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

Prevailing *Simulium* vectors, their biting rates and age-composition at different distances from their breeding sites

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Along the main water courses in the sparsely populated areas of the Sous-Préfecture of Tcholliré, the vectors of onchocerciasis were mainly *Simulium damnosum s. str.* and *S. sirbanum*, together with a small proportion of *S. squamosum*. Over a period of one to three years, vector biting rates were measured at 23 fly-catching sites in the vicinities of nine villages with different endemicities of onchocerciasis. Annual Biting Rates (ABR) on man were estimated as 26 100–83 800 fly-bites per man per year along the rivers Mayo Rey and Vina du Nord, and 11 000–37 400 at rainy season tributaries. Biting rates decreased rapidly at increasing distances from the river, and were between 10 700 and 2400 at 2–10 km cross-country from the breeding site. Lowest biting rates (50–6000) were measured at the village centres. The ABR varied from year to year in relation to the water-discharge of the main rivers, the coefficient of variation of the mean being 34–49%.

The parous rates were 64–73% at the perennial breeding sites and only 17–44% away from the breeding sites, indicating dispersal mainly of young nulliparous flies and a reduced flight-range after oviposition.

It is generally accepted that man–fly contact must be reduced to a very low level to interrupt transmission of onchocerciasis or to reduce it to levels at which serious clinical signs of the disease are unlikely to occur. Duke *et al.* (1975) and Thylefors *et al.* (1978) correlated the intensity of human infection in the Sudan-savanna of West Africa with the amount of man–fly contact (Annual Biting Rate, ABR*) and with the amount of transmission (Annual Transmission Potential, ATP†), but their studies were mostly carried out at sites with hyperendemic onchocerciasis (Prost *et al.*, 1979) and with a high prevalence of ocular lesions due to onchocerciasis.

The present study was designed to provide more information on the correlation of different levels of endemicity with the ABR and ATP in a typical Sudan-savanna focus, without previous control measures.

This first paper presents the study area, the localization of breeding sites, the vectors, with their age composition, and the ABR at 23 fly-catching sites.

MATERIALS AND METHODS

Description of the Areas and Villages

Onchocerciasis is widespread in North Cameroon along the upper courses of the rivers Benoué, Sanaga, Vina and Mbéré (Duke *et al.*, 1975; Anderson *et al.*, 1974; Le Bras *et al.*, 1976). The

These investigations received financial support from the WHO/UNDP/World Bank Onchocerciasis Control Programme and from the Filariasis component of the UNDP/World Bank/WHO Special Programme for Research and Training in Tropical Diseases.

*ABR: Estimated number of *Simulium damnosum s.l.* bites received by one person in one year at a given site, assuming that this person is exposed to the bites of the flies from dawn to dusk throughout one year and that all flies coming to land would actually take a bloodmeal.

†ATP: Estimated number of infective third-stage larvae of *Onchocerca volvulus* which could be inoculated into one person in one year, if all the infective flies biting him were to transmit their total load of infective larvae (Duke, 1968).

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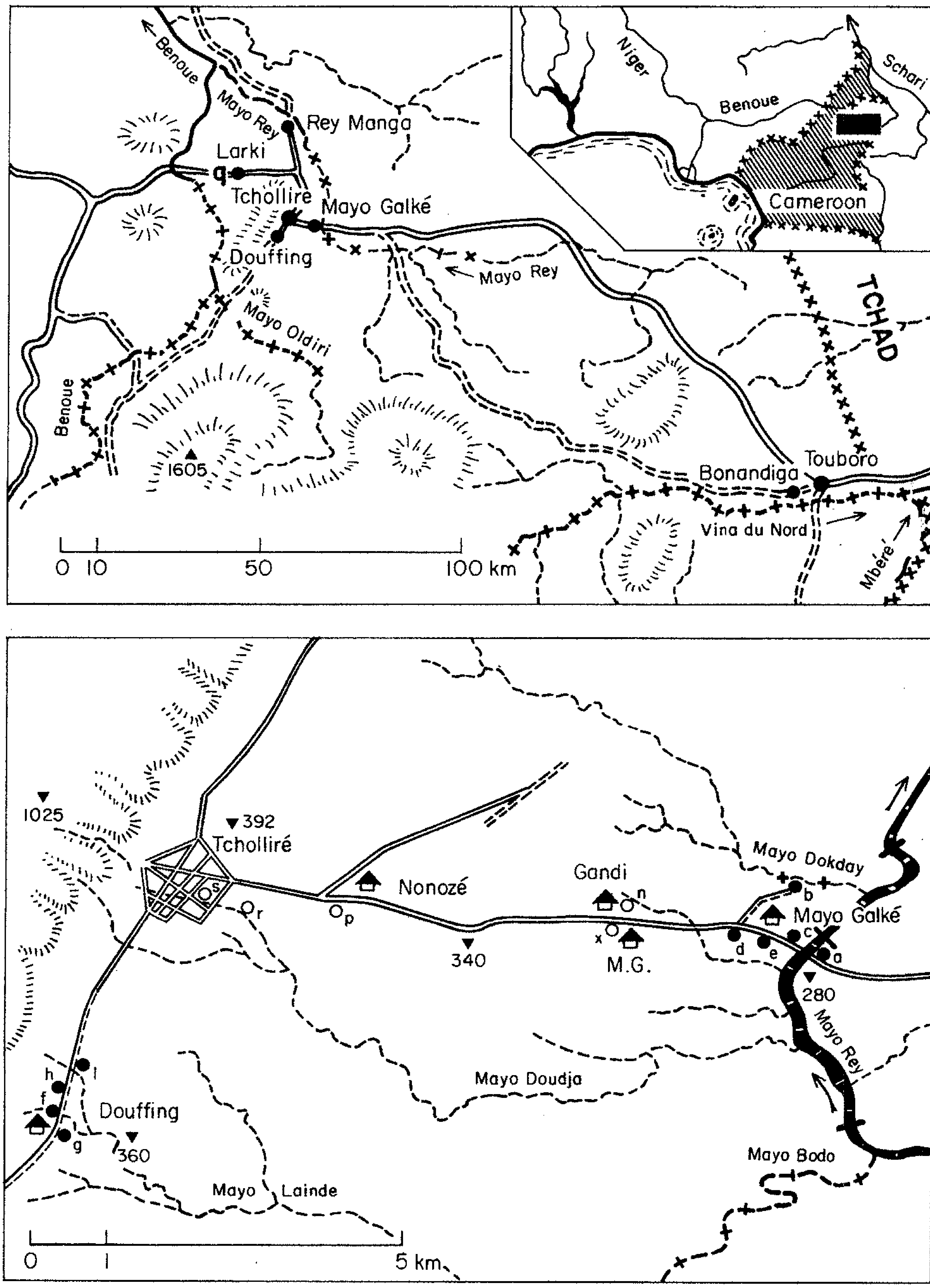
focus around Tcholliré (8°24′N, 14°10′E) and Touboro (7°46′N, 15°21′E) is situated between the Guinea-savanna area to the south (Adamaoua mountains) and the Sudan-savanna plains to the north towards Garoua, where onchocerciasis is not endemic.

