PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Progress in Controlling the Reinvasion of Windborne Vectors into the Western Area of the Onchocerciasis Control Programme in West Africa [and Discussion]

R. H. A. Baker, P. Guillet, A. Seketeli, P. Poudiougo, D. Boakye, M. D. Wilson, Y. Bissan, R. Garms, R. A. Cheke, R. Sachs, J. B. Davies, M. A. Howe, M. J. Lehane and A. L. Millest

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Progress in controlling the reinvasion of windborne vectors into the western area of the Onchocerciasis Control Programme in West Africa

By R. H. A. Baker†, P. Guillet, A. Sékétéli, P. Poudiougo, D. Boakye, M. D. Wilson‡ and Y. Bissan

Onchocerciasis Control Programme, B.P. 549, Ouagadougou, Burkina Faso

Since vector control began in 1975, waves of *Simulium sirbanum* and *S. damnosum s.str.*, the principal vectors of severe blinding onchocerciasis in the West African savannas, have reinvaded treated rivers inside the original boundaries of the Onchocerciasis Control Programme in West Africa. Larviciding of potential source breeding sites has shown that these 'savanna' species are capable of travelling and carrying *Onchocerca* infection for at least 500 km northeastwards with the monsoon winds in the early rainy season. Vector control has, therefore, been extended progressively westwards. In 1984 the Programme embarked on a major western extension into Guinea, Sierra Leone, western Mali, Senegal and Guinea-Bissau. The transmission resulting from the reinvasion of northern Côte d'Ivoire and Burkina Faso has been reduced by over 95%, but eastern Mali has proved more difficult to protect because of sources in both Guinea and Sierra Leone. Rivers in Sierra Leone were treated for the first time in 1989 and biting and transmission rates in Sierra Leone and Guinea fell by over 90%. Because of treatment problems in some complex rapids and mountainous areas, flies still reinvaded Mali, though biting rates were approximately 70% lower than those recorded before anti-reinvasion treatments started. It was concluded that transmission in eastern Mali has now been reduced to the levels required to control onchocerciasis.

1. Introduction

Since vector control started in 1975, waves of *Simulium sirbanum* and *S. damnosum s.str.* the principal vectors of severe blinding onchocerciasis in the West African savannas, have reinvaded treated rivers inside the original boundaries of the Onchocerciasis Control Programme in West Africa (OCP) (Le Berre *et al.* 1979). Larviciding of potential source breeding sites has shown that these 'savanna' species are capable of travelling and carrying *Onchocerca* infection for at least 500 km northeastwards with the monsoon winds in the early rainy season (Garms *et al.* 1979; Magor & Rosenberg 1980; Walsh *et al.* 1981; Johnson *et al.* 1985; Garms & Walsh 1987). Annual Transmission Potentials (ATP), as defined by Walsh *et al.* (1978), in communities near the original western borders of the Programme have remained above tolerable levels and human infection indices have decreased much more slowly than in central areas where this reinvasion has been controlled. Vector control has, therefore, been extended progressively westwards.

Garms *et al.* (1979) documented how experimental treatments of the Marahoué and Sassandra Basins in western Côte d'Ivoire during 1977 and 1978 markedly reduced the reinvasion of the Leraba and Upper Bandama Basins in the northeast of that country. In 1979,

† Present address: Wood View, Church Fields, Stonefields, Woodstock OX7 2PP, U.K.
‡ Present address: Department of Biological Sciences, University of Salford M5 4WT, U.K.

year-round control activities were extended to these river basins and substantial reductions in biting and transmission were recorded, although the Marahoué and Sassandra continued to be reinvaded (Walsh *et al.* 1981). In 1984, the Programme embarked on a major western extension into Guinea, Sierra Leone, western Mali, Senegal, and Guinea-Bissau. The first significant impact on reinvasion occurred in 1985 when the Upper Sassandra Basin in southeastern Guinea was treated with larvicides for the first time. Biting and transmission by re-invading flies in the Sassandra, Marahoué, Bandama and Leraba Basins decreased by over 90% (Baldry *et al.* 1985).

The Baoulé, Bagoé and Banifing tributaries of the River Niger in southeastern Mali and the extreme northwest of Côte d'Ivoire have been treated since 1977 but have proved to be more difficult to protect. The treatment of the Sankarani and Fié, the easternmost river basins in Guinea, had only a marginal effect on reinvasion (Baker *et al.* 1986). Further west, but still downwind and within 300 km of the re invaded areas, the Milo, Niandan, Kouya, Mafou and Niger Rivers were found to contain very large *S. sirbanum* breeding sites and flies collected from these sites were similar in size to those invading. Once the Inter-Tropical Convergence Zone (ITCZ) had been established to the north of the reinvasion zone, the periodicity of reinvasion could be related to changes in the height of these rivers, starting soon after their first rise at the end of the dry season and ending when they began to flood after the onset of the main rainy season. It was concluded that these rivers must be the principal sources of the reinvading flies (Baker *et al.* 1987).

This paper describes progress in discovering the sources, elucidating the migration pathways and controlling reinvasion in the western area of the OCP during 1987–1989. Progress in containing the reinvasion of the eastern area of the OCP has been presented by Garms *et al.* (1982); Cheke & Garms (1983) and Walsh (discussion after Le Berre, this symposium).

2. Study area

The area covered by this study (figure 1) extends through five countries and includes the Upper Niger River Basin in Mali and Guinea, the Sassandra, Bandama, Comoé and Black Volta River Basins in Côte d'Ivoire and Burkina Faso, together with coastal river basins in Sierra Leone such as the Great and Little Scarcies and Seli (Rokel). Descriptions of these areas have been given by Baldry *et al.* (1985) and Baker *et al.* (1986, 1987) and, for Sierra Leone, by Post & Crosskey (1985).

3. Methods

The gradual westward extension of OCP's vector control operations was preceded by extensive helicopter and ground prospections to determine the geographical and seasonal distribution of breeding sites for each vector species. A network of points (only a few of which are shown in figure 1) for 11-hour day collections of biting flies was progressively established along all the main rivers. Flies were dissected to determine parity and infection following a standard protocol (Walsh *et al.* 1979). Water-level gauges were installed or recalibrated on all the main watercourses, the most representative being fitted with Argos^{R} beacons, which transmitted river heights every 20 min to the aerial bases via satellite, to enable the accurate calculation of discharge rates.

