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Studies on the dynamics of transmission of onchocerciasis in a Sudan-savanna area of North Cameroon II

Seasonal and diurnal changes in the biting densities and in the age-composition of the vector population

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Near the perennial breeding sites in the main water courses the highest monthly biting rates were recorded from June to August (early rainy season) and again from December to February (dry season), but near the rainy season breeding sites in the affluents, or at fly-catching sites, more than 2 km inland from the nearest main river breeding site, the highest rates were recorded between August and December (mid-rainy to early dry season). The variation of the biting rates over the year depended on the waterflow of the main rivers and on the differential dispersal of the flies from the breeding sites during the dry and rainy seasons.

At the beginning of the rainy season, when the rivers started flowing, an immigration of non-local flies was observed at the river Mayo Rey near Tcholliré, presumably coming from *Simulium* breeding sites in the Adamaoua mountains to the South.

During three years 77 374 flies were caught by daily catches between 06.00 and 18.30 hours. During the dry season the biting activity of nulliparous and parous flies was highest between 09.00 and 10.00 hours and 16.00 and 17.00 hours, 9% and 22% of the total day-catches respectively. In the rainy season the peak biting rates occurred between 06.00 and 07.00 hours (9%) and again from 16.00 to 17.00 hours (14%). The lowest biting rates were observed between 11.00 and 12.00 hours in both dry and rainy seasons (4% and 3% of the total catch). Nulliparous flies showed higher variations in biting activity than did parous flies, leading to the highest proportion of parous flies during midday. These variations were not correlated with the temperature, though biting was reduced at values below 20°C.

Severe human onchocerciasis, and blindness as its most dangerous sequel, is the result of a continuous exposure of individuals to the bites of the *Simulium damnosum s.l.* vector flies. A valuable indicator for the degree of exposure is the estimated fly-biting rate on one man during one year (Duke, 1968; Duke *et al.*, 1975; Philippon, 1977; Walsh *et al.*, 1979; Renz and Wenk, 1987). However, the value of the Annual Biting Rate (ABR) gives no indication whether these bites were received during only a short period or were more or less evenly distributed over the year. Bertram (1964) suggested that the highly seasonal transmission of onchocerciasis in the savanna region of West Africa might be partially responsible for the higher prevalence of eye-lesions there, as opposed to the more continuous transmission of disease throughout the year in the rain-forest (Duke, 1968; Garms, 1973, 1983).

Seasonal variations in the fly-populations in the Sudan-savanna area were linked to the water-discharge of the breeding rivers, either by a synchronous unimodal, or a bimodal or an inverse type of correlation (Leberre, 1966). Optimum breeding conditions for the *Simulium* larvae, i.e. availability of turbulences and suitable support, are found at different seasons of the year in the large perennially-flowing rivers or in the rainy season tributaries. A good knowledge of the seasonal productivity of the breeding sites would be crucial for the successful control of the vectors by larvicides.

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Diurnal variations in the biting density have been related to variations in the temperature

(Leberre, 1966) and humidity (Häusermann, 1969) or to the intensity of light (Kaneko *et al.*, 1973). The variation in the biting activity of the flies, and in particular of the old, parous ones, delimits the hours of maximum or minimum danger of transmission of onchocerciasis.

The present paper describes the diurnal and the seasonal variations in the biting behaviour of the vectors (parous and nulliparous) of onchocerciasis around villages in the Sudan-savanna of North Cameroon. The Annual Biting Rates have already been reported (Renz and Wenk, 1987).

At the beginning of the rainy season, 'savanna' flies of the *S. damnosum* complex, namely *S. damnosum s. str.* and *S. sirbanum*, may migrate over considerable distances from the South to the North and repopulate rivers that had stopped flowing during the preceding dry season. This phenomenon was termed 're-invasion' when it was first described for flies invading the controlled areas of the WHO Onchocerciasis Control Programme (OCP) in the Volta river basin (Garms *et al.*, 1979). A similar invasion was observed during this study in the valley of the Mayo Rey in North Cameroon.

MATERIALS AND METHODS

The study area and the selection of the fly-catching sites in the areas of Tcholliré and Touboro, and also the methods of fly-catching and dissection, have been described in a previous paper (Renz and Wenk, 1987). For the present paper, evaluation data from the following main catching sites are used: Mayo Galké causeway, an almost perennial *Simulium* breeding site, Rey Manga causeway, about 9 km downstream from the nearest breeding sites in the Mayo Rey, and Douffing well, 7 km cross-country from the rainy season breeding sites in the Mayo Bodo and 10 km from the sites in the Mayo Rey. Fly-catching was carried out at these sites from April 1976 to May 1979. In the Touboro area the catching took place at the Vina bridge and at Bonandiga village centre. These latter sites were visited at about weekly intervals from February 1976 to May 1977.