The rainy season lasts some six months, beginning with heavy rainstorms in May. The annual rainfall averages 800–1400 mm. The dry season is relatively cold from November to January and then hot until the onset of rains.



Figs. 1 and 2. Locations of fly-catching sites (a–i, n–x) around Tcholliré and Touboro. +, *Simulium damnosum s.l.* breeding site.

The sparsely distributed population (34 000 km^2, 76 000 inhabitants) lives mainly in small hamlets of about a hundred inhabitants along the few roads (0·06 km km^{-2}). Dispersed in the

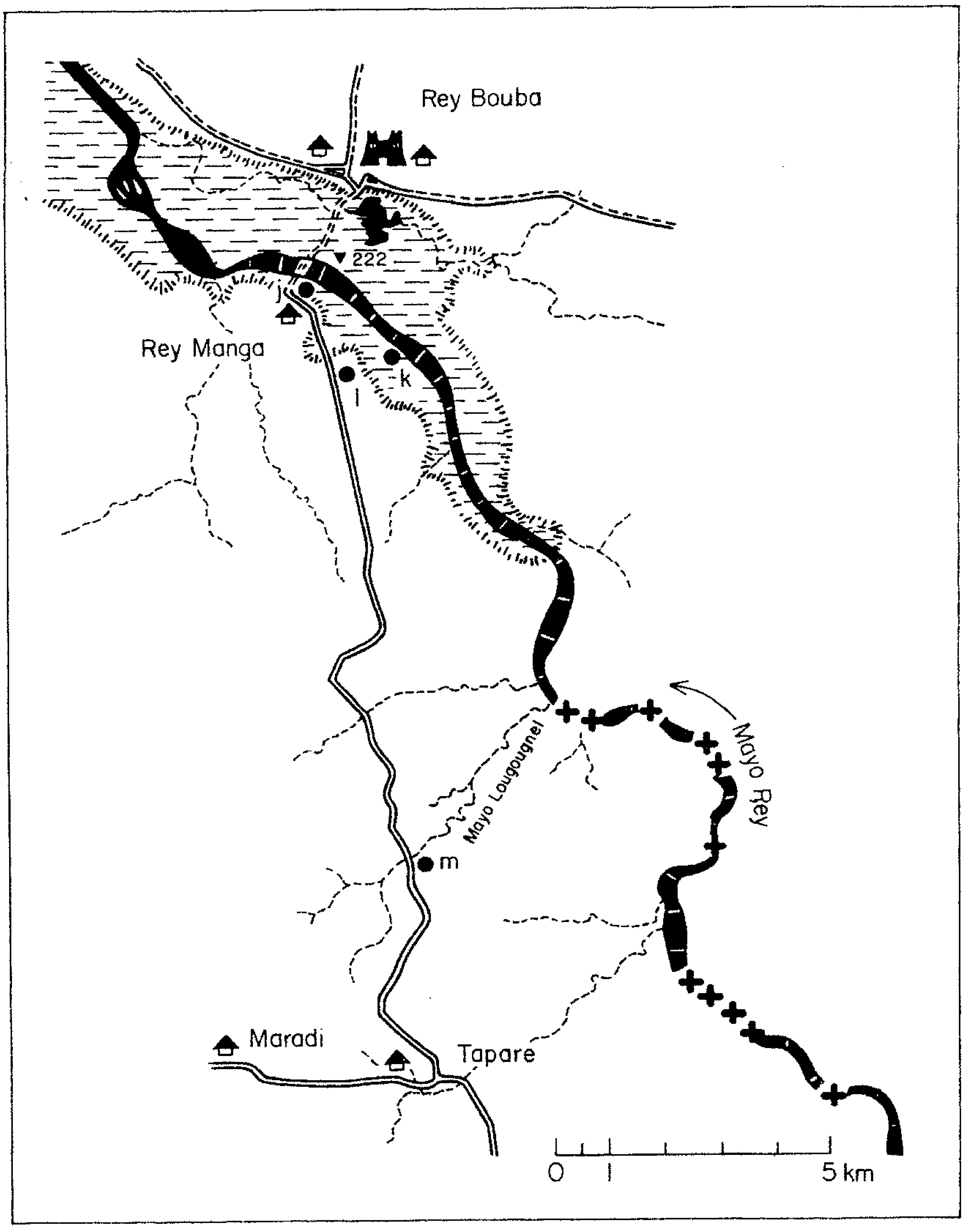


Fig. 3. Location of fly-catching sites (j–m) around Rey Manga.