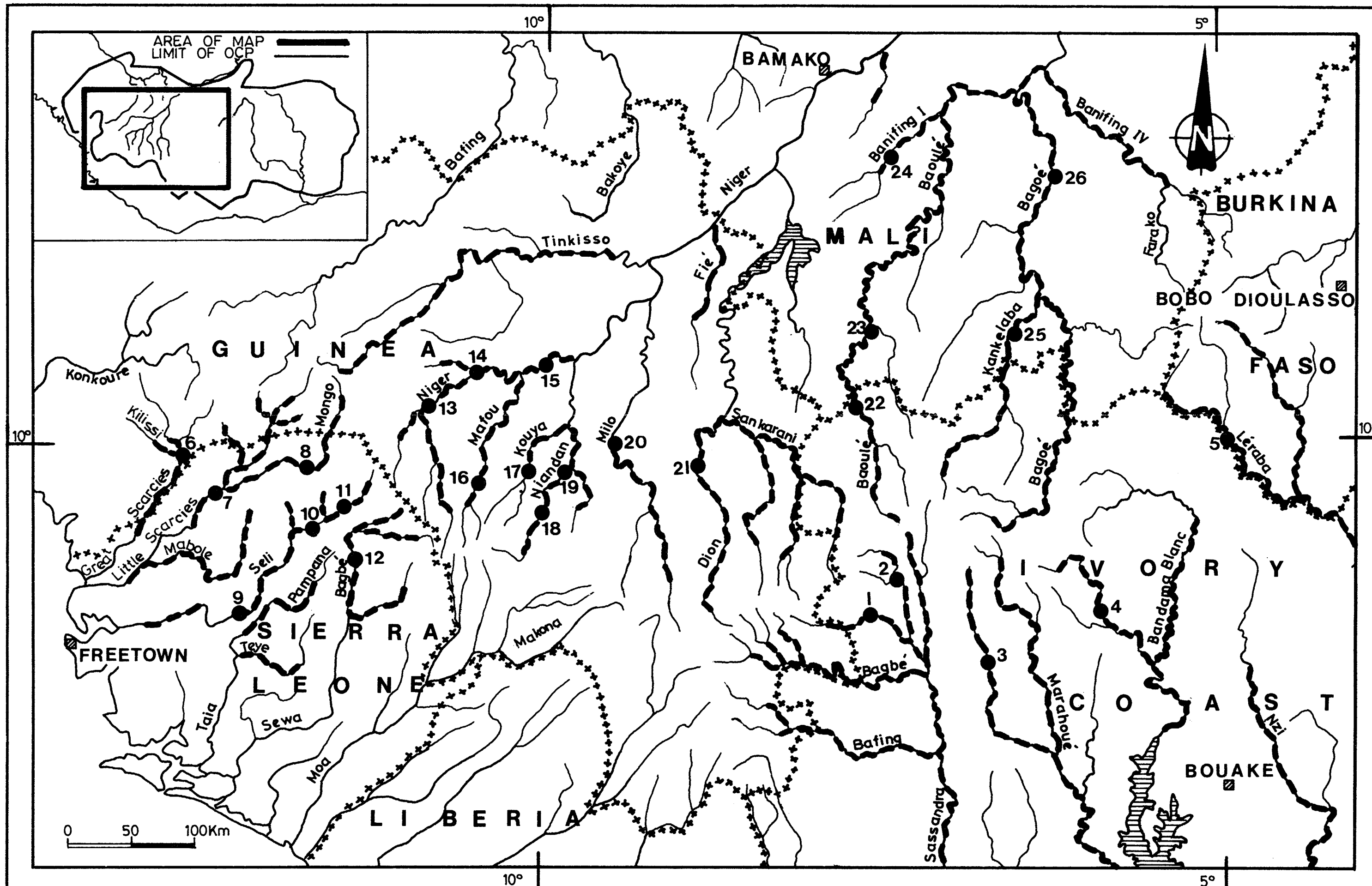

FIGURE 1. The Study Area showing: country boundaries (+ + + + +), the main rivers (thin lines), the river lengths (at maximum) treated in 1989 (thick dashed lines), and the capture points mentioned in the text (1, Niamotou; 2, Massadougou; 3, Kato, 4, Gîte 3; 5, Pont Leraba; 6, Badi Kanti; 7, Kaba Ferry; 8, Musaia; 9, Makpankaw; 10, Arfanya; 11, Yirafilaia; 12, Yifin; 13, Balandougou; 14, Banfarala; 15, Diaragbela; 16, Yalawa; 17, Kouya Laya; 18, Yradou; 19, Sansanbaya; 20, Morigbedougou; 21, Téré; 22, Madina; 23, Madina Diassa; 24, Mpiela; 25, Kankela; 26, Metela).

Cytotaxonomy of the larval polytene chromosomes (Vajime & Dunbar 1975) was the only unequivocal method of identifying savanna vectors, but adult females could generally be distinguished from 'forest' forms of the *S. damnosum s.l.* complex in this area by their pale wing tufts (Kurtak *et al.* 1981), pale fore-coxae and short, pale, compressed antennae (Garms *et al.* 1982; R. H. A. Baker *et al.*, unpublished). In Sierra Leone, *S. squamosum* were distinguished by electrophoresis (M. C. Thomson, unpublished).

Maps showing the distribution of each cytospecies were prepared and compared with graphs showing the strength and periodicity of reinvasion in the areas under vector control. In this way, the critical river stretches requiring priority treatment to prevent reinvasion were selected. To minimize the costs of vector control, only river stretches with rapids colonized by the savanna vector species were subjected to weekly aerial larviciding. Kurtak *et al.* (1987) have reviewed the insecticides, application methods and strategies involved. One biological (*Bacillus thuringiensis* serotype H14) and four chemical insecticides (temephos, chlorphoxim, permethrin, and carbosulfan) were carefully alternated to maintain effective control and minimize the development of insecticide resistance while preserving the ecological balance in the treated rivers. The insecticides were generally applied by helicopter, although a fixed-wing aircraft was sometimes used when river discharges were high.

In the Upper Sassandra Basin of southeastern Guinea, where anti-invasion larviciding had been so successful (Baldry *et al.* 1985), the same treatment limits were maintained, enlarging as each large tributary began to flow and contracting with the disappearance of savanna species.

As a result of the limited effects of vector control in the Sankarani and Fié Basins in 1984 and 1985 (Baker *et al.* 1986) and the discovery of the very large savanna breeeding sites along the lowland stretches of the other main rivers in the Upper Niger Basin in eastern Guinea (Baker *et al.* 1987), control operations had to be extended to these rivers. During 1986, *B. thuringiensis* (*B.t.*) H14 larviciding was carried out in the Sankarani Basin to contain insecticide resistance, while in the Upper Niger Basin, the network of capture points to monitor control became operational, base-line data were collected and the river gauges installed and calibrated. All stretches of rivers in the Upper Niger Basin harbouring savanna flies (figure 1) were included in anti-reinvasion treatment circuits from April–July in 1987, 1988 and 1989. In Sierra Leone, the collection of baseline data, the installation of river gauges and the training of the National Onchocerciasis Team began in 1988, and these results were used to determine the river stretches requiring priority treatment when vector control was initiated in April 1989 (figure 1).

To evaluate the achievements of an anti-invasion vector control campaign, the source breeding sites of any flies still biting within the treated area must be interpreted from the vector monitoring data. The possibility of local breeding within the treated area must first be excluded either directly by prospections of breeding sites or indirectly from the parous rates, with nulliparous rates above 20%, usually implying a control failure. The existence of additional re-invasion sources can be inferred when significant numbers of flies with high parous rates are collected at capture points near the westward treatment limits. Movements of these flies may be tracked northeastward by comparing graphs of biting densities per day at each capture point on their path (Johnson *et al.* 1985). Our incomplete knowledge of the factors initiating and terminating such long-distance movements, coupled with uncertainty as to the times of day and heights of travel in the air stream (reviewed by Garms & Walsh (1987)) make it difficult

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to back-track reinvasions accurately to their source and to predict their strength from year to year. Detailed interpretation was also limited by the incompleteness of the meteorological data from Guinea and Sierra Leone. These difficulties were compounded in this study by the limited sampling programme, with captures at most points restricted to one day per week. Capture frequencies were increased at heavily reinvaded sites but some points on the apparent reinvasion path, particularly those not situated close to large breeding sites, rarely recorded the passage of migrant flies.

4. Results

(*a*) *Reinvasion of Côte d'Ivoire* 1986–1989

Table 1 shows that since 1985, the treatments of the Upper Sassandra in southeastern Guinea have maintained their impact on biting and transmission during the critical April–June reinvasion period with 75–95% reductions in Monthly Biting Rates (MBRs) and 95–99% reductions in Monthly Transmission Potentials (MTPs) in comparison with the same period in 1982–84, when the treatment strategy in the reinvaded zones was most comparable. Annual Transmission Potentials (ATPs) (figure 2) were first reduced in 1979 when year-round vector control was undertaken in the Marahoué and Sassandra Basins and again when the Upper Sassandra in Guinea was added in 1985. The community microfilarial load in man, the geometric mean number of *O. volvulus* microfilariae per skin snip in adults of 20 years or older, for Massadougou was dropping rapidly (figure 3), and was approaching the trend predicted by a computer model (Remme *et al.* 1990).

(*b*) *Reinvasion of southeastern Mali* 1987–1988

(i) *Biting and transmission in Guinea and Mali*

Vector control in both 1987 and 1988 greatly reduced biting and transmission in Guinea at those points where collections were made in 1986 (table 2). Over 80% reductions in biting rate were recorded at Téré and Morigbedougou in the Sankarani and Milo Basins, and over 60% at Sansanbaya on the River Niandan. Despite these reductions, considerable numbers of parous flies were caught. At Sansanbaya an MBR of 24830 was obtained in May–July 1986, but 7579 and 10436 were still recorded in 1987 and 1988.