Catches were also made at the rainy season tributaries Mayo Lougougnel and Mayo Doudja in the area of Tcholliré. The water discharge of the rivers Mayo Rey at Mayo Galké and Vina du Nord at Touboro was based on information from the hydrological surveys of ORSTOM/ONAREST, Yaoundé.

The data for the calculation of the diurnal variation of the biting density and parous rate were taken from those catching sites only at which sufficient numbers of flies were caught and the catching hours were complete, from 06.00 to 18.30 hours.

Temperature readings were carried out regularly during the first year of studies (May 1976 to April 1977) in the shade of a tree near the fly-catching sites from 06.00 to 18.30 hours. From 48 readings during dry and rainy seasons the characteristic profiles for the daily variations of temperature were drawn.

RESULTS

Seasonal Variation of the Biting Densities (Fig. 1) and of the Parous Rate (Fig. 2)

At Mayo Galké causeway, near an almost perennial breeding site, the biting pattern was clearly bimodal, with peak Monthly Biting Rates (MBR) in the early rainy season during the months May to August (MBR 15 273 in July 1976; 10 256 in June 1977; 10 112 in May 1978), and with a second peak in the cold dry season from December to January (16 890 in January 1977; 4624 in December 1978 and 10 155 in January 1979). Biting densities were highest as the waterflow increased at the beginning of the rainy season and again as the flow decreased in the

middle of the dry season, but few flies were caught when the flow was more than 100 m^3 sec^{-1} at the height of the rainy season. No flies were caught during the late dry season, when the river had stopped flowing. A similar pattern, though at a much lower level, was observed at Rey Manga causeway, where the biting densities were highest in July 1976 (MBR 155), July 1977 (512) and May 1978 (248) and again in December (1976–1978, MBRs 1519; 155; 477).