bush before these roads were built, some of the villages moved only recently to their present sites. Nine villages in the areas of Tchollire and Touboro (Figs. 1–3) were selected according to their different distances from *Simulium damnosum s.l.* breeding sites. Table 1 gives village distances from the nearest *Simulium* breeding sites, population census, tribe and selection of fly catching sites, together with the prevalence of onchocerciasis and of ocular lesions.

The medical data come from a survey carried out in March (village Touboro) and October (all other villages) 1976 with the purpose of identifying suitable village populations (Fuglsang and Anderson, 1977). A census was taken by house to house visits, and at the same time two skin snips were taken from each person using a corneascleral punch, which gave an average weight of 1·4 mg (random sample tested on a torsion balance). One snip was taken near the outer canthus, and the other from the buttock. At Touboro these snips were taken from the left side of the body, but at the other villages they were taken from the right side. Each snip was placed in three drops of normal saline in a separate microtitre well, and left for about four hours under a plastic seal. The snips were then removed with a pin, and the saline containing the microfilariae that had emerged was transferred by pipette to a slide. Each well was washed by an additional drop of saline, which was added to the appropriate slide. The microfilariae were then counted under the microscope. The snipping and the transfer and counting were done by the same

TABLE 1

Study-villages and fly-catching sites

Village	Population ex./census	Prevalence of oncho-cerciasis (%)*†	Mean mff density per snip *‡	Prevalence of ocular lesions (%)*§	Prevalence of blindness* (no. of persons): Total		Prevalence of blindness* (no. of persons): Due to oncho-cerciasis only		Tribe	Remarks	Fly-catching sites‖
					bi-lateral (%)	uni- or bilateral (%)	bi-lateral (%)	uni- or bilateral (%)			
Tchollirá	48/*ca.*2000	48·4	16	1·2	0·0 (0)	0·7 (1)	0·0 (0)	0·0 (0)	Mixed	Administrative town, 8 km from the river Mayo Rey. One quarter of the population near the Sultans's palace examined	Tcholliré East Mayo Doudja (r) Tcholliré centre banana garden (s)
Rey Manga	88/94	50·7	17	0·9	0·0 (0)	1·1 (3)	0·0 (0)	0·0 (0)	Mixed	9 km downstream from breeding sites in the river Mayo Rey. 500 m from causeway	Rey Manga causeway (j) 2 km upstream from causeway (k) Village fields, 1·5 km from the river (l) Tributary Mayo Lougougnel (m)
Larki	42/51	64·4	24	2·3	1·1 (1)	6·0 (5)	0·0 (0)	1·1 (1)	Dourou	6 km from perennial breeding sites along the river Benoué. During the dry season, the inhabitants hunt and fish	Village well, 100 m from the village (q)
Douffing	93/112	60·8	35	1·7	0·0 (0)	0·7 (2)	0·0 (0)	0·7 (2)	Dourou	10 km from the river Mayo Rey and 7 km from rainy season breeding sites in the tributary Mayo Bodo	Village well, at tributary (t) Waterhole (g) Village fields (h) Small tributary (i)
Nonozé	67/79	74·1	56	11·1	4·5 (3)	5·4 (4)	4·5 (3)	4·5 (3)	Mixed	6 km from the river Mayo Rey. Recently built near the protestant mission. High prevalence and eye-lesions probably acquired elsewhere	Well of campment, 6·5 km from Mayo Rey (p)

Gandi	1. 53/72 2. 124/157	83·1 70·1	89 65	22·4 5·0	5·7 (4) 2·8 (5)	12·7 (10) 3·9 (8)	3·7 (3) 0·7 (2)	9·4 (8) 1·3 (3)	1. Mboum 2. Dourou	2·5 km from the breeding sites in the Mayo Rey 1. Part of Mayo Galké until 1968 2. Local population	Village well, 2·5 km from Mayo Rey (n) In the village 2·5 km from Mayo Rey (x)
Touboro	244/ *ca.*1500	69·4	94	7·1	0·3 (1)	1·1 (2)	0·3 (1)	1·1 (2)	Mixed	Administrative town and cotton factory. 2 km from perennial breeding sites along the Vina river. 3 village quarters examined	River Vina bridge (t) Touboro South, tributary (u) Touboro centre near the hospital (v)
Mayo Galké	114/145	89·5	101	20·3	7·6 (3)	11·8 (6)	7·6 (3)	11·8 (6)	Mboum	500 m from breeding sites at disused causeway across the river Mayo Rey, and 1 km from a rainy season breeding site in the tributary Mayo Dokday	Mayo Galké causeway (a) Tributary Mayo Dokday, 1 km from Mayo Rey (b) 250 m from causeway, fields (c) 900 m from the causeway (d) In the village, 600 m from causeway (e)
Bonandiga	88/108	83·3	107	19·0	5·0 (5)	9·3 (8)	3·7 (4)	5·0 (5)	Mboum	2 km from perennial breeding sites at the river Vina du Nord. Probably additional rainy season breeding in the nearby tributary Bome	Village centre, 2 km from the Vina (w)

*Adjusted for age and sex, OCP standard population.
†Positive skin snip.
‡Arithmetic mean number of microfilariae at the buttock per person examined.
§Ocular lesions, due to onchocerciasis only, including sclerosing keratitis, any degree of iritis, optic nerve disease and choroidoretinitis.
‖See Figs 1–3 for the location of fly-catching sites.

person (H.F.) at all villages except Touboro, where the counting was done by a laboratory assistant.

