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

Infection rates of the *Simulium* vectors and *Onchocerca volvulus* transmission potentials

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Populations of *Simulium damnosum s.str.* and *S. sirbanum* were examined for infections with filarial parasites during three years in the areas of Tcholliré and Touboro, at sites at different distances from *Simulium* breeding rivers, and in relation to villages with different endemicities of onchocerciasis. A total of 60 353 flies from 23 fly-catching sites were dissected.

The overall infection rate was low, 11·8% of 35 357 parous flies dissected. 1681 flies (4·8% of the total parous) contained 3557 infective larvae, 68·8% of which were morphologically indistinguishable from *Onchocerca volvulus* and 31·2% were infective 'Type D' larvae of non-human origin, indicating a high degree of zoophily of the fly populations. It was estimated that only 20–40% of all bloodmeals were taken from man.

The majority (54%) of all infective *O. volvulus* larvae were found in the heads of the flies, the remainder being in the thorax (34%) and abdomen (12%). Only 54% of the *O. volvulus* infective larvae left their vectors during a bloodmeal which, however, was not completed in most cases.

During the rainy season infection rates with *O. volvulus* infective larvae were 3·5% of the total parous flies, as compared with 1·8% during the dry season. The average number of infective larvae of *O. volvulus* per infective fly was 2·6 and 2·2 during the rainy and dry seasons respectively.

These variations in the vectorial efficiency of the fly populations, as well as variations from one site to another, could be explained by different survival rates and man-biting habits of the various vector populations during the dry and rainy seasons and in different regions, rather than by different endemic profiles of onchocerciasis in the human population.

The intensity of transmission varied seasonally and was highest (1609 to 3076 infective larvae/man/year) near the main breeding sites, where transmission was almost perennial. At distances of more than 3 km from the river transmission was mainly restricted to the rainy season and the Annual Transmission Potential was below 200, whereas low to zero levels of transmission were measured inside villages more than 3 km distant from the river. The coefficient of variation of the Annual Transmission Potentials over the three years of studies was from 31% to 192% of the mean, being higher that the variations in the corresponding levels of the biting rates, due to the low numbers of infective flies dissected at sites with low transmission.

The frequency distribution of infective larvae *O. volvulus* in infective flies could be adequately described by the truncated form of the negative binominal distribution.

Previous work has shown that the infection rates of *Simulium damnosum s.l.* vectors in the Sudan-savanna of North Cameroon are low, and that they are more closely related to the prevalence of onchocerciasis and to the number of parous flies than to the mean concentrations of microfilariae in the skin or to the total number of flies caught (Duke *et al.*, 1975).

The human host-choice of the vectors, their rate of survival to the infective age, and the mean number of infective larvae developing from one bloodmeal on a microfilarial-positive person are the main factors influencing the vectorial efficiency of a fly population (Garrett-

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Jones, 1964; Dietz, 1982). Seasonal variations in vectorial efficiency are likely to occur, following changes in the species composition and in the dispersal pattern of the fly population (Renz and Wenk, 1987; Renz, 1987; Duke, 1975). Thus, at the same man–fly contact rate, the resulting *O. volvulus* transmission potentials may vary considerably from one place to another or from the rainy to the dry season.

The Annual Transmission Potential (ATP) is an estimate of the total number of infective larvae of *O. volvulus* which could be inoculated into one man in one year, if all the infective flies biting him were to transmit their total load of infective larvae (Duke, 1968). This parameter is largely used to quantify the intensity of transmission of onchocerciasis at a given place (Duke, 1968; Garms, 1973; Duke *et al.*, 1975; Philippon, 1977; Thylefors *et al.*, 1978).

The present study was therefore aimed at investigating the seasonal and year to year variations in the infection rates and transmission potentials, found at varying distances from the *S. damnosum s.l.* breeding sites, and in relation to villages with different degrees of endemicity of disease.

In Togo, *S. damnosum s.l.* is also a potential vector of *Onchocerca ochengi*, a filarial parasite of cattle (Omar *et al.*, 1979). Up to 40% of all infective larvae found in wild-caught *S. damnosum s.l.* from a savanna area in Mali were histochemically different from *O. volvulus* (Omar and Garms, 1981). Non-*O. volvulus* infective larvae of animal origin were also found in *S. damnosum s.l.* in North Cameroon (Duke, 1967; Franz and Renz, 1980). These larvae should be distinguished from those of *O. volvulus* when calculating onchocerciasis transmission potentials.

Detailed descriptions of the study area, the selection of the fly-catching sites, and the dynamics of the vector populations (mainly *S. damnosum s.str.* and *S. sirbanum*) have been given previously (Renz and Wenk, 1987; Renz, 1987). The correlation between Annual Transmission Potentials and the endemic levels of onchocerciasis will be presented in a later paper.

MATERIALS AND METHODS

Nineteen fly-catching sites in the region of Tcholliré (8°24′ N, 14°14′ E) and four catching sites in the region of Touboro (7°46′ N, 15°21′ E) were visited at weekly, biweekly or monthly intervals for one to three years from February 1976 to May 1979. Details of the location of the catching sites and the selection of study villages are given by Renz and Wenk (1987), where the Annual Biting Rates (ABRs) and the age-composition of the vector populations are also described.

Filarial infections found during the dissection of the flies were classed into developing infections (sausage stage larvae L_1, and preinfective larvae L_2) and infective stages (L_3; Bain, 1969). Double infections, stemming from larvae ingested at two subsequent bloodmeals, were recorded when L_1 and L_3 were found in the same fly, whereas infections with L_2 and L_3 were not included in this group.

Infective larvae were classed as (1) indistinguishable from *O. volvulus* or (2) infective 'Type D', according to their morphology, length and movements (Duke, 1967; Franz and Renz, 1980), but developing stages of the two filariae could not be distinguished.