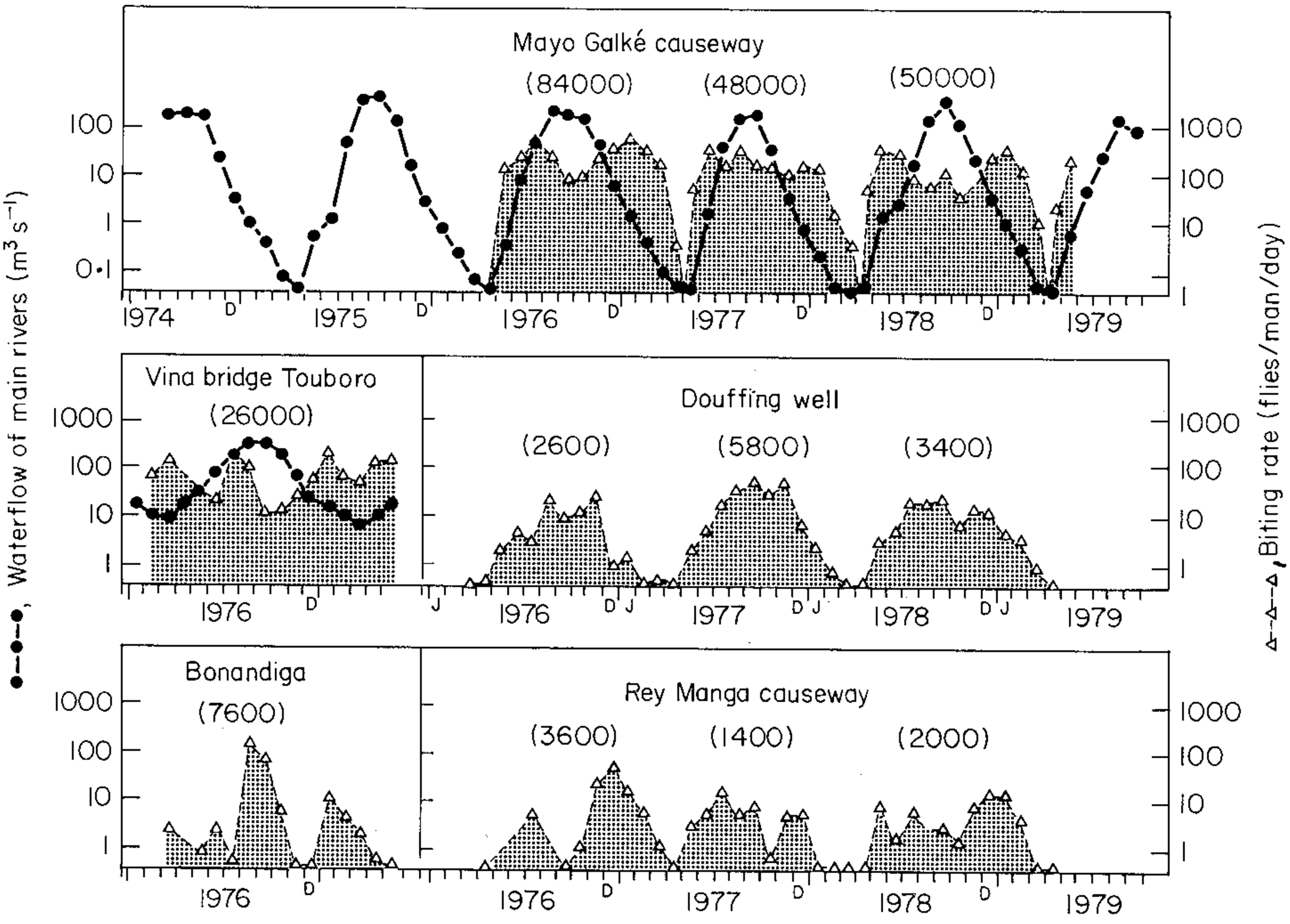

Fig. 1. The variation of the *Simulium damnosum s.l.* biting rate on man (flies/man/day, on a monthly average) over one to three years at Mayo Galké causeway and Touboro bridge (catching sites near *S. damnosum s.l.* breeding sites in the rivers Mayo Rey and Vina du Nord), at Rey Manga causeway (9 km downstream from the next breeding sites) and at Bonandiga and Douffing (2 and 7 km inland from the next breeding sites). When compared to the waterflow of the main rivers (m^3 s^{-1}) the pattern of the variation was bimodel at Mayo Galké causeway and synchronous at Douffing. Figures in brackets give the estimated values of the Annual Biting Rates (sum of 12 monthly biting rates from May to the end of April of the following year).

At Douffing, 7 km cross-country from the nearest breeding river, the biting density reached high levels only during the late rainy season and early dry season, with peak monthly biting rates in August and September, and again in November, interrupted only by a slight reduction in October (1976: August, 719; November, 800. 1977: September, 1425; November, 1376. 1978: September, 668; November, 462). There was very little biting during the dry season from February to May.

At the river Vina, near Touboro, the biting densities were at their lowest level during the rainy season in October 1976 (MBR 315) and were high in March 1976 (4278), July 1976 (6006), January 1977 (5589) and April 1977 (3956). The river Vina was flowing throughout the year, the monthly averages of the flow varying from 325 m^3 sec^{-1} in August 1976 to 7 m^3 sec^{-1} in March 1977.