The 1987–1988 reinvasion in Mali, as represented by cumulative May–July MBRs, constituted a 72% reduction at Madina Diassa and a 36% reduction at Mpiela, but only a 10% reduction at Kankela and Madina, when compared with 1977–1983 when no treatments were conducted in Guinea (table 3). At Metela there was a 35% increase. However, estimates of the reductions in biting and transmission achieved by spraying source breeding sites can only be very approximate, because MBRs and MTPs have varied considerably from year to year (figures 4 and 5) and it has not been possible to predict the strength of the annual reinvasion.

(ii) *Effectiveness of treatments in Guinea and Mali*

Parous rates at capture points beside treated river stretches in Guinea and Mali remained very high in both 1987 and 1988. In 1987, during the period when flies were invading Mali, however, some local breeding was reported in several of the complex rapid systems on the River Niandan and River Niger in Guinea, which had been treated with *B.t.* H14. Formulations of this insecticide could have a relatively short 'carry' and treatment failures

TABLE 1. CUMULATIVE APRIL–JUNE MONTHLY BITING RATES AND CUMULATIVE MONTHLY TRANSMISSION POTENTIALS IN THE CÔTE D'IVOIRE REINVASION ZONE 1982–1989, TOGETHER WITH MEAN VALUES FOR 1982–1984 AND 1985–1989 FOR BOTH INDICES AND PERCENTAGE REDUCTIONS BETWEEN THE TWO PERIODS

capture point and map number (figure 1)	1982	1983	1984	1985	1986	1987	1988	1989	mean 1982–84	mean 1985–89	percentage reduction
Monthly biting rates (MBR)											
Niamotou (1)	16892	14536	6919	808	230	270	1082	516	12782	581	95.5
Massadougou (2)	12372	3762	4613	209	1372	1068	711	173	6916	707	89.8
Kato (3)	13782	3540	7905	189	224	1094	946	1387	8409	768	90.9
Gîte 3 (4)	7102	1233	2761	111	288	744	1106	1599	3699	770	79.2
Pont Leraba (5)	2423	259	705	20	459	269	351	323	1129	284	74.8
Monthly transmission potentials (MTP)											
Niamotou (1)	808	986	551	20	0	0	15	0	782	7	99.1
Massadougou (2)	476	66	179	2	8	15	6	0	240	6	97.4
Kato (3)	410	154	211	1	0	17	5	2	258	5	98.1
Gîte 3 (4)	452	30	177	11	0	22	13	9	220	11	95.0
Pont Leraba (5)	161	18	36	0	4	3	0	0	72	1	98.0

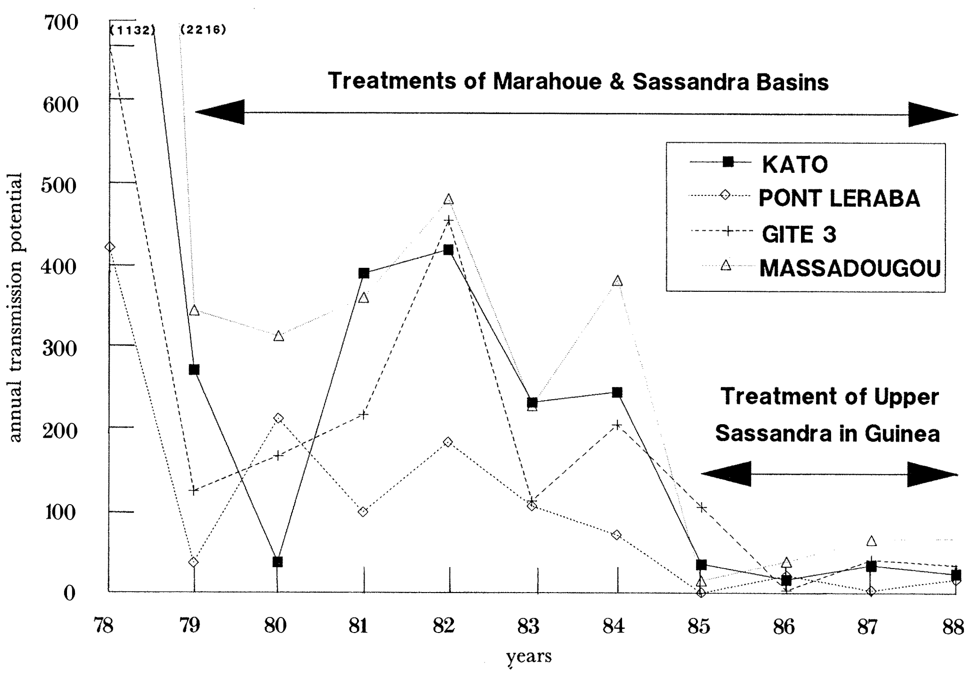

FIGURE 2. The effect of insecticide treatments of the Marahoué and Sassandra Basins followed by the Upper Sassandra in Guinea, on Annual Transmission Potentials at four capture points in the Côte d'Ivoire reinvasion zone.

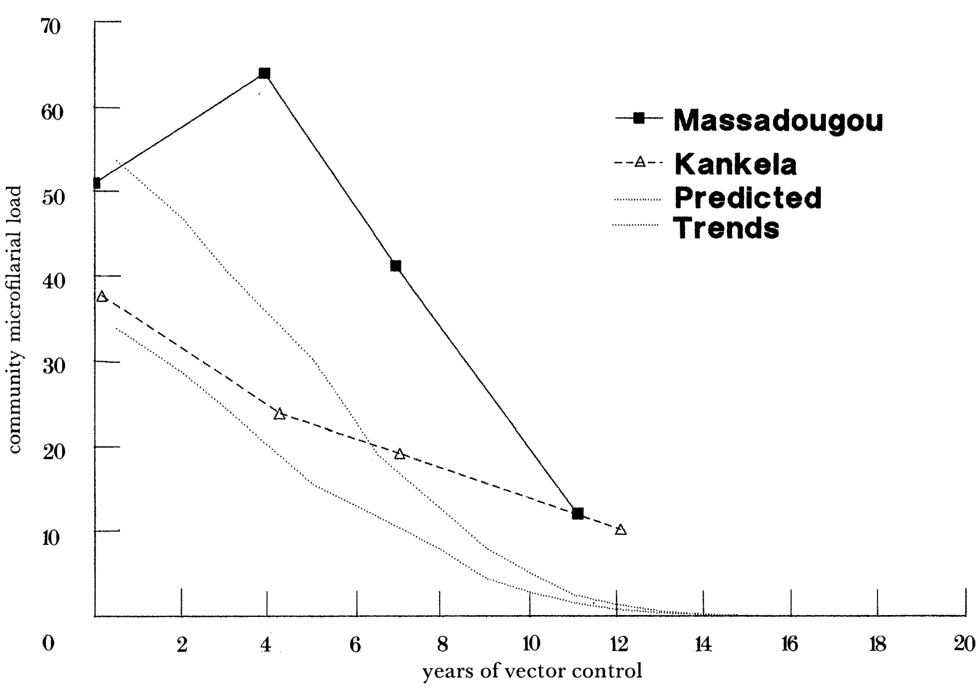

FIGURE 3. Epidemiological trends in the reinvasion zones. The predicted trends are those of Remme *et al.* (1990).