After the recording and snipping the patients were examined (left eye at Touboro, right eye at the other villages) with a Haag-Streit 900 slit lamp placed in a centrally located hut. The numbers of microfilariae in the cornea and anterior chamber (without positioning of the patient) were recorded, together with the lesions of the anterior segment. Since posterior segment lesions in onchocerciasis rarely occur without some evidence in the anterior segment (particularly low-grade iritis and abnormalities of pupil reaction), it was not difficult to select patients for examination of the posterior segment. For the purposes of this study eye lesions include sclerosing keratitis, any degree of iritis, optic nerve disease and choroidoretinitis. Blindness was defined as the inability to count fingers accurately at 3 m with the better eye. All ophthalmological examinations were done by the same person (J.A.).

Fly-catching and Dissections

Simulium flies were caught in hourly samples by seated fly-collectors, exposing their legs to the flies and catching them with a sucking tube as they came to land. A team of two collectors worked simultaneously at a distance of 20–50 m from each other at one catching site from 06.00 to 12.00 hours local time (GMT + 1 hour). They were replaced by a second team which took their place from 12.00 to 18.30 hours. The fly-catches were therefore carried out during 12.5 hours per day from soon after dawn to dusk, covering almost all hours of the diurnal activity of blood-sucking flies. Care was taken to assemble teams of comparable efficiency by pairing collectors with different skill and degree of attractivity to the flies. Around Tchollirë, where the collectors were usually brought to their stations by car, one complete day of catching could be performed. Around Touboro, where there were no transport facilities, only half-day sessions could be made on one day, and then were completed on the following day.

Catches were made on one to four days per month at 14 sites which were regularly visited in the first year of studies (May 1976 to April 1977). Twelve sites were visited in the second year (May 1977 to April 1978) at more or less weekly intervals, and six sites were still visited at weekly intervals in the third year (May 1978 to April 1979). Catchings were interrupted at the end of the dry season around Tchollirë, when the rivers stopped flowing and the biting densities became very low.

During dissection of the flies, which was carried out following standard routine (Walsh *et al.*, 1979), the following was recorded: nulliparous, parous* and old parous (category 4 of Häusermann 1969, recorded only from May 1977), trace of fresh bloodmeal, and infections by filarial or other parasites. If all the flies caught could not be dissected, a random sample of 10–20 flies per hour and per vector collector was dissected. Dissections were made by D. Tom† at Touboro and by R. Oguama† and the author at Tchollirë. From June 1978 to May 1979 all dissections were made by the author. Whenever possible the dissected flies were cross-checked by a second person or by the dissector himself after ten minutes.

The fly-catching sites (a–x, Figs. 1–3) were selected as follows: 1. Near *S. damnosum s.l.* breeding sites, along the perennial rivers, where the biting density was likely to be high. 2. In the open fields away from the rivers, where the biting density was likely to be low. 3. At rainy season tributaries, which were expected to form the routes of fly-migration and to provide suitable *S. damnosum s.l.* breeding sites at their lower reaches. 4. At the village well or waterhole, often situated near a rainy season tributary; it was frequently visited by the village populations and was attractive also to the flies, due to the humidity and the dense vegetation there. 5. At the village centre between the huts, where the people spent much of their time. Additional fly-catching sites not mentioned in Table 1 were visited along the perennial rivers Oldiri (Taboun

*Before, or respectively after, the first oviposition indicating the first (nulliparous) or a subsequent (parous) attack for bloodfeeding.

†Staff of the Medical Research Centre, Kumba, experienced dissectors of *S. damnosum s.l.* flies.

causeway) and Benoué (Buffle Noir and Grand Capitaine), but regular follow-ups were not feasible during the rainy season.

Calculation of Biting Rates

The flies caught in hourly samples by the fly-collectors were killed with chloroform vapour and the number of flies counted per hour was divided by the number of collectors working simultaneously to give the hourly biting rate per man. The Daily Biting Rate (DBR) was then the sum of 13 hourly values from catches between 06.00 and 18.30 hours.

The Monthly and Annual Biting Rates (MBR, ABR) were calculated according to Walsh *et al.* (1979), the ABR being the sum of 12 monthly biting rates during one hydrological year, from the beginning of the rainy season in May to the end of the following dry season in April. During the dry season, when the rivers stopped flowing and the biting rates became very low, the catches were interrupted. The MBR was then estimated. To give an example; fly-catches at Mayo Galké causeway were suspended in February 1978 after the river stopped flowing, and the biting rates had decreased from 41 flies/man/day on the 4th to 13, 12·5 and 3 flies/man/day on the 10th, 13th and 17th respectively. No catches were made from 18 February throughout March and April. The river started flowing again by the end of April, and the fly-catches were resumed on 2 May at weekly intervals, giving Daily Biting Rates (DBR) of 376, 252·5, 370, 235·5 and 397 flies/man/day. The MBR for March and April 1978 was then estimated arbitrarily to be 100 and 1500 respectively by interpolation.