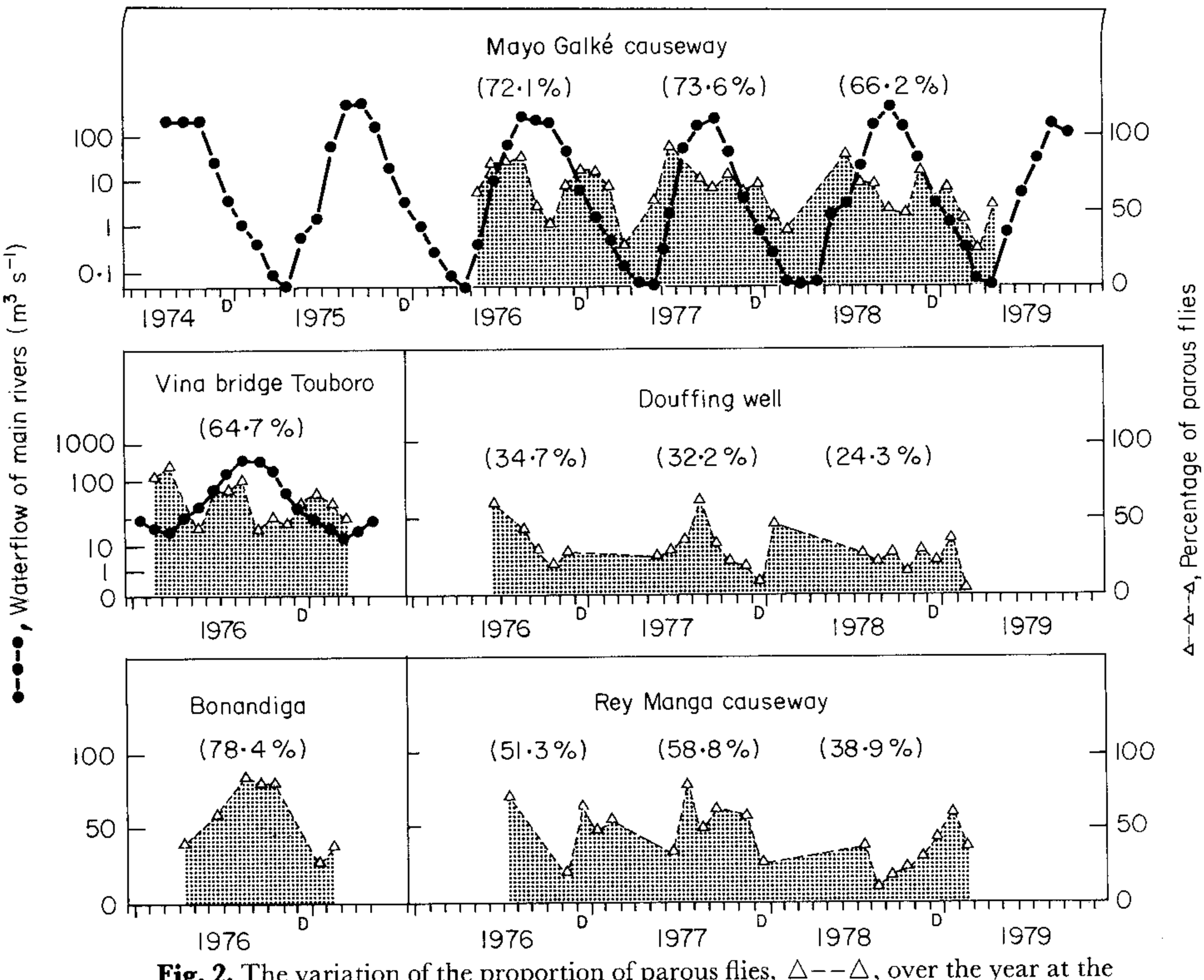

Fig. 2. The variation of the proportion of parous flies, △– –△, over the year at the same sites as in Fig. 1. Figures in brackets give the estimated proportion of parous flies for the total Annual Biting Rate. The parous rate for those months, where insufficient numbers of dissected flies were available (less than ten), was interpolated between those of the months before and after. Note that the proportion of parous flies is positively correlated with the biting rate: peak monthly biting rates coincide with highest parous rates.

Bonandiga, situated at about 2 km from the river Vina, followed the biting rates, measured at the river, though the peak biting densities during the dry season were lower (1976: August, 4600. 1977: January, 388). No flies were caught in November and December.

Other catching sites, situated at more than 2 km cross-country and which are not mentioned in Fig. 1, followed more or less the same pattern of variation, but two exceptions are worth mentioning: at the rainy season tributaries Mayo Dokday and Mayo Lougougnel (2 and 3 km from the river Mayo Rey respectively), biting densities were highest in December in the middle of the dry season in 1978 (Mayo Dokday, MBR 6823; Mayo Lougougnel, 14 217). At both sites, in 1978, the biting rate was low during the rainy season (maximum MBR 3309 and 314 respectively). The year before, in 1977, the pattern was inverse, with highest biting densities in August (14 307) at Mayo Dokday and in June (3705) at Mayo Lougougnel, but with much lower densities in the dry season (1488 and 1880 respectively).

The variations in the age-composition of the fly-population were closely linked to the variation in the total biting density, the highest parous proportions being observed when the biting rates were highest (Fig. 2). At Mayo Galké causeway at the beginning of the rainy season 82–93% of the total MBR were parous flies, and the percentage decreased at the height of the river's flow (41–76% during September and October). At the beginning of the dry season a second increase was observed, as the biting rates increased, though the proportion of

parous flies remained lower than at the beginning of the rainy season. During the hot dry season the parous proportions were low (24–67% in February and March).

At Rey Manga causeway and Douffing well the seasonal variation of the proportion of parous flies followed the same pattern, but the parous proportions were on the whole much lower.

Immigration of Non-local Flies during the Rainy Season

At the end of the dry season the river Mayo Rey stopped flowing every year for a few weeks. The *Simulium* populations disappeared completely, in the larval as well as in the adult stages, as evidenced by the absence of biting flies on man at the site Mayo Galké ford. However, at the moment of the onset of the rainy season, when the river started flowing after the first heavy rains, considerable numbers of flies were caught on man, even before any larvae or pupae were found in the river. This phenomenon was first observed in May 1976 and was followed in 1977, 1978, 1979. To give an example, the results from the year 1977 are presented here (see Figs. 1–3 in Renz and Wenk, 1987, for location of the sites).