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TABLE 2. CUMULATIVE APRIL–JULY MONTHLY BITING RATES AND CUMULATIVE MONTHLY TRANSMISSION POTENTIALS IN THE UPPER NIGER BASIN IN GUINEA 1986–89

capture point and map	pre-treatment 1986	all Upper Niger Basin treated 1987	1988	1987–88	Sierra Leone added 1989	percentage reduction 1987–88 and 1986	1989 and 1986	1989 and 1987–88
				Monthly biting rates (MBR)				
Tere (21)	28097	3373	2647	3010	1466	89.3	94.8	51.3
Morigbedougou (20)	23675	4026	3315	3671	2144	84.5	90.9	41.6
Sansanbaya (19)	24830	7579	10436	9008	2276	63.7	90.8	74.7
Yradou (18)	—	3881	7424	5653	2262	—	—	60.0
Kouya Laya (17)	—	7471	8769	8120	2587	—	—	68.1
Yalawa (16)	—	6986	8489	7738	3069	—	—	60.3
Diaragbela (15)	—	5978	2320	4149	470	—	—	88.7
Banfarala (14)	—	8140	15945	12043	716	—	—	94.1
Balandougou (13)	—	4955	8459	6707	1336	—	—	80.1
				Monthly transmission potentials (MTP)				
Téré (21)	559	116	14	65	9	88.4	98.4	86.2
Morigbedougou (20)	636	176	78	127	41	80.0	93.6	67.7
Sansanbaya (19)	1168	242	363	303	106	74.1	90.9	65.0
Yradou (18)	—	205	154	180	23	—	—	87.2
Kouya Laya (17)	—	204	71	138	93	—	—	32.4
Yalawa (16)	—	126	151	139	133	—	—	4.0
Diaragbela (15)	—	370	102	236	14	—	—	94.1
Banfarala (14)	—	420	347	384	0	—	—	100.0
Balandougou (13)	—	39	407	223	69	—	—	69.1

TABLE 3. CUMULATIVE APRIL–JULY MONTHLY BITING RATES AND CUMULATIVE MONTHLY TRANSMISSION POTENTIALS IN THE MALI AND NORTHWESTERN CÔTE D'IVOIRE REINVASION ZONE 1977–89

capture point and map number	mean MBR pre-Guinea treatments 1977–83	mean MBR Sankarani treatments 1984–86	mean MBR Upper Niger treatments 1987–88	percentage reduction after Sankarani treatments	after Upper Niger treatments	after Sierra Leone treatments
			Monthly biting rates (MBR)			
Madina (22)	4798	7115	4278	(a)	10.8	83.6
M-Diassa (23)	8965	12699	2497	(a)	72.1	71.1
Mpiela (24)	1864	1176	1189	36.9	36.2	86.1
Kankela (25)	5120	4372	4586	14.6	10.4	65.2
Metela (26)	1768	1243	2387	29.7	(a)	68.7
			Monthly transmission potentials (MTP)			
Madina (22)	107	54	41	49.2	61.6	87.8
M-Diassa (23)	425	387	66	9.1	84.6	83.3
Mpiela (24)	220	110	28	50.0	87.5	95.5
Kankela (25)	409	229	168	43.9	59.0	83.1
Metela (26)	23	7	15	67.9	34.4	86.9

(a) No reduction.

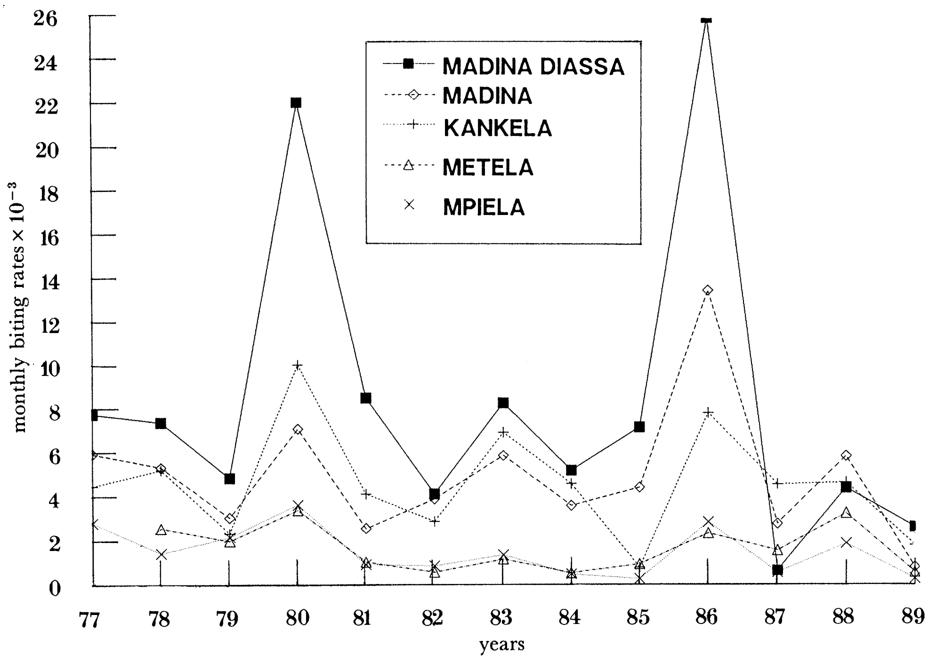

FIGURE 4. May–July cumulative Monthly Biting Rates at five capture points in the Mali/northwestern Côte d'Ivoire reinvasion zone from 1977–1988.

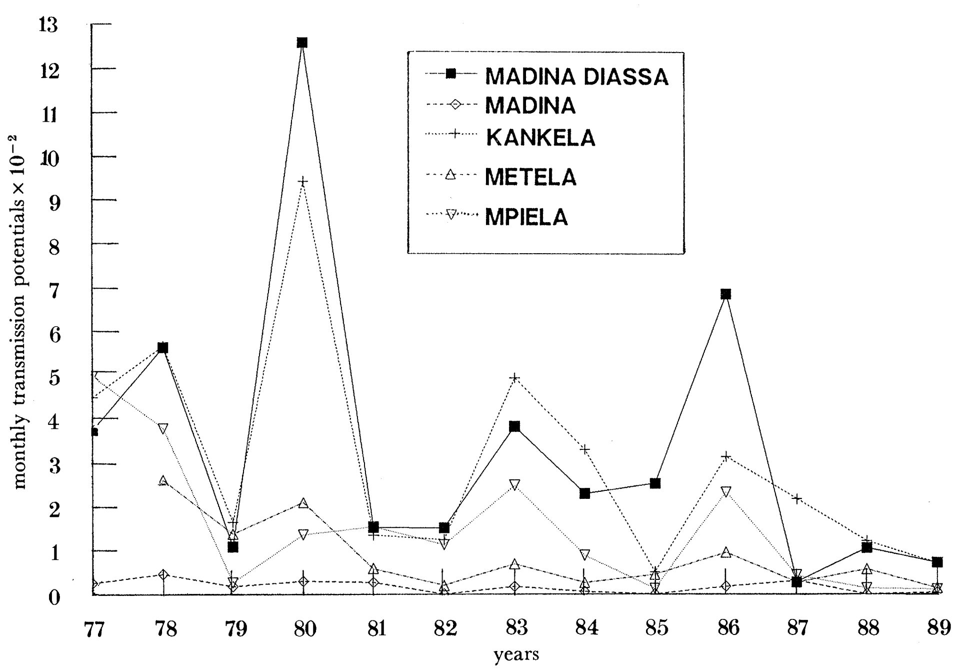

FIGURE 5. May–July cumulative Monthly Transmission Potentials at five capture points in the Mali/northwestern Côte d'Ivoire reinvasion zone from 1977–1989.

could occur when complex rapid systems were treated for the first time. With greater experience and more accurately calibrated river gauges this problem was largely eliminated in 1988.