The standard deviation of the results of the sample of DBRs measured per month was divided by the square root of the number of catching days executed to give the standard error of the DBR. This was then extrapolated to give the variance of the MBR according to the formula:

$$\text{Variance}_{(\text{MBR})} = \text{Variance}_{(\text{sample})} \times (\text{days per month})^2/\text{no. of catching days}$$

i.e. the percental standard error of the DBR was extrapolated to the standard error of the MBR. In the above mentioned example, the mean DBR in May was 326·2, the variance 5767, the S.E. 33·96 (10·4% of the DBR), and the variance of the total MBR (10 112 flies/man/month) was 1 108 480 (S.D. 1053 = 10·4% of MBR).

Accordingly, the ABR being the sum of 12 MBRs, the variance of the ABR is the sum of the variances of these 12 MBRs, and the square root of this is the S.D. (S.E.) of the ABR.

The calculations of the proportions of the parous and old-parous flies were based on an extrapolation of the number of parous or old-parous flies found at dissection to the total number of flies caught per hour, day, month and year. The results from about 25 000 man-catching-hours during 1916 man-catching-days had to be evaluated. Since the same method of extrapolation was used later on to calculate the infection rates and transmission potentials, all data from the fly-catchings and dissections were stored in a computer to facilitate the subsequent evaluation.

Samples of larvae of *S. damnosum s.l.* from various breeding-sites were preserved in Carnoy for cytotaxonomic identification of the salivary gland chromosomes (Vajime and Dunbar, 1977). Pupae were kept in breeding cages (Wenk and Raybould, 1972). The morphology of alcohol-preserved flies, which were either caught on man or were reared from pupae in a breeding cage, was examined following criteria given in Dang and Peterson (1980) and Garms *et al.* (1982).

RESULTS

Breeding sites of *S. damnosum s.l.*, Identification of Larvae and Adults

Abundant perennial breeding sites existed along the main rivers Vina du Nord and Mbéré in the region of Touboro, and along the Benoué and Oldiri in the region of Tchollìré (Figs. 1–3).

The highest larval population densities were at the beginning of the rainy as well as of the dry season, when the waterlevel was at an intermediate height. Similar dynamics were shown by the *Simulium* larval populations in the river Mayo Rey, although breeding was interrupted there at the end of the dry season (February to April), when the river stopped flowing. *S. damnosum s. str.* was the most common species in the larval populations at these sites during the rainy season, although *S. sirbanum* was always found at the same sites and its proportion in the region of Tcholliré increased markedly during the dry season (Table 2). Three larvae of *S. squamosum* were recorded in the area of Tcholliré in samples from the rivers Mayo Rey and Benoué in November 1976, but none was found at Touboro in a small sample.

Rainy season breeding sites were productive during the months of August and September at the lower reaches of the tributaries Mayo Dokday and Mayo Bodo in the Tcholliré region. Only *S. damnosum s. str.* larvae were identified in a sample from the Mayo Bodo in October 1977.

Almost all the adult female flies caught on man were identified, according to their morphology, as belonging to the group *S. damnosum s. str./S. sirbanum*. The wing-tufts and post-cranial hairs were pale, and the antennae were short, compressed and pale. Flies with 'mixed' wing-tufts (class C,D; Kurtak *et al.*, 1981) and longer antennae were caught in the Tcholliré region during the late rainy season and during May 1977 at Touboro. They were probably *S. squamosum*. During the three years of studies, a total number of five male *S. damnosum s.l.* were caught on man, where they had probably followed a female fly. Two of these males were very pale and showed a scutal pattern, typical for *S. damnosum s. str.* and *S. sirbanum* (Type H, Meredith *et al.*, 1983; Dang and Peterson, 1980). The other three males had dark wing-tufts and post-cranial hairs and their scutal pattern was very different in two of the individuals (pattern A and B). According to the key of Dang and Peterson (1980) these males would belong to the group *S. soubrense/S. sanctipauli*. No similar male was seen in 88 males which emerged in the breeding cage from pupae of various breeding sites.

Estimated Annual Biting Rates and Age-composition

From February 1976 to May 1979 a total of 1916 man-catching-days was achieved, 90 553 flies were caught, and 60 453 flies were dissected. Table 3 shows the annual totals of the numbers of flies caught and dissected, as well as the estimated ABR and the extrapolated proportion of parous and of old parous flies. Near the main breeding sites, the ABR was between 26 100 (site t, Touboro) and 47 900–83 800 (site a, Mayo Galké causeway 1976 to 1979). At rainy season tributaries, the ABR was 11 100–20 500 at the Mayo Lougougnel (site m) and 27 700–37 400 at Mayo Dokday (site b). At the other catching sites, situated cross-country away from the rivers, the biting rates depended mainly on the distance from the next breeding site, and they were generally lower in the open fields near the villages than at a nearby well or waterhole, located in a sinking and covered by dense vegetation. Lowest biting rates were measured inside the villages (50–730 at Touboro, sites u,v; 360 and 1000 at Tcholliré, sites r,s; 2100 at Gandi, site x), although the ABR was as high as 6000 flies at Mayo Galké village centre (site e) and 7600 at Bonandiga (site w) due to the proximity of *Simulium* breeding sites and because of the small size of these hamlets.