The river Mayo Rey had stopped flowing on 21 April 1977 and the fly-population disappeared almost completely during April. On 16 May 1977 the daily biting rate on man was one fly, and on 22 May 1977 it was 0·5 flies. After heavy rainfall between the 26 and 28 May 1977 the biting rate went up suddenly, to 141 flies/man/day on 29 May 1977 and to as high as 690 on 6 June 1977. However, the river Mayo Rey started flowing at Mayo Galké causeway only on 3 June 1977 and no larvae or pupae of *S. damnosum s.l.* could be found before mid-June. This would indicate that these flies came from non-local breeding sites. As concerns the possible routes of immigration, the biting densities at the fly-catching sites at Rey Manga, some 30 km downstream north from Mayo Galké causeway, and at Douffing, some 10 km inland west, provide some further information. At Rey Manga the dynamics of the biting densities followed more or less a similar pattern, though at a much reduced level: On 27 May 1977 the biting rate was one fly/man/day, and it went up to 8·5 on 1 June 1977 and was 30 on 7 June 1977. At Douffing the biting density never reached high levels: two flies/man/day were caught on 26 May 1977 and on 31 May 1977, one fly was caught on 2 June 1977 and the maximum was 5·5 flies on 10 June 1977. At all three catching sites the biting densities went down in mid-June and only reached similar high (and even higher) levels by the end of June.

The nearest *Simulium* breeding sites during this period were in the river Mayo Oldiri, 32 km south from Mayo Galké, and in the Benoué, 25 km west behind the mountain of Tcholliré. These rivers were flowing throughout the year. On 30 May 1977 the biting rate at the causeway crossing the Mayo Oldiri was 349 flies/man/day. No data were available from the river Benoué for this period, but from catches during other seasons of the year the biting density at the Benoué is known to be about equal to that observed at the Oldiri.

The proportion of parous flies amongst the day-catches at Mayo Galké causeway increased during late May to early June from 57% on 29 May 1977 to 90% on 6 June 1977 and was as high as 97% on 14 June 1977. It remained high and only fell to 81% on 29 June 1977, probably as a result of local breeding in the river Mayo Rey.

Morphologically, all flies examined were identified as members of the group *S. damnosum s. str.* and *S. sirbanum*. These species are also known to be mainly involved in the reinvasion into the western and north-eastern areas of the Onchocerciasis Control Programme (OCP) in West Africa (Garms *et al.*, 1979, 1982; personal observation).

Diurnal Variation of the Biting Density and Parous Rate (Figs. 3 and 4)

From the analysis of 77 374 flies caught at 23 catching sites throughout the seasons of three consecutive years, the overall diurnal pattern of the total biting rate was calculated as shown in the Table. About equal numbers of flies were caught during the rainy and dry season (55% of total catches between May to October, 45% between November to April).