(iii) *Sierra Leone savanna populations and reinvasion of Mali*

During 1988, the search for additional sources of reinvasion further upwind in Sierra Leone was intensified. Post & Crosskey (1985) showed that savanna vectors were mostly limited to the extreme north of the country, but in May 1988, breeding populations of *S. sirbanum* were found in all the main river basins, though northern rivers were more heavily colonized (figure 6). Biting savanna flies were recorded at all capture points, with a maximum of 650 per day on the River Seli at Arfanya in late May. During June, *S. soubrense* B began to dominate in biting

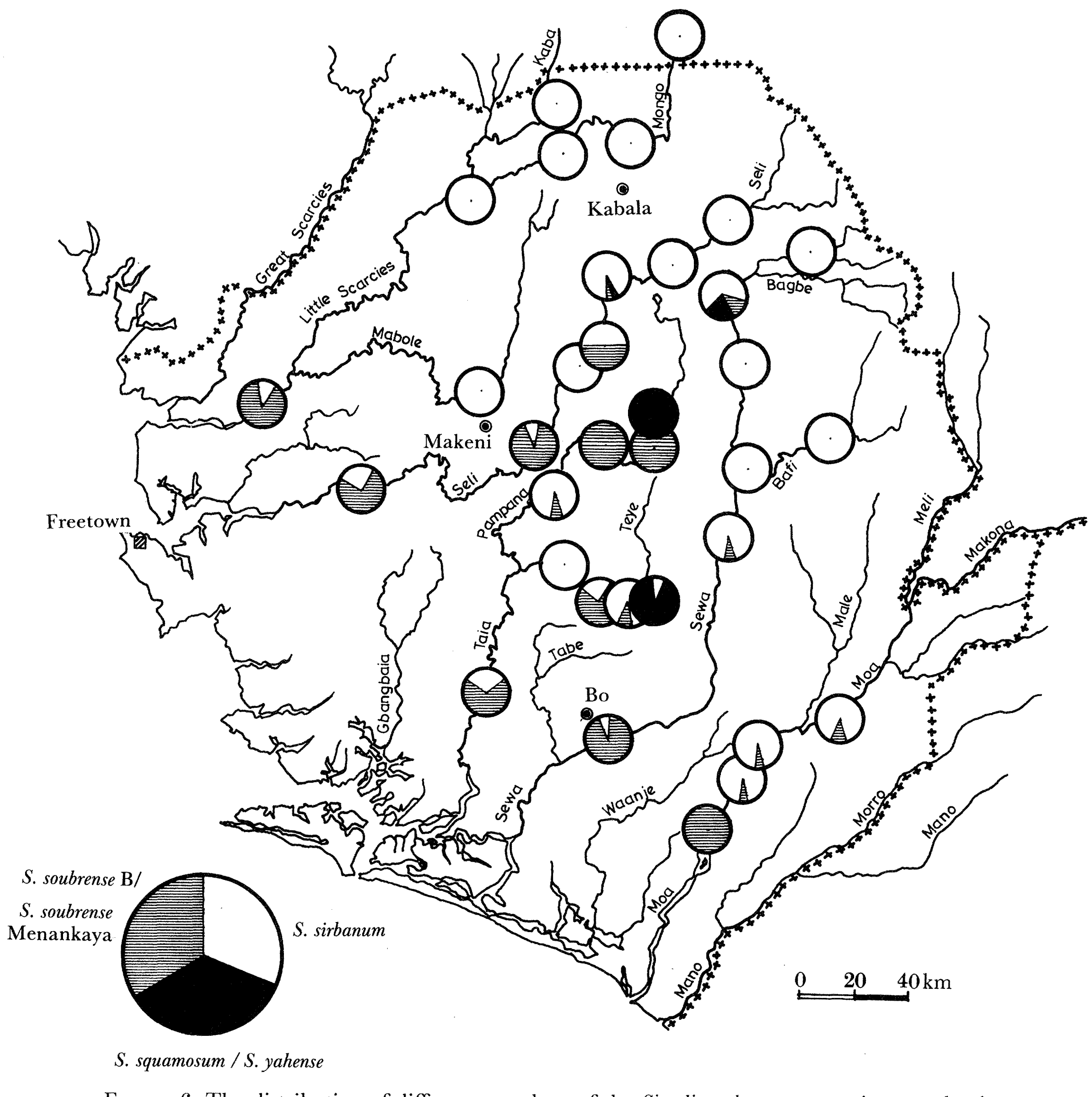

FIGURE 6. The distribution of different members of the *Simulium damnosum* species complex in Sierra Leone in April–May 1988, identified by larval cytotaxonomy.

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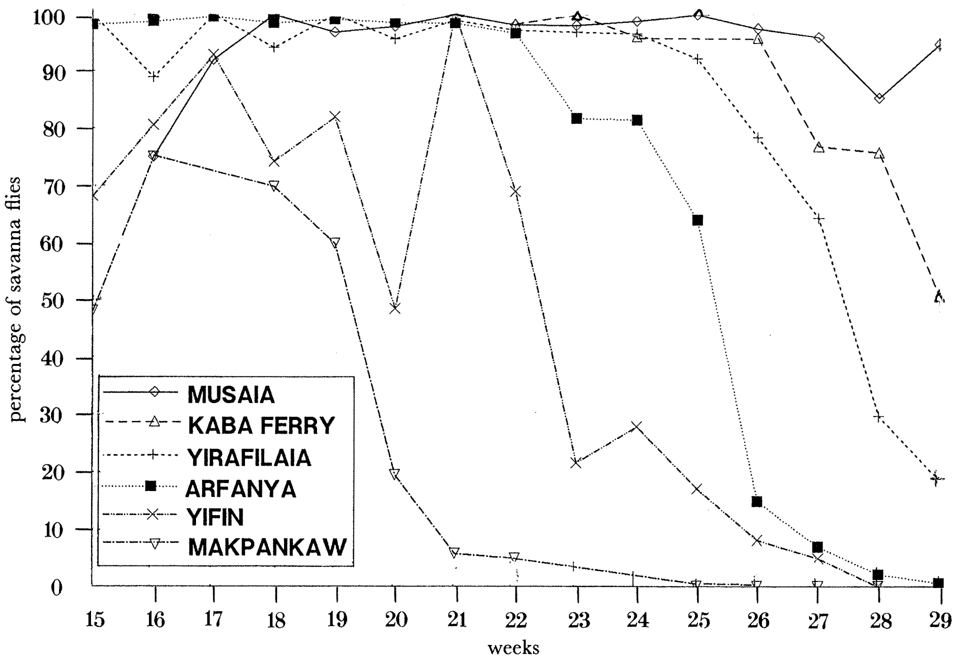

FIGURE 7. Percentage of savanna biting flies in weekly catches at six capture points in Sierra Leone during calendar weeks 15–29, 1988.

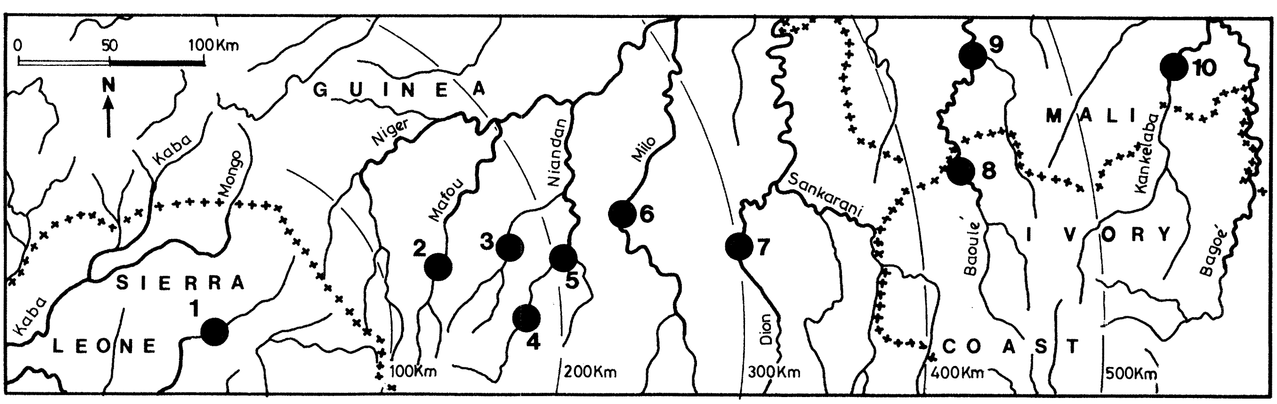

FIGURE 8. Map situating the capture points (1, Arfanya; 2, Yalawa; 3, Kouya Laya; 4, Yradou; 5, Sansanbaya; 6, Morigbedougou; 7, Téré; 8, Madina; 9, Madina Diassa; 10, Kankela) on the reinvasion axis between Sierra Leone and Mali as used in figures 9 and 10.

collections until, by the end of July, biting savanna flies were virtually restricted to the Little and Great Scarcies Basins in either side of the border with Guinea (figure 7).