The S.D. of the ABR (Table 3), as defined for the purpose of this study, is an indicator of the precision of its assessment by fly-catching at monthly, bi-weekly or weekly intervals. In the present study it varied from 8% (Mayo Galké causeway, 1978) to 54% (Gandi village centre, 1976) of the ABR, and was highest for low values of the ABR or when only few catching sessions were carried out during one year.

The decrease in the biting rates with increasing distances from the breeding river is shown, for the area of Tcholliré and the river Mayo Rey, in Fig. 4(A). The biting density decreased to less than half of its original level at the river within a few hundred metres inland, and went down to 10% at about 5 km distance.

TABLE 2

Seasonal variation in the cytotaxonomic composition of the Simulium damnosum s.l. *larvae populations. The results were combined from collections during the years 1976–1978*

	Rainy season (May–October)			*Dry season (November–April)*		
Region (River)	S. sirbanum *(%)*	S. damnosum s. str. *(%)*	S. squamosum *(%)*	S. sirbanum *(%)*	S. damnosum s. str. *(%)*	S. Squamosum *(%)*
Tchollirê (Mayo Rey, Oldiri, Bodo, Benoué)	1	99 (122 larvae identified)	0	27	71 (172 larvae identified)	2
Touboro (Vina du Nord)	9	91 (11 larvae identified)	0	7	93 (54 larvae identified)	0

Cytotaxonomic identification by Dr. Vajime.

TABLE 3

The results of catches and dissections of Simulium damnosum s.l. *in the environs of the nine villages and various parameters derived from these*

Village	*Fly-catching site*	*Year*†	*Days spent fly-catching*	S. damnosum s.l.		*Estimates for whole year*			
				Caught	*Dissected*	*ABR*‡	*±SD*§	*% parous*‖	*% old-parous*≡
Mayo Galké	Causeway (a)	1976	85	18 641	14 891	83 800	9400	72·1	—
	Causeway (a)	1977	68	9864	6255	47 900	6200	73·6	9·9
	Causeway (a)	1978	102	14 416	4644	49 600	4100	66·2	7·4
	Mayo Dokday (b)	1977	63	8105	4583	37 400	6300	45·3	4·4
	Mayo Dokday (b)	1978	95	7886	4733	27 700	2500	48·5	2·9
	250 m from causeway (c)	1977	64	2925	2546	14 400	1700	52·3	4·5
	900 m from causeway (d)	1977	59	2319	2176	12 000	1200	43·9	3·7
	In the village (e)	1976	48	869	832	6000	760	51·5	—
Douffing	Well (f)	1976	53	552	547	2600	320	34·7	—
	Well (f)	1977	62	1270	1065	5800	1100	32·2	2·6
	Well (f)	1978	93	970	891	3400	390	24·3	1·7
	Waterhole (g)	1977	66	834	791	3200	570	35·7	3·9
	Waterhole (g)	1978	95	706	605	2500	340	26·5	0·2
	Fields (h)	1977	58	759	745	3400	800	36·7	2·8
	Tributary (i)	1977	63	601	541	2300	500	35·4	2·5
Rey Manga	Causeway (j)	1976	20	272	272	3600	1700	51·3	—
	Causeway (j)	1977	55	265	265	1400	250	58·8	9·4
	Causeway (j)	1978	79	456	360	2000	350	38·9	2·4
	2 km upstream (k)	1977	48	900	789	4500	1400	71·9	11·8
	Fields (l)	1977	49	260	260	1400	150	39·9	4·3
	Mayo Lougougnel (m)	1977	53	2090	1850	11 100	2500	54·1	5·4
	Mayo Lougougnel (m)	1978	80	5062	1635	20 500	3500	38·6	0·7
Gandi	Well (n)	1976	49	598	573	4200	530	38·2	—
	In the village (x)	1976	16	87	87	2100	1140	35·1	—
Nonozé	Well (p)	1976	50	467	464	2400	470	44·8	—
Larki	Well (q)	1976	26	720	677	10 700	4520	36·3	—
Tcholliré	Mayo Doudja (r)	1976	37	215	215	1000	240	27·6	—
	In the village (s)	1976	32	53	50	360	90	20·2	—
Touboro	Vina bridge (t)	1976	95	6395	5239	26 100	5500	64·7	—
	Tributary (u)	1976	34	65	60	730	340	38·9	—
	In the village (v)	1976	41	5	5	50	16	17·0	—
Bonandiga	In the village (w)	1976	78	1926	1917	7600	1500	78·4	—

*See Figs 1–3 for the location of fly-catching sites.
†Corresponds to the period 1 May–30 April.
‡ABR: Annual Biting Rate rounded to nearest 100.
§±S.D. of the ABR.
‖Estimated proportion of parous flies, including older parous flies.
≡Old parous flies were only recorded from May 1977.