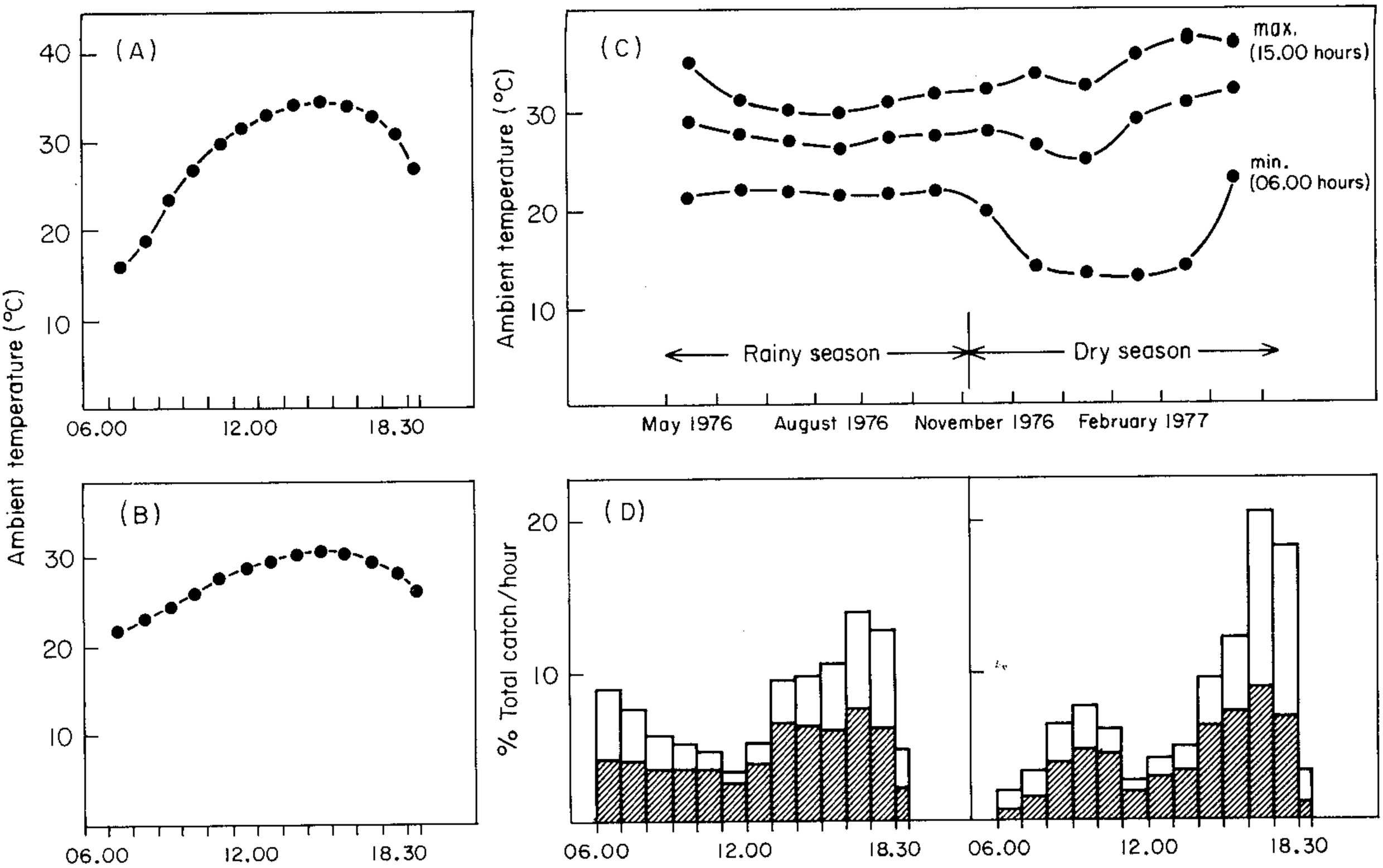

Fig. 3. The variation of the ambient temperature at the fly-catching sites over the day (06.00 to 18.30 hours) during the (A) dry and (B) rainy season. (C) The monthly averages of the daily temperatures (average 06.00 to 18.30 hours, minimum and maximum temperatures) over the year. (D) The proportion of the day-catch of *S. damnosum s.l.* (parous and nulliparous flies) during the hours of the day in the dry and rainy season. In the dry season, the variation of the range of daily temperatures, was more marked than in the rainy season, as was the variation of the biting activity of the flies. Parous flies showed less variation in the biting activity than did the nulliparous flies. ▨, Parous flies, □, nulliparous flies.

The highest biting densities were recorded between 16.00 and 17.00 hours (16·7% of the total day-catch) and the lowest densities were found between 11.00 and 12.00 hours (2·9%). During the morning hours from 06.00 to 11.00 hours the biting density was almost constant. 5·8% of the total day-catch was caught between 06.00 and 07.00 hours and 3·9% between 18.00 and 18.30 hours. Hence, 9·7% of all flies were caught during those hours of the day, which are not covered by an 11 hour catching period (from 07.00 to 18.00 hours). Seasonal variations in the diurnal biting pattern were marked (Fig. 3). During the rainy season (May to October) the biting density was already high between 06.00 and 07.00 hours (8·9% of total day-catch), and it gradually decreased towards midday. The highest density was observed from 16.00 to 17.00 hours (13·8% of total). By contrast, during the dry season, the biting densities were very low in the early morning, increasing until 09.00 to 10.00 hours, and decreasing again during the middle of the day. A maximum (20·6% of total) was reached, as during the rainy season, between 16.00 and 17.00 hours. The proportion of parous flies reached its highest level during the mid-day hours, indicating that nulliparous flies were much more influenced by the daily rhythm than the older, parous flies.

This pattern of the variation in the diurnal biting activity of nulliparous and parous flies was similar in both regions around Tcholliré and Touboro, and it did not vary significantly between catching sites situated near the river or across country away from the river. However, there was much variation from one catching day to another due to changing meteorological