The Annual Transmission Potentials were calculated from the total number of infective larvae in the fly, regardless of their position in the head, thorax or abdomen (Duke, 1968). In order to estimate the standard deviation of the ATP, the following assumptions were made: the ATP is the product of the estimated ABR ($=A$), the average proportion of infective flies amongst the flies dissected (NIF/NFD$=B$) and the average number of infective larvae *O. volvulus* per infective fly (NIL/NIF$=C$), corresponding to the formula:

$$\mathrm{ATP} = ABC.$$

The variance of the ATP is derived, assuming independence of A, B and C:

$$V(\mathrm{ATP}) = B^2C^2V(A) + A^2C^2V(B) + A^2B^2V(C).$$

A method for the calculation of the variance of the ABR ($V(A)$) has been given in Renz and Wenk (1987). The variance of the average number of infective flies per biting fly ($V(B)$) is taken from the negative binomial distribution of the proportion of infective flies found at dissection:

$$V(B) = \mathrm{NIF}/\mathrm{NFD}^2 - \mathrm{NIF}^2/\mathrm{NFD}^3; \text{ or, if } \mathrm{NFD} \gg \mathrm{NIF},: V(B) = \mathrm{NIF}/\mathrm{NFD}^2.$$

The variance of the average number of infective larvae per infective fly ($V(C)$) is taken from the truncated negative binomial distribution of the distribution of infective larvae in infective flies (see text), w and k being the two parameters of the distribution:

$$V(C) = \mu((1 + k(1-w))/w - \mu)/\mathrm{NIF},$$

with μ being the average number of infective larvae per infective fly (NIL/NIF):

$$\mu = k(1-w)/(w(1-w^k)).$$

RESULTS

Infection Rates and Transmission Potentials

Table 1 summarizes all 23 fly-catching sites which were visited during the three year period in the vicinity of nine villages, the numbers of flies dissected and classed parous, infected (containing L_1 or L_2 or L_3), developing infected (with L_1 or L_2) and infective (with L_3), together with the total number of infective larvae, morphologically indistinguishable from *O. volvulus*, found in the infective flies, and the estimated values of the ABR and ATP.

On average, 4184 of 35 357 dissected parous flies (11·8%) carried filarial infections, of which 2624 (7·4% of the total parous) were developing infections, 1681 (4·8%) carried infective larvae of either *O. volvulus* or Type D, and 121 (0·3%) were double-infected. Of the infective flies, 1011 (2·9% of parous) carried infective larvae of *O. volvulus*, and 670 (1·9%) contained infective larvae of Type D. The average number of infective larvae per infective fly was 2·4 for *O. volvulus* and 1·7 for Type D. From this, an average number of 0·07 infective larvae *O. volvulus* per parous and 0·04 infective larvae per dissected (parous and nulliparous) fly was calculated.

The standard deviation of the ATP (Table 1, last column) was high, exceeding 100% of its value at those sites where the ATP was low. Thus, it may be calculated that the S.D. of an ATP of 100 is as high as 55, since its calculation is based on six infective larvae only, caught during one year if there was one catching day per week. From one year to another, the variation of the ATP was high even at the same place (Table 2) and depended on the variation of the water-flow of the breeding river.

Seasonal and Place-dependent Variations in the Infection Rates

Considerable differences were observed in the infection rates at sites at different distances from the river and at different seasons of the year. In order to have a sufficiently large sample of dissected flies, the results from catching sites around the nine villages were grouped into six categories (Table 1). Mayo Galké (sites a–e): at or near the breeding sites of the rivers Mayo Rey and Mayo Dokday. Rey Manga (sites j–m): 8–10 km downstream from the nearest breeding sites in the river Mayo Rey. Douffing (sites f–i): 6–8 km cross-country from the nearest breeding sites in the rivers Mayo Rey and Mayo Bodo. Tcholliré, Gandi, Nonozé, Larki (sites n–s,x): 2–10 km from the nearest breeding sites in the rivers Mayo Rey or Benoué

TABLE 1

Results from catching and dissections of Simulium damnosum s.l. *at 23 fly-catching sites around nine villages in the Sudan-savanna of North Cameroon. Numbers of flies dissected, parous and infected (including infections by* Onchocerca volvulus *and 'Type D') and the derived Annual Biting Rates (ABR ± S.D.) and Annual Transmission Potentials (ATP ± S.D. based on infective larvae, morphologically indistinguishable from* O. volvulus *in the head, thorax and abdomen of the flies)*

			Number of Simulium damnosum s.l.					O. volvulus *only*					
Village	*Fly-catching site**	*Year†*	*Dissected*	*Parous*	*Infected*	*Developing infected*	*Infective*	*Infective flies*	*Infective larvae*	*ABR*	± S.D.	*ATP*	± S.D.
Mayo Galké	Causeway (a)	1976	14 891	10 541	1119	624	522	282	603	83 800	9400	3076	483
	Causeway (a)	1977	6255	4473	653	384	280	147	319	47 900	6200	2402	423
	Causeway (a)	1978	4644	2890	295	185	116	51	134	49 600	4100	1609	245
	Mayo Dokday (b)	1977	4583	2357	361	220	158	101	262	37 400	6300	2104	392
	Mayo Dokday (b)	1978	4733	2267	239	165	82	35	71	27 700	2500	377	110
	250 m from causeway (c)	1977	2546	1343	166	100	72	53	116	14 400	1700	670	114
	900 m from causeway (d)	1977	2176	989	105	65	48	31	65	12 000	1200	355	98
	In the village (e)	1976	832	458	59	40	22	12	20	6000	760	109	77
Douffing	Well (f)	1976	547	197	23	15	11	5	12	2600	320	68	48
	Well (f)	1977	1065	356	49	32	19	12	37	5800	1100	177	93
	Well (f)	1978	891	223	22	19	3	3	6	3400	390	19	30
	Waterhole (g)	1977	791	295	26	17	10	9	15	3200	570	54	58
	Waterhole (g)	1978	605	156	11	10	2	1	1	2500	340	4	19
	Fields (h)	1977	745	256	30	21	9	6	15	3400	800	77	54
	Tributary (i)	1977	541	191	20	16	5	3	27	2300	500	157	34
Rey Manga	Causeway (j)	1976	272	123	11	7	4	2	3	3600	1700	46	49
	Causeway (j)	1977	265	162	21	12	9	5	10	1400	250	65	29
	Causeway (j)	1978	360	138	9	4	5	4	4	2000	350	19	27
	2 km upstream (k)	1977	789	576	81	43	41	21	36	4500	1400	220	91
	Fields (l)	1977	260	102	7	4	3	2	3	1400	150	12	18
	Mayo Lougougnel (m)	1977	1740	917	79	51	29	10	17	11 100	2500	91	54
	Mayo Lougougnel (m)	1978	1635	643	33	25	8	5	16	20 500	3500	185	68
Gandi	Well (n)	1976	573	224	31	24	7	2	22	4200	530	105	47
	In the village (x)	1976	87	39	2	2	0	0	—	2100	1140	0	—
Nonozé	Well (p)	1976	464	200	31	23	9	6	18	2400	470	77	60
Larki	Well (q)	1976	677	223	16	13	4	3	4	10 700	4520	79	138
Tcholliré	Mayo Doudja (r)	1976	215	68	6	4	3	1	5	1000	240	17	21
	In the village (s)	1976	50	10	2	1	1	0	—	360	90	0	—
Touboro	Vina bridge (t)	1976	5239	3380	450	323	139	139	444	26 100	5500	2767	520
	Tributary (u)	1976	60	23	0	0	0	0	—	730	340	0	—
	In the village (v)	1976	5	1	0	0	0	0	—	50	16	0	—
Bonandiga	In the village (w)	1976	1917	1536	227	175	60	60	161	7600	1500	578	194

*See Figs 1–3, Renz and Wenk, 1987 for the location of fly-catching sites.