When the 1988 mean daily biting rates per week at capture points in Sierra Leone, Guinea and Mali (figure 8) were plotted on the same graph (figure 9), a wave of savanna flies could be followed northeastwards from Arfanya through Yalawa (101–150 km) on the R. Mafou, Kouya Laya on the River Kouya and Yradou on the River Niandan (151–200 km), Sansanbaya on the R. Niandan and Morigbedougou on the River Milo (201–250 km), Téré on the R. Dion (251–300 m) and reaching Madina in northwestern Côte d'Ivoire (401–450 km), Madina Diassa (451–500 km) and Kankela in Mali (501–550 km) in calendar week 24–25. Another wave was observed two weeks later passing through Balandougou,

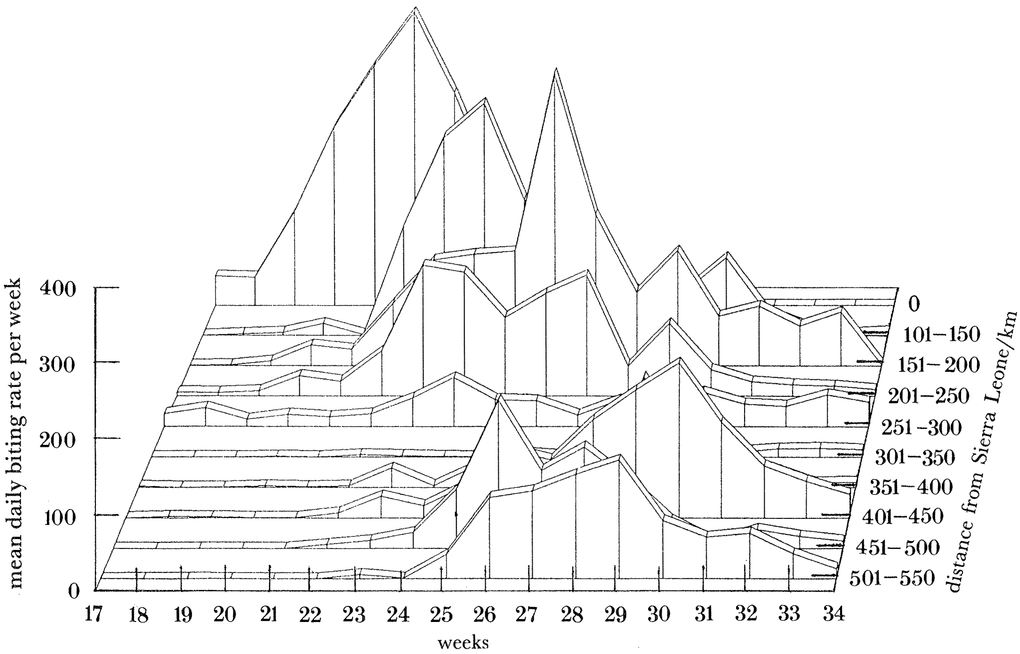

FIGURE 9. Three-dimensional representation of the mean daily biting rate per week at increasing distances from Sierra Leone in 1988.

Banfarala and Diaragbela on the River Niger some 100 kms further north. Flies were thus apparently taking 2–3 weeks to reach Mali from the Mafou and Niandan Basins in Guinea and 4–5 weeks to travel the approximately 500 km from Sierra Leone to Mali, a rate of one day per 15–20 km. This is within the estimate of 7–35 km made by Johnson *et al.* (1985) for migrating flies in Côte d'Ivoire and Burkina Faso.

(*c*) *Reinvasion of southeastern Mali* 1989

(i) *Biting and transmission in Sierra Leone, Guinea and Mali*

Figures 4 and 5 and table 3 show that the principal points in Mali and northwestern Côte d'Ivoire were still reinvaded in 1989 despite the treatment of all known savanna breeding sites upwind. Significant numbers of parous invading flies were recorded at Madina Diassa, Kankela and Mpiela with maximum mean daily biting rates of 145, 91 and 94, respectively. However, very few flies were caught at Madina (maximum mean daily biting rate per week of 31, and a May–July MBR of 788), the best result ever recorded. In 1989, May–July MBRs were 65–86 % and MTPs 83–95 % less than means for 1977–1983, before any control was undertaken in the Western Extension.

The 1989 treatments also further reduced biting and transmission in the Upper Niger Basin (table 2). This effect was most noticeable at Sansanbaya where the cumulative May–July MBR of 2276 was 78 % lower than that recorded in 1988, 70 % lower than 1987 and 91 % lower than 1986. MBRs on the River Niger were reduced by over 80 % compared to the 1987–1988 mean and, at all points where 1986 data were collected, MBRs in 1989 were also reduced by at least 80 %. On the Kouya, Upper Niandan and Mafou, MBRs remained at between 60–70 % of the 1987–1988 mean.

MTPs followed the same trend. At Sansanbaya, the MTP of 106 was 70 % lower than

1988, 55% lower than 1987 and 91% lower than 1986. Over 65% reductions compared to the 1987–1988 mean were recorded in the Sankarani, Milo, Niandan and Niger Basins, but there was little or no change on the Kouya and Mafou. In May, ivermectin, a microfilaricidal drug potentially capable of reducing transmission by up to 75% in isolated endemic communities (Remme *et al.* 1989), was delivered to hyperendemic communities in the Milo, Niandan, Mafou and Niger Basins, but no consistent effect on vector infectivity was recorded.

Vector control also greatly depressed biting and transmission rates in northern Sierra Leone. At Arfanya, the May–July MBR dropped by 97% (from 25420 to 680, with forest vectors making up 27% of the residual MBR) and the MTP by 98% (from 1810 to 1833). Low savanna vector biting rates and high parous rates were observed at all points except those in the Upper Great and Little Scarcies Basins near or north of the Guinea border.

(ii) *Effectiveness of treatment in Sierra Leone, Guinea and Mali*

Parous rates remained high at virtually all capture points beside treated river stretches in Sierra Leone, Guinea and Mali. However, some local breeding may have occurred for a short time in Mali near Madina Diassa because on the two days when the highest numbers of flies (238 and 200) were caught, only 76% and 67% were parous although by the next day the parous rate had reverted to 98%. This suggests that reinvasion at Madina Diassa was less important than the biting levels imply. Parous rates at Kankela and Madina were very high throughout and these two points may be better reflections of the reinvasion events.

Savanna vector breeding was not, however, completely eliminated in Sierra Leone. This was again partly because of difficulties in applying *B.t* H14 to complex breeding sites for the first time, but mainly to the problems encountered in treating tributaries of the Great and Little Scarcies which, at a critical time, were dry near their confluence with the main river, but flowing productively upstream. Biting rates on the Great Scarcies River at Badi Kanti increased rapidly from week 23, well before the river began to flow. Substantial breeding by *S. sirbanum* was found two weeks later in the River Kilissi, a major tributary in Guinea, which

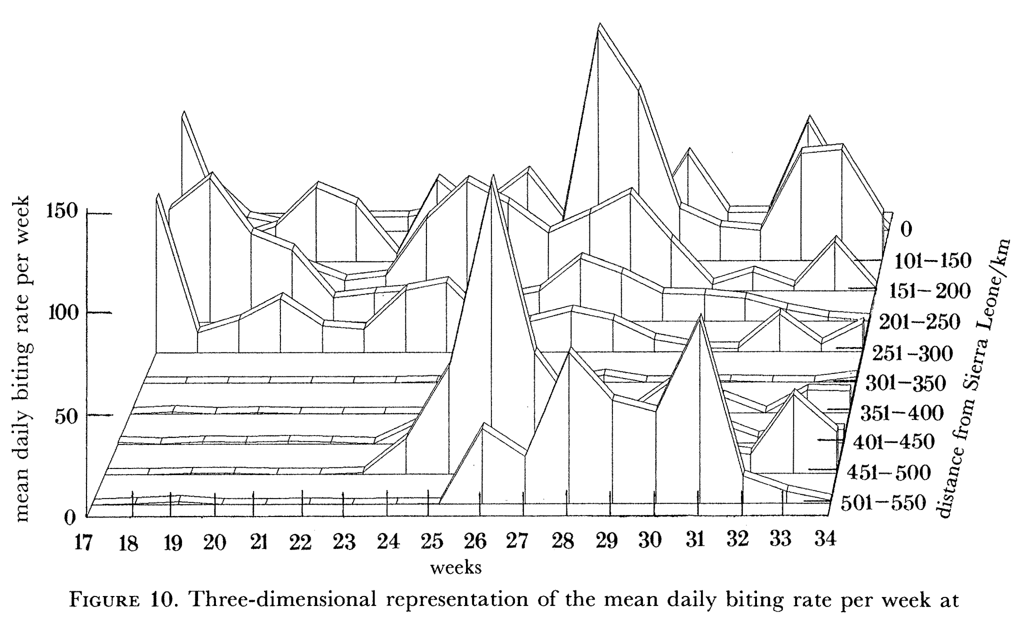

FIGURE 10. Three-dimensional representation of the mean daily biting rate per week at increasing distances from Sierra Leone in 1989.

was then included in the treatment circuit. However, catches at Badi Kanti peaked at 230 per day and were clearly an important potential source of invading flies.