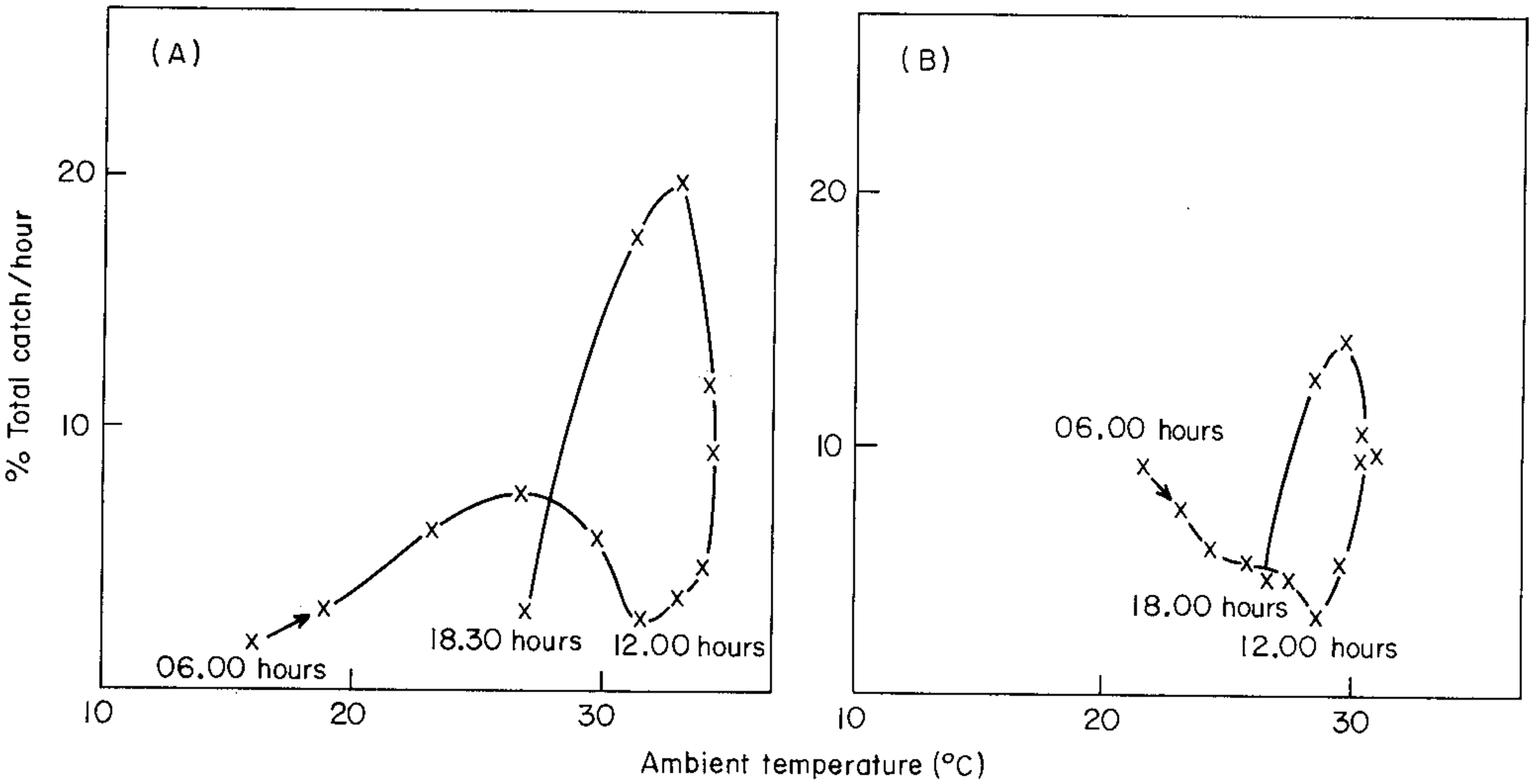

Fig. 4. The influence of the ambient temperature on the biting activity of the flies during (A) the dry and (B) the rainy season. Although low temperatures limited the biting activity of the flies, there was no upper range of temperature showing a similar effect, and the pattern of biting was rather related to the hour of the catches than to the daily course of temperature.

TABLE

*The variation of the fly-biting density (*S. damnosum s.l. *caught per hour, proportion of total day-catch) over the day*

Time	*Total number of* S. damnosum s.l. *caught*	*Percentage of total day-catch*
06.00–07.00	4464	5·8
07.00–08.00	4309	5·6
08.00–09.00	4659	6.0
09.00–10.00	4793	6·2
10.00–11.00	3973	5·1
11.00–12.00	2259	2·9
12.00–13.00	3571	4·6
13.00–14.00	5718	7·4
14.00–15.00	7390	9·6
15.00–16.00	8631	11·2
16.00–17.00	12 956	16·7
17.00–18.00	11 602	15·0
18.00–18.30	3049	3·9

A total of 77 374 flies were caught at 23 fly-catching sites over three years (788 fly-catching days) in the Sudan-savanna of North Cameroon. More than 40% of all flies came to bite between 15.00 and 18.00 hours.

conditions, especially during the rainy season or in the early dry season when there was harmattan (dry dust mist coming from the sahara).