†Corresponds to the period 1 May–30 April of the following year.

TABLE 2

Comparison of the year-to-year variation of the annual water-flow of the river Mayo Rey at Mayo Galké causeway (m^3/year) with the variation of the Annual S. damnosum s.l. *Biting Rate (ABR) and the Annual* O. volvulus *Transmission Potential (ATP)*

Location		*ABR*	*ATP*	*Mayo Rey* m^3/*year*
Mayo Galké causeway	1976	83 800	3076	$1{\cdot}62 \times 10^9$
	1977	47 900	2402	$0{\cdot}98 \times 10^9$
	1978	49 600	1609	$2{\cdot}04 \times 10^9$
	$\bar{x}$	60 433	2362	$1{\cdot}55 \times 10^9$
	C_v (%)	34	31	35
Douffing well	1976	2600	68	Seasonal
	1977	5800	177	tributary
	1978	3400	19	flowing
	$\bar{x}$	3933	88	from July to
	C_v (%)	42	92	November
Rey Manga causeway	1976	3600	46	
	1977	1400	65	See
	1978	2000	19	Mayo Galké
	$\bar{x}$	2333	43	causeway
	C_v (%)	49	53	

The fly-catching site Mayo Galké causeway lies near the breeding sites, Douffing well is situated 6 to 10 km cross-country away from the river and Rey Manga causeway is located 9 km downstream from the nearest breeding sites in the river Mayo Rey. The coefficient of variation (C_v) is ratio of the standard deviation of the three annual values divided by the mean value ($\bar{x}$) and multiplied by 100.

(Larki). Touboro (sites t–v): at the breeding sites of the river Vina (t) or 1·5–2·5 km inland from them (u,v). Bonandiga (site w): at the village, 2·5 km from the river Vina.

In these six groups of villages, the infection rate and the average number of *O. volvulus* and 'Type D' infective larvae per infective fly varied from rainy to dry season, and from one area to another (Table 3). In the rainy season, the percentage of *O. volvulus* infective flies was more than twice as high as in the dry season (3·5 and 1·8% of parous) whereas the corresponding percentage of flies with developing larvae was only slightly higher (7·9 and 6·6%). Likewise, in the rainy season the percentage of Type D infections was more than three times higher than in the dry season (2·6–0·7%).

The low general infection rate with infective stage larvae during the dry season was related to the lower proportion of parous, and in particular of old parous, flies. This indicates a much reduced rate of survival of the flies during the dry season, where the daily temperatures were either at a minimum during December–January or were highest in March and April (Renz, 1987). However, the high parous rate of the fly populations along the breeding rivers during the rainy season is also due to the preferential dispersal of nulliparous flies across country away from the river, and possibly to an immigration of old parous flies coming from other breeding sites south (Renz, 1987).

Differences in the average infective load per infective fly were not so marked between the two seasons (2·5 and 2·2 during rainy and dry seasons respectively for *O. volvulus* and 1·7 and 1·5 for Type D), but they varied from one site to another, as did the infection rates.

There was a connection, but no clear-cut correlation, between the proportion of infective parous flies and either the prevalence of onchocerciasis (Fig. 1(A)) or the microfilarial density

TABLE 3

The variation of the parous and infection rates of Simulium damnosum s.l. *flies during the dry and rainy season at different sites in the Sudan-savanna of Cameroon*

Place	*Total numbers of* S. damnosum *flies examined**		*% of examined flies* Parous		*Old-parous*		*% of parous flies carrying developing filarial larvae‡*		*% of parous flies carrying infective larvae* O. volvulus *(95% confidence limits)*		*Arithmetic mean number of infective larvae per infective fly*		*% of parous flies carrying infective larvae 'Type D' (95% confidence limits)*		*Arithmetic mean number of infective larvae per infective fly*	
	RS	*DS*	*RS*	*DS*	*RS*	*DS*	*RS*	*DS*	*RS*	*DS*	*RS*	*DS*	*RS*	*DS*	*RS*	*DS*
Mayo Galké	24 773	15 887	63·6	60·3	7·7	3·5	7·3	6·6	3·5 (3·2–3·7)	1·8 (1·5–2·1)	2·3	2·0	3·2 (2·9–3·5)	0·8 (0·6–1·0)	1·7	1·6
Douffing	3504	1681	36·6	23·4	3·1	0·8	8·4	5·6	2·7 (1·9–3·8)	1·0 (0·3–2·8)	2·9	2·5	1·3 (0·7–2·1)	1·0 (0·3–2·8)	2·2	1·3
Rey Manga	2590	2731	59·6	40·9	8·5	1·7	6·8	3·7	2·3 (1·7–3·2)	1·2 (0·6–2·0)	1·9	1·5	2·5 (1·8–3·5)	1·0 (0·5–1·8)	1·6	1·5
Gandi, Nonozé, Larki, Tcholliré	1423	643	34·5	42·5	—	—	9·0	8·4	1·6 (0·7–3·3)	1·5 (0·5–4·0)	4·5	3·3	1·8 (0·9–3·6)	1·1 (0·2–3·5)	1·7	1·0
Touboro	2252	3052	66·2	62·7	—	—	11·4	8·0	6·4 (5·3–7·8)	2·3 (1·6–3·0)	3·3	3·0	0	0	—	—
Bonandiga	1823	94	82·7	29·8	—	—	11·4	10·7	4·0 (3·1–5·1)	0 (0–15·1)	2·7	—	0	0	—	—
∑ all sites	36 365	24 088	60·6	55·2	7·2	2·8	8·0	6·7	3·5	1·8	2·5	2·2	2·6	0·7	1·7	1·5

*RS: rainy season (May to October); DS: dry season (November to April).
†Old-parous flies were only recorded starting May 1977.
‡Developing filarial larvae were not distinguished into '*O. volvulus*' and 'Type D'.