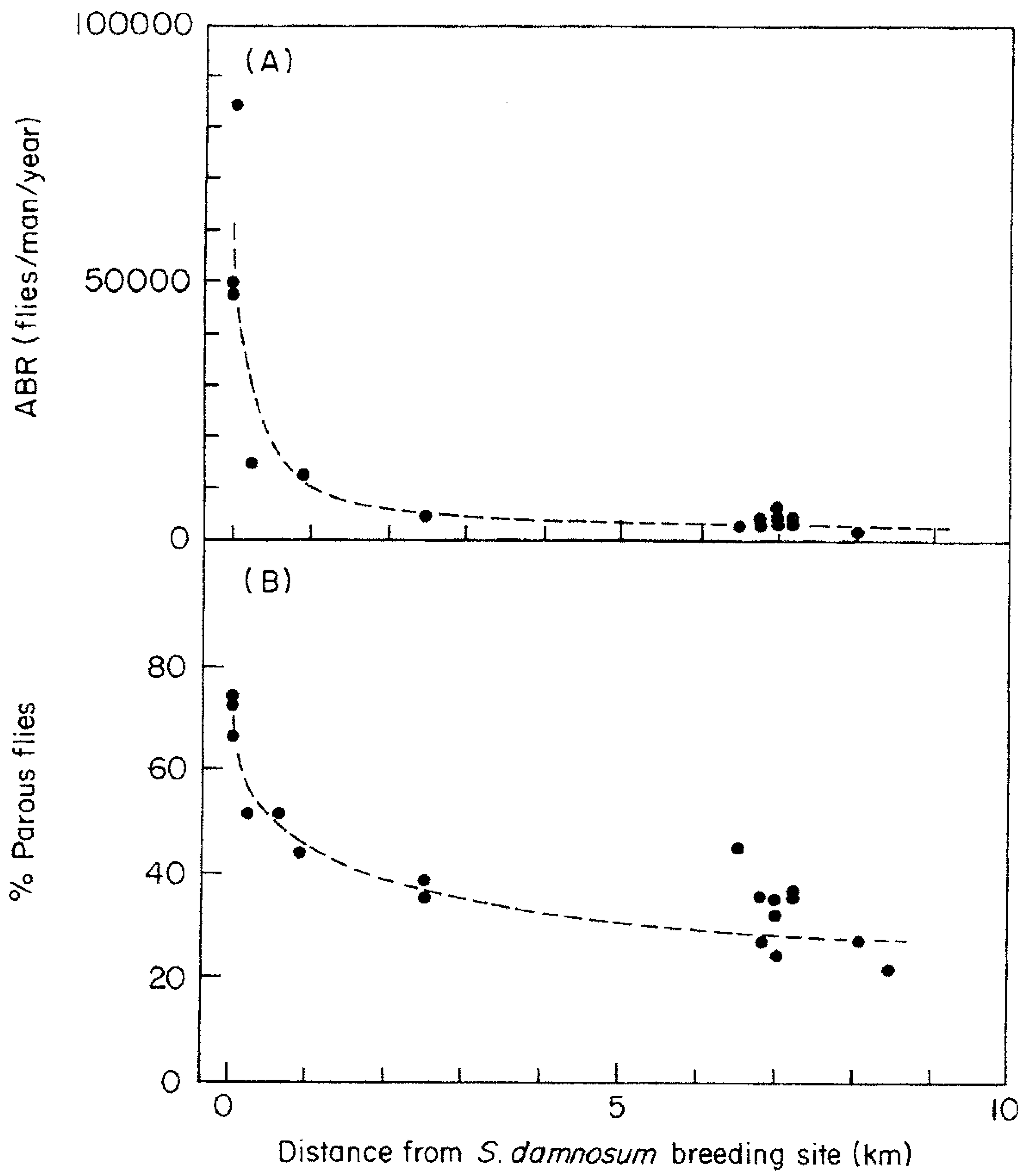


Fig. 4. Dispersal of flies away from the Mayo Rey river at Tchollire. (A) ABR: flies/man/year; (B) Percentage parous flies.

The percentage of parous and old parous flies was highest (64–73% parous and 7–9% old parous flies of the total ABR) at the main breeding sites, and decreased to 30–40% parous (0·2–4·3% old parous) at the catching sites inland (Fig. 4(B)). Although the biting rates in 1978 were similar to or only slightly lower than those in 1977, the proportion of parous, and in particular of old parous, flies was much lower in 1978, indicating a reduced life-expectancy of the fly-population during that year, when the rainfall was more than twice as high as in 1977.

Year to Year Variation in the Annual Biting Rates

At the catching sites at Mayo Galké causeway, Douffing well and Rey Manga causeway, the year to year variation in the ABR was of the same order (coefficient of variation 34, 42 and 49% respectively) for the years 1976–1978 and was similar to the variation in the water-discharge of the river Mayo Rey at Mayo Galké during the same period (35%). In 1976, when the total water-flow per hydrological year (April to March) was at an average level ($1{\cdot}62 \times 10^9$ m^3), the biting rate was highest at Mayo Galké and Rey Manga causeways. At both sites the biting rate was lower in 1977 (when the water-flow was low, $0{\cdot}98 \times 10^9$ m^3) and in 1978 (when the water-flow was high, $2{\cdot}04 \times 10^9$ m^3). An inverse situation was observed at Douffing, about 6 km from the nearest breeding sites in the rainy season tributary Mayo Bodo, where the biting rates were highest in 1977.

DISCUSSION

The location of *S. damnosum s.l.* breeding sites and their accessibility is of importance when control measures are desirable, as in this area with severe onchocerciasis. The worst affected villages were situated close to perennial breeding sites in the main water courses which were accessible to cheap *Simulium* control measures. However, treatment of the inaccessible breeding sites in the tributaries during the rainy season is only feasible by air.

The high prevalence of ocular lesions at Mayo Galké, Bonandiga and Nonozé is similar to the findings of Duke *et al.* (1975) and Anderson *et al.* (1974, 1978) in a neighbouring area of North Cameroon. It was linked to the vectors *S. damnosum s. str.* and *S. sirbanum*, as in Sudan-savanna areas in Upper Volta (Philippon, 1977; Quillevere, 1979), Nigeria (Budden, 1963; Crosskey, 1979) and Southern Sudan (Baker and Abdelnur, 1986).