(iii) *Sources of reinvasion in* 1989

A graph of biting rates along the reinvasion axis for 1989 (figure 10) was much less clear cut than for 1988 (figure 9). In week 22 the situation looked excellent with about 10 flies per day at all points (25 at Sansanbaya). Then in weeks 23 and 24 daily biting trebled or quadrupled at Yalawa, Yradou, Kouya Laya and Téré, though remaining stable at Sansanbaya and Morigbedougou. Such rises could be correlated with the increases in Mali during weeks 25 and 26, but it is not clear why they were not detectable at Sansanbaya and Morigbedougou, both points where reinvasion had been very important in previous years. An additional rise in weeks 27 and 28 can, however, be detected at all points on the southern Guinea axis.

Along the Niger River fly numbers gradually increased at Balandougou in weeks 25–27, peaking at Balandougou, Banfarala and Diaragabela in week 27. A second peak at Balandougou was observed in week 31.

5. Discussion

(*a*) *Côte d'Ivoire*

Since treatments began in the Upper Sassandra Basin in Guinea, May–July MBRs in the Sassandra, Marahoué, Bandama and Leraba Basins in Côte d'Ivoire have been maintained at 4–25% and MTPs at 1–5% of pre-1985 levels. Epidemiological indices (figure 3) have fallen rapidly and, with ATPs below 100 since 1985 (figure 2), this trend should continue.

Potential reinvasion sources still exist to the southwest of the Côte d'Ivoire reinvasion zone. Garms (1987) and discussion after this paper has collected adults and larvae of both savanna vector species from several rivers in Liberia. A large population of breeding and biting savanna flies (maximum 335 per day in late May 1988) was found on the River Moa in southeastern Sierra Leone in both 1988 (figure 6) and 1989. However, since biting rates and transmission potentials have now been maintained at low levels for five reinvasion seasons and epidemiological indices are rapidly improving, it would appear that reinvasion from Liberia or southeastern Sierra Leone does not play an important role in the transmission of onchocerciasis in Côte d'Ivoire.

(*b*) *Mali and northwestern Côte d'Ivoire*

In 1989, for the first time, biting and transmission at all points were consistently low throughout the Mali and northwestern Côte d'Ivoire reinvasion zone and over 65% less than recorded before OCP began insecticide treatments in Guinea. In previous years, the strength of reinvasion had varied unpredictably (figure 4), with up to sixfold differences in biting rates between the years. Until 1987, reinvasion biting rates had always been highest at Madina Diassa, but in that year 72% less than the 1977–1983 mean were caught. However, in 1987 the River Baoulé only started to flow on 6 July, six weeks later than usual. Capture points beside slow flowing river stretches rarely caught migrating flies and if, as seems likely, these flies, which were believed to migrate gravid (Bellec 1976), were attracted to the vicinity of rapids then this behaviour could explain the low catch at Madina Diassa in 1987. If years with unusually late flow by the capture points are excluded (together with Kankela in 1985, which may have been affected by treatments of the Sankarani Basin (Baker *et al.* 1986)), the 1989 reinvasion was lower than ever before at all points. In 1989, cumulative May–July MTPs (figure 5) were below 100 for the first time. Epidemiological indices, which have only been slowly decreasing in this area (figure 3 for Kankela) should improve rapidly if this trend of low MTPs is maintained.

(*c*) *Sources of reinvasion in* 1989

The key questions would appear to be to determine the source of the flies invading Mali during the main peak, which started in week 24 and was at a maximum 2–3 weeks later. If we accept that flies do take at least 4 weeks to travel the 500 km from northeastern Sierra Leone to Mali, then the flies breeding in the poorly treated tributaries of the Great and Little Scarcies, 100–150 km further west, should take even longer. This makes it unlikely that these flies, which first appeared in week 23, were the main contributors to this invasion.

An alternative hypothesis is based on the increase in biting rates observed in the Mafou, Kouya, Upper Niandan and Dion Basins during weeks 23–24, but this is confounded by the stability of the biting rates at Sansanbaya and Morigbedougou during the same period. Could the occasional poorly treated breeding site in Sierra Leone and Guinea have been responsible for the 30–40 flies per day in the southern part of the Upper Niger Basin and could these flies have produced 150 per day at Madina Diassa? If we assume that the Madina Diassa peak was inflated by local breeding, because of the relatively low parous rate in week 26, and if wind conditions favoured long distance movement on particular days, thus increasing densities in the reinvaded zones, we may have a partial explanation. There were no other obvious potential source rivers.

Breeding sites in the Upper Great and Little Scarcies were probably responsible for the wave of invading flies that passed through capture points in the Niger River in weeks 26–27 and maintained relatively high biting rates in Mali and northwestern Côte d'Ivoire until weeks 34–35.

With the experience obtained in treating complex breeding sites and partially flowing rivers in Sierra Leone during 1989 and with the evidence for the existence of source areas there, future reinvasions of Guinea and Mali should be further minimized by the appropriate insecticide treatments.

In a programme of the scale of OCP it is impossible to acknowledge all the individuals who contributed to the work described here. Special thanks are extended to: Mr I. Sesay, Entomologist of the Sierra Leone National Onchocerciasis Team and his staff; Messrs R. Lama, A. Sagno and Dr K. Kaba, entomologists of the Guinea National Onchocerciasis Team; Dr A. Akpoboua, OCP Bouaké, Sector Chief, his Sub-Sector Chiefs and their staff; Messrs I. Diallo and Y. Diarra, OCP Sub-sector Chiefs at Bamako and Bougouni, and their staff, Mr M. Kassambara, OCP Bobo Dioulasso, and his staff; Mr. S. Dramane, Dr K. Doucouré, Dr L. Toé, and Mr B. Tele for detailed surveys in Sierra Leone; Dr M. C. Thomson for electrophoretic identifications; Mr A. Soumbey and Dr S. Doumbia for data analysis; Dr C. Back for comments on the manuscript; Drs G. De Sole, K. Y. Dadzie and J. Remme for epidemiological information; Messrs A. Sib and Y. Coulibaly for cytotaxonomic assistance; Mr A. Belli and the administrative services for logistic support; the pilots of Viking Helicopters Ltd. and Evergreen Helicopters Inc. and the OCP aerial operations staff.

We acknowledge the key roles played by Dr B. Philippon and Dr D. Quillévéré, past and present Chiefs of the Vector Control Units; Dr D. A. T. Baldry and Mr P. Kaboré, past and present Chief Aviation Officers; Dr J. Grunewald, Research Coordinator; D. G. Zerbo, Chief Entomological Evaluation and Dr H. Agoua, Chief Central Zone.

Finally, we are grateful to Dr E. M. Samba, Programme Director for his continuing encouragement and permission to publish.

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Discussion

R. Garms,[1] R. A. Cheke[2] and R. Sachs[1] ([1] *Bernhard Nocht Institute for Tropical Medicine, Bernhard-Nocht-Strasse* 74, *D*-2000 *Hamburg* 36, *F.R.G.*; [2] *Overseas Development Natural Resources Institute, Chatham, U.K.*). Baker *et al.* described movements in a northeastward direction of savanna members of the *Simulium damnosum* species complex from uncontrolled areas. Little is known about whether savanna flies also move in the opposite direction from north to south, from the savanna into the forest. Some recent observations in Liberia are therefore of interest.