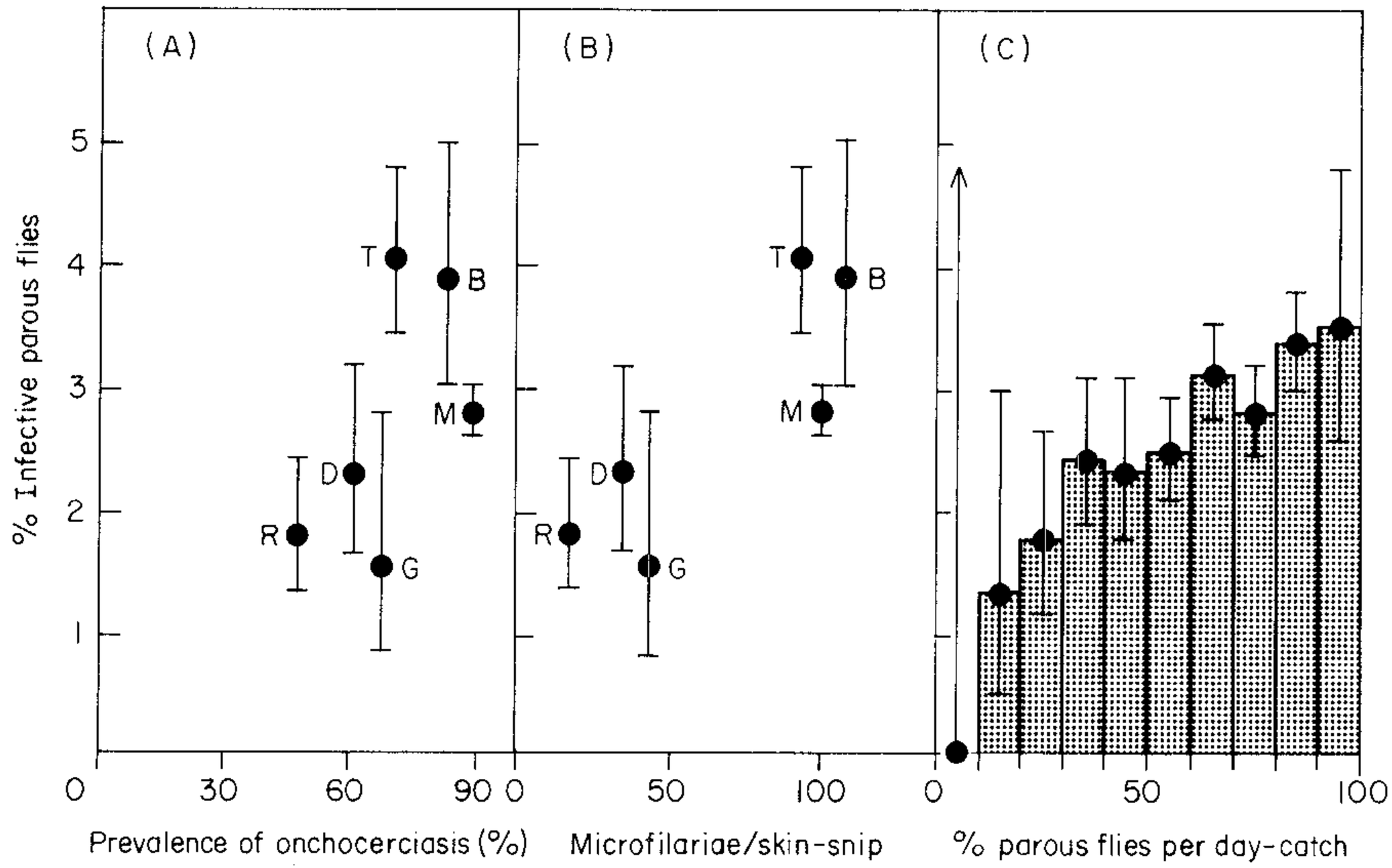

Fig. 1. The prevalence of infective parous flies in relation to: (A) The prevalence of onchocerciasis (positive skin-snip) at the study villages. (B) The intensity of human infection (arithmetic mean number of microfilariae per skin-snip). (C) The age-composition of the biting fly population (proportion of parous flies per day-catch). The villages were: R: Rey Manga (prevalence of onchocerciasis 51%); D: Douffing (61%); G: Gandi + Larki + Tcholliré + Nonozé (63%); T: Touboro (69%); B: Bonandiga (83%); M: Mayo Galké (90%). The length of the vertical lines indicates the 95% confidence interval.

(Fig. 1(B)). This could be explained by the seasonal variation in the proportion of infective parous flies. Since this proportion was much lower during the dry season, the annual average of the proportion of infective parous flies depended mainly on the proportion of the total annual catch dissected during the rainy or dry season respectively. At Rey Manga, where the majority of flies were caught during the dry season, the annual average of the infective rate was lower than, for example, at Douffing, where two-thirds of the flies stemmed from the rainy season, though the infection rates were not very different at the two sites during the respective seasons of the year. At Touboro and Bonandiga, the high proportion of infective flies is explained by a higher degree of anthropophily of the fly population, as is also evidenced by the absence of Type D infections. The close correlation between the percentage of infective parous flies and the overall percentage of parous flies per day-catch (Fig. 1(C)) underlines the crucial importance of the rate of survival of the flies on their vectorial efficiency.

In order to have a simple index for the correlation between the intensity of human infection (average microfilarial density of the exposed population) and the vectorial efficiency of the flies, Fig. 2 shows: the average number of infective larvae of *O. volvulus* (A) per fly dissected, (B) per parous fly only and (C) per infective fly. Whilst the vectorial efficiency seems to increase with increasing microfilarial densities, the average number of infective larvae per infective fly decreases at high intensities of infection. However, since the villages were all different with respect to their distance from the nearest *Simulium* breeding sites and to the degree of zoophily of the fly populations, it is difficult to decide the significance of these differences. In addition, changes in the species-composition of the vector population during the dry and rainy season and in different river systems might be of importance. Higher infective loads were observed when the vector population was mainly *S. damnosum s.str.*, as in the region of Touboro and Bonandiga or during the rainy season in the region of Tcholliré (Renz and Wenk, 1987).