Although no other vector species were found during the present study, the occurrence of *S. mengense* (Vajime and Dunbar, 1977) must be considered as this species was identified (1981) from the river Faro at Poli in a nearby area, close to the Nigerian border (Walsh and Meredith, personal communication). Little is known about the morphology and vectorial efficiency of these flies. It is possible that the three dark male flies, caught on man, belonged to this species.

The importance of the ABR as an indicator of the risk of disease transmission, especially during a *Simulium* control campaign (Walsh *et al.*, 1978) raises the question of the accuracy of its assessment. It follows from the data presented in Table 3 that the value of an ABR assessed by fly-catches at weekly intervals should be expected to lie, in about 67% of all cases, roughly within a range of $\pm 20\%$ of the value measured.

Several causes are responsible for the high S.E. of the assessment of the ABR. Some are due to the sampling bias, like the efficiency of the fly-collector, which was partly eliminated by pairing two collectors of different attraction to the flies and by exchanging this team at midday by a second team, so that one DBR was usually the result of the catches of four different collectors. Also the choice of the catching site on a sandbank, on rocks or in the shade under a tree influences the visibility and thereby the attractiveness of the collectors. The fly-collectors sat at different places at the same catching site during the various seasons of the year, according to the water-level of the river and to the height of the growing vegetation. Other causes like heavy rain, bushfire, or insecticide-spraying of the cotton-fields also accounted for a high variation between the DBRs within one month, even when the birth-rate of the fly-population was presumably fairly constant. Similarly, invasion of non-local flies from other breeding sites far away by wind-borne movements suddenly increased the DBR, especially during the early rainy season. All these causes of variation can only be controlled by increasing the number of catching days. Therefore the variation of the DBRs within one month appears to be due in most cases to those environmental factors rather than to an actual increase or decrease in the 'real' size of the local fly-population which should result in a constant raise or fall in the DBR over some weeks and which would lead to an overestimate of the S.E. by the method employed. On the other hand, the variation in the MBRs over the year is best explained by changes in the size of the fly-population, expressed by generally increasing or decreasing MBRs (Renz, 1987).

The differential dispersal of nulliparous and parous flies away from the riverside corresponded to similar observations of Leberre (1966) at the Red Volta in Upper-Volta and of Duke (1975) in the same area in North Cameroon. At the Red Volta the proportion of parous flies, taken as an average over one complete year, was 65% at the breeding site and decreased to 41% at a distance of 6 km inland. Our data indicate an even higher reduction in the parous-proportion, from 64–73% at the breeding sites to 20–44% some 5–10 km inland. In its epidemiological consequences, the wider flight-range of nulliparous flies indicates that these flies take their bloodmeals from a widespread section of the human and animal population, including the low-infected population of the villages situated further inland, whereas parous flies stay near their sites of oviposition, and hence feed and transmit the disease near the river.

On a few occasions an inverse pattern of dispersal was observed, with biting rates at inland sites higher than at the river. This was mainly seen in the months October to early December, but occurred at all rivers examined: At Mayo Galké causeway the biting rate was 35 flies on 26 October 1977, whereas 139 flies were caught at Douffing on 24 October 1977. At the Benoué at Boukma bridge the biting rate was 14 flies, as opposed to 100 flies caught at Larki (both on 22

November 1977). At the Mayo Oldiri the biting rate was 20 flies at the river on 16 November 1977, but 75 flies were caught at the village Taboun, some 3 km from the river. A similar situation was seen in the Touboro area in the middle of September, when a similar number of flies were caught at the river Vina and at the village of Bonandiga, about 2 km from the river. It remains unclear whether this different dispersal behaviour was due to a particular meteorological situation at the beginning of the dry season, or to a change in the composition of the fly-population. Coincidentally, a few larvae of *S. squamosum* were identified from samples collected during this period. This species, which predominates in the Cameroon Guinea-savanna and in the rain-forest, is known to have a higher dispersal potential (Duke, 1968).

The low biting rate at sites far away from the riversides does not necessarily mean that only a small proportion of the total bloodmeals of the whole fly-population are taken there. On the contrary, the large extension of the area with a similar, though low biting density of flies suggests a rather large number of bloodmeals taken from this area as a whole, whilst the high biting density at the river is limited to a fairly restricted area of a few hundred metres at both sides of the river. Similarly, the high parous-proportion at the breeding sites (64–78%), if taken as a parameter for the survival of a fly-population (Coz *et al.*, 1961), overestimates the proportion of old flies within the whole population. Taking into consideration the wide range of dispersal of nulliparous flies, the parous-proportion within the whole fly-population is probably not much higher than 50% on an annual average.

The on-going Onchocerciasis Control Programme in West Africa considers that an ABR of 1000 represents the maximal tolerable biting rate in a controlled area (Walsh *et al.*, 1979). In the present study the values of the ABR were above this level at all the fly-catching sites outside the villages, corresponding to the high endemicity of onchocerciasis. Even higher levels of ABR (22 000–207 000) have been measured by Duke *et al.* (1975) in the Touboro area near the villages Ndiki, Mbai-Mboum, Koumban and Bedera, where the prevalence of blindness in persons over 20 years ranged from 0 to 10%. However, it cannot be completely ruled out that there has been a general decrease in the biting rates during the past decade, due to the increasing drought and the reduced waterflow in the main rivers, especially during the dry season. Such a decrease is seen in the dry-season water discharges of the river Benoué at Garoua, where hydrological measurements date back to 1950 (Olivry and Borel, 1974).

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