* 2]
Culex (*Eubonnea*) *amazonensis* (Lutz) [*Culex* 5]
Culex (*Carollia*) *urichii* (Coquillett)
Culex (*Culex*) *quinquefasciatus* Say
Culex species

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