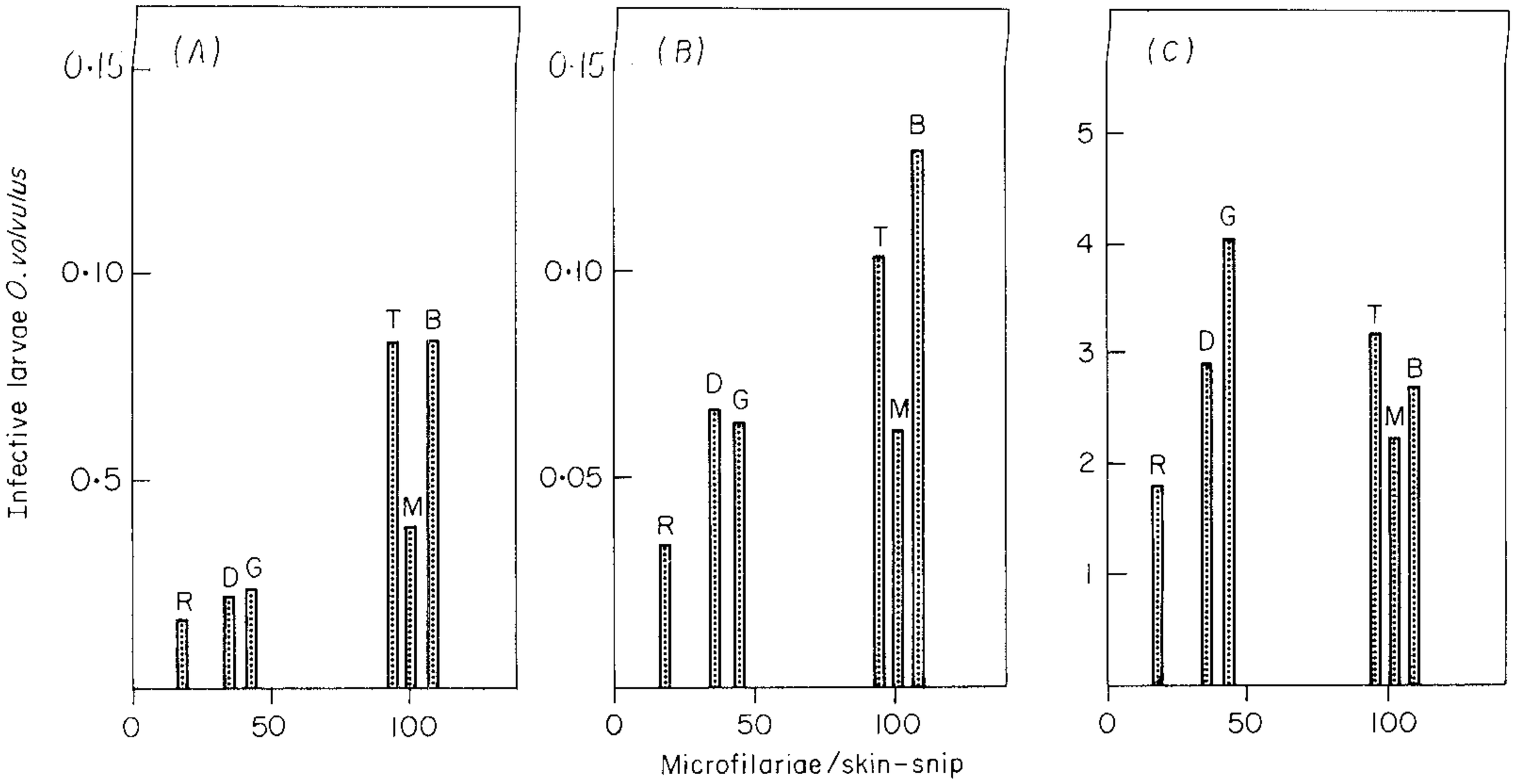

Fig. 2. Histograms comparing the study-villages with regard to the number of *O. volvulus* infective larvae (A) per *S. damnosum s.l.* dissected, (B) per parous fly only and (C) the arithmetic mean number of *O. volvulus* larvae per infective fly. The villages are arranged from left to right according to their adjusted arithmetic mean microfilarial density at the buttock: R: Rey Manga (16 mff/snip, without Mayo Lougougnel); D: Douffing (35 mff/snip); G: Gandi + Larki + Tcholliré + Nonozé grouped together (43 mff/snip, weighted by the ABR); T: Touboro (95 mff/snip); M: Mayo Galké (101 mff/snip); B: Bonandiga (109 mff/snip).

The Number and the Location of the Infective Larvae *O. volvulus* in Infective Flies

Of the total of 2446 infective larvae dissected out of 1011 flies, 1325 larvae (54·2%) were located in the head of the flies, 820 (33·5%) were in the thorax and 301 (12·3%) in the abdomen. 64·9% of all infective flies carried infective larvae in the head (2·02 infective larvae per infective head).

The frequency distribution of the total number of infective larvae per infective fly could be adequately described by the truncated form of the negative binomial distribution, the parameters (w, k) of which were calculated by maximum likelihood estimators (Table 4). Non-infective flies were observed much more frequently than expected by the zero-class of the distribution $(p_0 = w^k)$. The exception was Rey Manga where only a few infective flies were dissected. The low value of parameter k at this site indicates that the distribution could also be described by a log-series distribution.

The Loss of Infective Larvae during a Bloodmeal of the Flies

From May 1977, the presence of traces of a fresh bloodmeal was recorded during the dissection of the wild-caught flies. Of 18 334 parous flies dissected, 2278 flies (12·43%) had taken, at least partially, one bloodmeal, which in the case of incomplete meals, might have been taken either on the fly-collector or elsewhere. According to Table 5, the flies lost about 54% of their total load of *O. volvulus* infective larvae during this bloodmeal (loss from head, thorax and abdomen 68, 31 and 57% respectively). 2·85% of the parous flies without a bloodmeal (457/16 056) carried infective larvae of *O. volvulus*, but only 1·84% (42/2278) had infective larvae after the bloodmeal. This means that 35% of the infective flies lost all infective larvae during the bloodmeal. If one takes into consideration that most of our flies had taken only incomplete bloodmeals, these results are comparable to those published by Duke (1973) and Philippon

TABLE 4

Fitting the observed frequency distribution of infective larvae O. volvulus *in infective* S. damnosum s.l. *flies to the truncated negative binomial distribution*