The relationship between diurnal biting pattern and ambient temperature is shown in Fig. 4. Though temperatures below 20°C restricted the biting activity of the flies, there was no upper range of temperature with a similar effect.

DISCUSSION

With regard to the control of *Simulium* breeding sites by insecticides, the degree of breeding at different seasons would determine the period of the year at which control would be most effective. It would probably not be necessary to treat the river Mayo Rey at the period of maximum water levels ($> 100\ m^3\ sec^{-1}$), since the biting rates indicated that the breeding was much reduced then and that most flies came from smaller, rather inaccessible breeding sites in the rainy season tributaries (Renz and Wenk, 1987).

The sudden increase in both biting rates and parous proportions at the beginning of the rainy season indicates an invasion of non-local flies, the amount of which still remains to be determined. Similar observations on invasions from outside have been made in the controlled areas of the OCP in West Africa (Garms *et al.*, 1979, 1982), and after *Simulium* control in a neighbouring region on the river Mayo Kebbi in Tchad, when the breeding sites were quickly repopulated (Tauflieb, 1955, 1956). The sources of the invading flies in the region of Tcholliré are not known, but the low biting rate at Rey Manga would suggest that the flies came from the south rather than from the north or by flying up the river Mayo Rey from its junction with the Benoué. On the other hand, the very low biting density at the catching sites near Douffing, which would be located on the hypothetic flight-route of an immigration from the south (Mayo Oldiri) or from the west (river Benoué), indicates that the flies either flew too high to be attracted, or that the flies are only stimulated to bite in the near vicinity of a river and a potential breeding site. A similar situation could also be explained by the suggestion of Garms *et al.* (1979) that the invading flies may arrive gravid, oviposit and only then bite the vector collectors. It is a common phenomenon that re-invading flies concentrate near potential oviposition sites along fast-flowing rivers (personal observation in Togo).

The low proportion of parous flies at the beginning of the invasion is in contrast to the high parous percentages observed during the re-invasion into the western areas of the OCP (Garms *et al.*, 1979), where the flies presumably came from untreated breeding sites some hundreds of kilometers south. This could indicate a much shorter flight-distance for the invading flies in the region of Tcholliré, suggesting that they probably came from the river Oldiri. Abundant further breeding sites are in the rivers of the southern flank of the Adamaoua mountains (Vina du Sud, Mbéré, Faro) in the region south of Ngaoundéré, but the contribution of these fly-populations to the invasion along the river Mayo Rey remains still to be determined.

The seasonal variations of biting rates in relation to the water level of the breeding rivers were similar to the patterns described by Leberre (1966), being synchronous with the water level at the catching sites inland and bimodal at the perennially flowing rivers. However, the maximum monthly biting rates in the present study were more evenly distributed over the year, from the mid-rainy season to the mid-dry season, depending on the localization of the sites near perennial (Vina), almost perennial (Mayo Rey) or seasonal (Mayo Lougougnel, Mayo Dokday) watercourses. They changed considerably from one year to another.

The close relationship between the increase in biting rates and in the proportion of parous flies at all catching sites cannot be satisfactorily explained only by an increased life-expectancy of the flies, but is probably also due to the differential dispersal of nulliparous and parous flies from the breeding sites (Duke, 1975; Renz and Wenk, 1987). Thus parous flies, which stay near the breeding sites after oviposition, were not common at the river Mayo Rey at Mayo Galké causeway when the breeding sites were flooded in the middle of the rainy season, and when the

flies laid their eggs presumably in the smaller tributaries like the Mayo Dokday and the Mayo Bodo.

In this study catches were carried out for 12·5 hours per catching day, i.e. from 06.00 to 18.30 hours local time (G.M.T. + 1 hour), thus covering almost the complete day from dawn to dusk. If the catches had been restricted to an 11 hour period from 07.00 to 18.00 hours, as adopted by the OCP in West Africa, then it can be calculated that almost 10% of the total day-catch would have been overlooked, assuming that the flies in search of a bloodmeal would not have waited until the fly-collector was available. This bias, although small, should be kept in mind when comparing Annual Biting Rates and Transmission Potentials.

Low temperatures limit the activities of blood-searching flies, as shown by Leberre (1966), Häusermann (1969) and Philippon (1977), but the different behaviour of nulliparous and parous flies, and the variation of the biting density in the afternoon, were governed by other, probably innate, parameters.

Early morning and late afternoon hours were the most dangerous times with respect to the exposure to the bites of the flies and to transmission. If these hours could be avoided, a considerable reduction of exposure could be obtained.

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