Number of flies not infective		*Gandi, Larki, Douffing Tcholliré, Nonozé*		*Touboro Bonandiga*		*Mayo Galké*		*Rey Manga*	
		Observed 2015	*Estimated 93*	*Observed 6922*	*Estimated 326*	*Observed 39 948*	*Estimated 2130*	*Observed 5272*	*Estimated 320 000*
Number of infective larvae *O. volvulus* per infective fly	1	19	19·87	81	79·06	350	357·86	31	29·78
	2	13	10·16	36	40·32	178	155·04	10	9·91
	3	5	6·21	28	24·40	70	80·88	4	4·40
	4	2	4·10	13	15·93	42	45·77	1	2·19
	5	6	2·83	11	10·85	25	27·11	1	1·17
	6	0	2·01	7	7·60	16	16·54	0	0·65
	7	0	1·45	8	5·43	12	10·30	0	0·37
	8	1	1·07	4	3·93	8	6·51	1	0·22
	9	2	0·79	2	2·88	3	4·16	1	0·13
	10	1	0·59	2	2·12	1	2·69	0	0·08
	11	0	0·45	2	1·58	1	1·75	0	0·05
	12	0	0·34	0	1·18	1	1·14	0	0·03
	13	1	0·26	2	0·89	2	0·75	0	0·02
	14	1	0·20	1	0·67	1	0·50	0	0·01
	15	0	0·15	1	0·51	0	0·33	0	0·01
	16	0	0·12	1	0·39	0	0·22	0	0·00
	17	0	0·09	0	0·29	0	0·15	0	0·00
	18	0	0·07	0	0·22	1	0·10	0	0·00
	19	0	0·05	0	0·17	1	0·07	0	0·00
	20+	0	0·19	0	0·56	0	0·13	0	0·00
Total infective flies		51		199		712		49	
m_a infective larvae/fly		3·157	3·157	3·040	3·040	2·233	2·233	1·816	1·817
Estimate of w			0·1914		0·2044		0·3015		0·3346
Estimate of k			0·2655		0·2819		0·2405		0·00014
χ^2 (df)		1·6 (2)		3·41 (7)		10·43 (8)		0·26 (1)	
α		0·46		0·86		0·26		0·57	

Observed: observed number of flies in the corresponding class

Estimated: estimated number of flies, from the calculated distribution

χ^2 (df) $= \dfrac{(\text{observed-estimated})^2}{\text{estimated}}$; the brackets indicate values taken together for the calculation of χ^2

df: degrees of freedom.

α: probability of coincidence between observed and estimated distribution; 0: no coincidence; 1: identical.

Formula of the truncated negative binominal distribution: $P(s) = w^k(1-w)^s\,(k+s-1)!/(k-1)!s!(1-w^k)$; $s = 1,2,3\ldots$.

(1977), who both found a loss of 80% of the infective load when the flies were allowed to take a complete bloodmeal on a volunteer.

TABLE 5

The escape of infective larvae during a bloodmeal of their vectors

	Infective larvae O. volvulus *in* S. damnosum s.l.		*Infective larvae Type D in* S. damnosum s.l.	
No. of parous flies examined	*Without bloodmeal 16 056*	*With bloodmeal 2278*	*Without bloodmeal 16 056*	*With bloodmeal 2278*
Total for head, thorax, abdomen:				
No. flies with infective larvae	457	42	358	42
Total no. infective larvae	1083	71	610	74
No. infective larvae/parous fly	0·0675	0·0312	0·0380	0·0325
Loss of infective larvae during bloodmeal (%)	53·8		14·5	
Head only:				
No. heads with infective larvae	277	17	158	11
Total no. infective head-larvae	548	25	220	14
No. infective larvae/parous head	0·0341	0·0110	0·0137	0·0061
Loss of infective head-larvae during bloodmeal (%)	67·7		55·5	
Thorax only:				
No. thorax with infective larvae	243	27	188	23
Total no. infective thorax-larvae	370	36	234	29
No. infective larvae/parous thorax	0·0230	0·0158	0·0146	0·0127
Loss of infective thorax-larvae during bloodmeal (%)	31·3		13·0	
Abdomen only:				
No. abdomen with infective larvae	118	9	110	19
Total no. infective abdomen-larvae	165	10	156	31
No. infective larvae/parous abdomen	0·0103	0·0044	0·0097	0·0136
Loss of infective abdomen-larvae during bloodmeal (%)	57·3		−40·2	

Infective larvae of Type D were much less successful in leaving the vector, though they were usually found more actively curling during dissection than the infective larvae of *O. volvulus*. Only about 15% of these larvae left their vectors during a bloodmeal on the human host, and there were even more larvae in the abdomen in flies with a bloodmeal as compared to those without. However, these results are based on small samples and it seems risky from a statistical point of view to postulate that these infective larvae did not leave their vector because it was feeding on an unsuitable host.

From the proportion of parous flies that had taken a bloodmeal, and from the proportion of infective larvae that left the vector during that bloodmeal, it could be calculated that 6·7% of the total infective load had left the vector during the bloodmeal taken immediately before being caught. Assuming that all these bloodmeals were effectively taken on the fly-collectors, this would mean that a fly collector is exposed to about 0·5% of the calculated ATP (one catching-day per week, half-day shifts), and if he worked for five days a week about 2·5% of the average ATP would be transmitted to him.

Monthly and Annual Transmission Potentials

The variations in the Monthly Transmission Potentials are given for three consecutive years of fly-catching at Mayo Galké causeway, Douffing well and Rey Manga causeway in the

Tcholliré area, and for the Touboro Vina bridge and Bonandiga village in the Touboro area (Fig. 3).

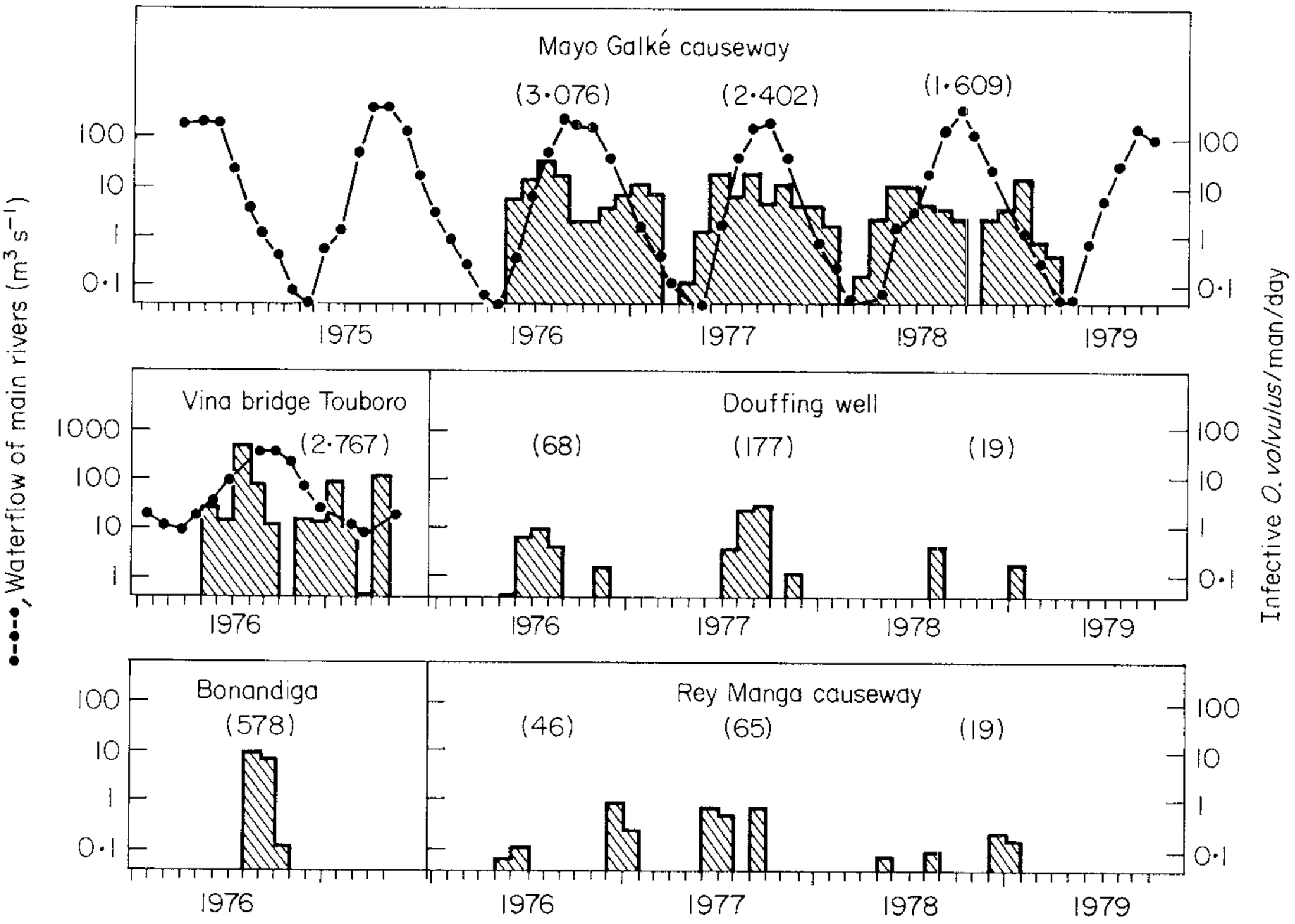

Fig. 3. The monthly variations of the *O. volvulus* transmission potentials (infective larvae *O. volvulus*/man/day) and the waterflow of the breeding rivers Mayo Rey at Rey Manga causeway and Vina du Nord at Touboro bridge (m^3 s). The values in brackets give the estimated ATP.

Three patterns of seasonal fluctuations in the transmission of *O. volvulus* could be distinguished:

All-year-long transmission near the perennial *S. damnosum s.l.* breeding sites at Mayo Galké causeway and the Vina bridge, with highest Monthly Transmission Potentials of about 500 infective larvae man/month at the beginning of the dry and rainy seasons. The ATPs at these two places were between 1609 and 3076.

Rainy season transmission during the months of June to September as a result of additional breeding sites in the rainy season tributaries, as well as of a different dispersal of parous flies during the rainy season. The Monthly Transmission Potentials were moderate and the ATP did not exceed 200 at the villages Douffing, Gandi and Nonozé, but was rather high at Bonandiga.

Moderate seasonal transmission at the beginning of the rainy and dry seasons, with the highest transmission in December and January. The ATP was between 20 and 70 at Rey Manga causeway. The transmitting flies probably came exclusively from perennial breeding sites in the river Mayo Rey, which were most productive at the beginning of the dry and rainy seasons.

Seasonal Variations in the Ratio of Infective to Infected Flies

Seasonal variations in the age-composition of the fly populations, as indicated by the change in the ratio of infective to developing infected flies, are shown in Fig. 4, for increasing distances

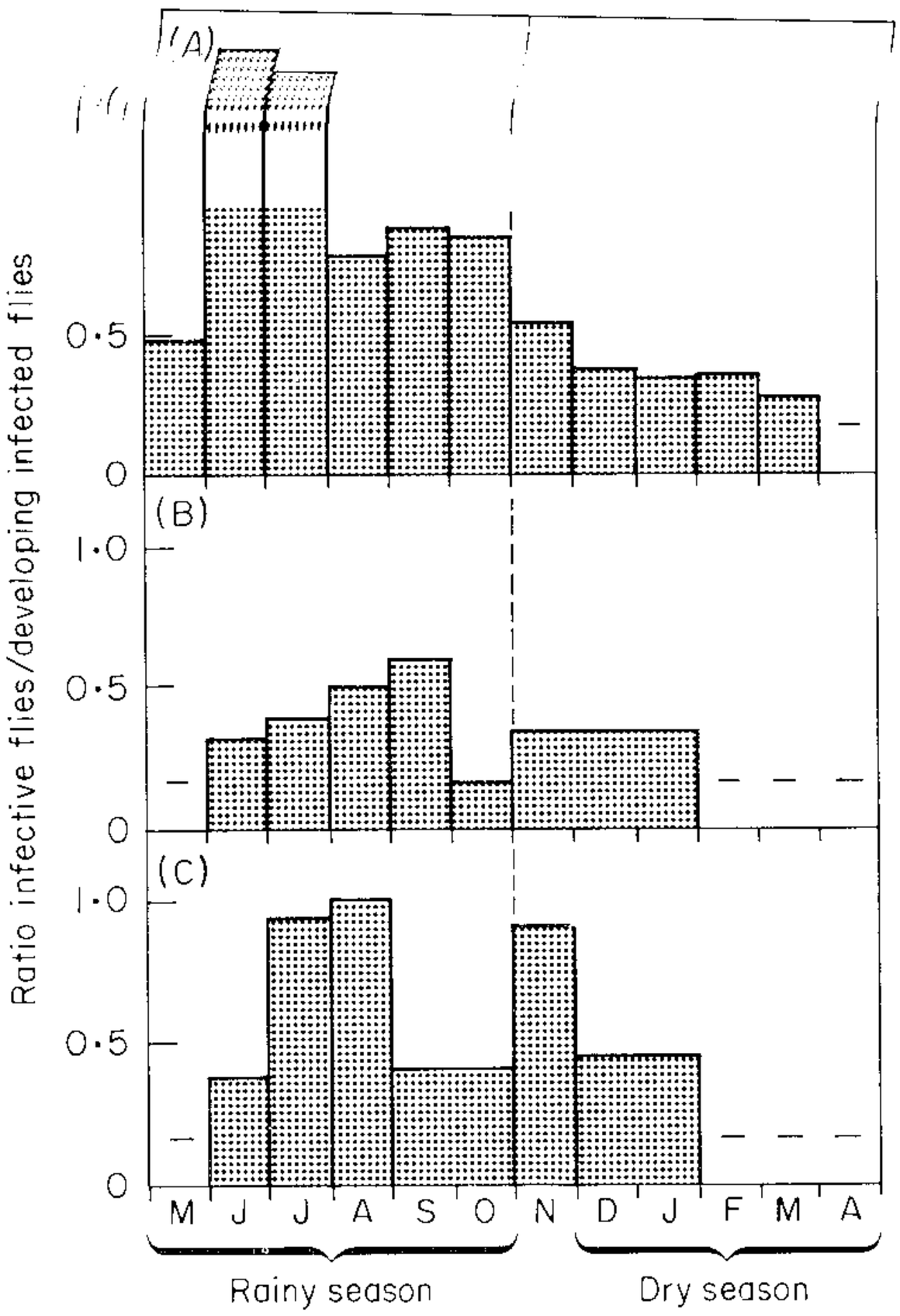

Fig. 4. Showing the monthly variation of the ratio of infective to developing infected flies coming to bite on man over the year at (A) Mayo Galké (8 place-years; 1783 flies infected; 1300 flies infective), near to an almost perennially productive *S. damnosum s.l.* breeding site; (B) Douffing, Gandi, Larki, Nonoze and Tcholliré (13 place-years; 197 flies infected; 83 flies infective), some 2–10 km cross-country away from the nearest breeding sites, and (C) Rey Manga (7 place-years, 146 flies infected, 99 flies infective) 3–9 km downstream from the breeding sites in the river Mayo Rey. Infected flies, containing developing stage larvae are supposed to attack for their second or subsequent bloodmeal, whereas infected flies are on their third or subsequent meal.

, less than ten infected flies dissected.

from the *Simulium* breeding sites in the river Mayo Rey. At the breeding site there were even more infective than infected flies during the months of June and July, and a similar situation was seen in August at Rey Manga, about 9 km downstream from the nearest breeding sites. Douffing, Gandi, Nonozé, Tcholliré and Larki never reached such high ratios. At all sites this ratio decreased during the dry season, and it reached low values in the hot dry season. The average ratio for the whole year was 0·77 at Mayo Galké causeway, 0·68 at Rey Manga (wihout Mayo Lougougnel) and 0·42 at the other sites. These ratios corresponded to a decrease in the overall parous rates at these sites, situated at increasing distances from the *Simulium* breeding sites (69, 57 and 37% parous flies respectively of the total flies dissected).

DISCUSSION

The low infection rates of parous flies with *O. volvulus* contrasted with infection rates reaching 20–30%, as seen in the Togo savanna (unpublished observation), and from those of reinvading flies at Leraba-bridge in Upper Volta, where more than 15% of the total biting fly population carried infective larvae morphologically indistinguishable from *O. volvulus* (Garms *et al.*, 1979). However, they were similar to the results of Duke *et al.* (1975) from a neighbouring area at Touboro, where only 3·3–4·4% of parous flies carried developing infections and where 2·9% of

the flies were infective. This can be explained by a high degree of zoophily of the flies, as also evidenced by the frequent infections with Type D infective larvae. Duke (1967) also found similar high infection rates with Type D larvae (30% of infective flies) during the dry season at Mayo Boki, a tributary of the river Benoué northwest of Tcholliré, but those larvae were found only rarely in the region of Touboro (2·0% of infective flies, Duke *et al.*, 1975). During the present study no infective larvae of Type D were observed near Touboro or Bonandiga, though it is not impossible that some infections were overlooked since one infection was found in a sample of flies from the Vina bridge near Touboro, not included in the present evaluation. The adult hosts of Type D filariae are still unknown. A rather haphazard survey for animal filariae showed the presence of microfilariae in buffaloes (*Synerus caffer*) and cattle (*O. armillata, O. gutturosa* and *Setaria sp.*), in the rock hyrax (*Procavia capensis*) and in a majority of the larger bird species examined (mff. positive: *Streptopelia senegalensis, Columba guinea, Lamprotornis purpureus, Oriolus auratus, Crinifer piscator, Centropus senegalensis*).

In contrast to the low density of the human population in the study area (less than two inhabitants per km^2), game animals and birds were abundant in the neighbouring hunting zones and in the national parks surrounding Tcholliré (13 to 19 large game animals per km^2, Van Lavieren and Esser, 1979). Evidence of the feeding of *S. damnosum s.l.* on animals was found by Disney and Boreham (1969) from precipitin examination of bloodgorged wild-caught flies from Mayo Boki in North Cameroon: of three bloodmeals examined, two were identified to be of avian origin and the third had been taken from a primate.

If one assumes that the overall prevalence of onchocerciasis in that part of the human population having the closest contact with the fly population averaged around 70% (cf. Table 1 in Renz and Wenk, 1987), and that only 40 to 50% of all flies feeding on a microfilarial positive person will contain developing larvae at the time of the subsequent bloodmeal (Philippon, 1977; Quillévéré, 1979), then 28 to 35% of all parous flies would be expected to carry developing stages of *O. volvulus*. This figure is much higher than the percentage of *O. volvulus* infected flies observed (4·5 to 11·4% by calculation), after the subtraction of the estimated proportion of Type D infection (0 to 40%). This would suggest that only 20% (at Tcholliré) to 40% (at Touboro) of all bloodmeals were taken on man.

As a corollary, if the density of the human population were to increase, or if the availability of non-human hosts were to decrease, there would be a potential danger that the flies would turn more to the human host, thus giving a much higher ATP at the same Annual Biting Rate. Prost *et al.* (1979) showed that hyperendemic onchocerciasis was common when the population density fell below the threshold level of 35 inhabitants per km^2. This implies that the population density in the area of the present study would have to be raised considerably in order to reach this safe level.

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