Savanna species were known to occur and occasionally breed in northern Liberia (Garms & Vajime 1975), but they were not found elsewhere in the country until the dry season of 1985, when a few flies were caught biting man at sites beside the St Paul River in the evergreen rainforest zone. They were thought to have arrived from northern sites assisted by the northeasterly harmattan winds (Garms 1987). Three years later, during the dry season of 1988, residents of the Bong iron ore mine complained about a serious nuisance caused by blackflies biting them within the mine's concession area as much as 10 km away from the St Paul River, where flies had been extremely rare in previous years. Fly catches in May and June 1988 confirmed that biting densities were very high (more than 500 in 7 h). Morphological identifications showed that practically all of these flies were savanna members of the *S. damnosum* species complex.

This phenomenon of mass biting did not recur in the dry season of 1989 when regular fly catches were performed at four sites within and five sites outside the Bong Mine concession area. However, some savanna flies were present, but they were only caught in small numbers within the concession area. Their source could be traced to the Yea Creek, a small stream emerging from the Bong Mine's tailings pond. Larvae collected on 20 March, 21 and 22 April were cytologically identified as 39 *S. damnosum s.str.*, 19 *S. sirbanum* and 2 *S. soubrense* (G. K. Fiasorgbor, personal communication). Interestingly, they were associated with *S. adersi*, another savanna species, which had not been recorded from the area before. It is probable that the savanna species had invaded the region from the north with the harmattan winds, had encountered favourable breeding conditions and were able to establish themselves in the area for at least a few generations. They were not found in any of six streams and rivers around the concession area which were regularly checked.

It is not known why the outlet of the tailings pond, a unique and highly artificial environment, is such an attractive breeding site for the savanna species but not for the local forest species. Most of the water originates from the St Paul river from where it is pumped through a pipe line *ca.* 10 km long to the concentrator of the Bong Mine. From there the water, heavily loaded with inorganic material, is passed to a large impondment area, the tailings pond, where the solid wastes settled prior to the release of clean water to the river. The water leaving the tailings pond is characterized by constant high temperatures of 30 °C and several chemical characteristics, in particular hardness, which are quite distinct from those of the natural watercourses. It is very rich in microorganisms, probably produced by the drowning forests and decaying trees within the impondment area.

It is not yet clear whether or not the invasion by savanna species and their colonization of the Bong Range will have any epidemiological consequences.

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R. H. A. Baker. Despite the potential threat of savanna flies re-invading the Sassandra, Marahoué and Bandama Basins from isolated seasonal breeding sites in Liberia, described by Dr. Garms *et al.* and southern Sierra Leone (figure 6), biting and transmission rates in the reinvasion zones have been maintained at low levels for the past five years (since the treatment of the Upper Sassandra in southeastern Guinea began). This was true even in 1988, when the savanna flies were most numerous at the Bong Mine in Liberia. Rivers in southern Sierra Leone will be included in treatment circuits from 1990, further diminishing this threat.

R. A. Cheke[1], M. A. Howe[2], M. J. Lehane[2], A. L. Millest[2], T. Kone[3] R. H. A. Baker[3] ([1]*Overseas Development Natural Resources Institute, Chatham, U.K.*; [2]*School of Animal Biology, University College of North Wales, Bangor, Gwynedd U.K.*; [3]*WHO Onchocerciasis Control Programme. B.P. 549, Ouagadougou, Burkina Faso*). Baker *et al.* suggested that the migrant *Simulium sirbanum* reaching Madina Diassa in Mali during the 1988 wet season were 4–5 weeks old. The basis for their conclusions were analyses of the time sequences of waves of flies traversing a series of sites between Madina Diassa and their likely sources, 450–500 km away in Sierra Leone. We have recently estimated the ages of a sample of *S. sirbanum*, caught near Madina Diassa in June 1988, by analysis of their pteridine concentrations. Our results, based on this biochemical technique, agree very well with the conclusions of Baker *et al.*

Pteridine concentrations are known to increase with age and fly size in different members of the *S. damnosum* species complex (Cheke *et al.* 1987, 1989). Such variation was established for Malian populations of *S. sirbanum* by experiments with flies emerged from pupae, collected at Tienfala (12° 44′ N, 08° 00′ W; 40 km E of Bamako) in the Niger River. The flies were maintained at different temperatures (20–33 °C), killed at daily intervals, measured for size, and pteridine concentrations estimated by fluorescence spectrometry. Although, surprisingly, temperature had no effect ($P = 0.99$), a significant multiple regression was obtained relating pteridine concentrations in the flies' heads to fly age and size, as follows: Log PTHD = 0.0113 age (days) + 0.2158 fly thorax length (mm) + 0.53 ($P < 0.0001$), where PTHD is the pteridine concentration in the head capsule. This equation was then used to estimate the ages of 199 flies caught at Kanibougoula, 10 km upstream of Madina Diassa, on 22 and 23 June 1988. A histogram of the results is shown in figure 1. The mean of this distribution was 29.08 days (s.d. = 8.99), within the range of 4–5 weeks suggested by Baker for his flies caught nearby during the same period. A few flies were estimated as being less than two weeks old and some others more than six weeks, with a maximum of 67 days. This maximum is more than twice the previous longevity record, estimated by pteridines, of 27 days for a female *S. damnosum s.str.* (Cheke *et al.* 1989). However, it is recognized that conclusions about individual flies must be treated with caution as the method is best restricted to populations (Cheke *et al.* 1989). As such

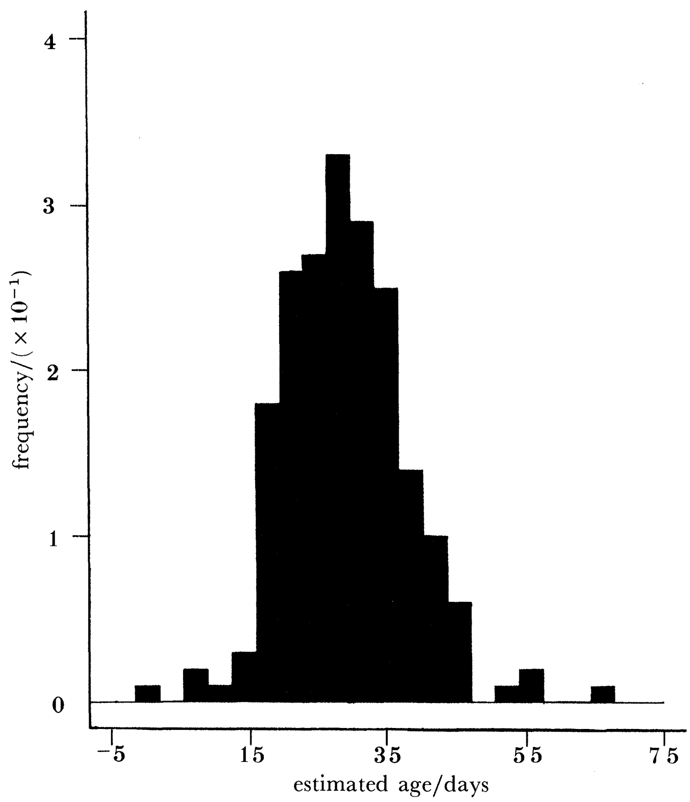

FIGURE 1. A frequency histogram of the estimated ages of *Simulium sirbanum*, caught at Kanibougoula on 22–23 June 1988. (Average age, $\bar{x} = 29.08$ days; s.d. = 8.99.)

a population analysis, the results in figure 1 provide good supportive evidence for the conclusion of Baker *et al.* that *S. sirbanum* take about a month to migrate 500 km.

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J. B. DAVIES (*Medical Research Council and School of Tropical Medicine, Liverpool, U.K.*). I am extremely interested in Dr Baker's observation that flies were taking 4–5 weeks at average speeds of 15–20 km per day, to travel 500 km or so, and note how this is supported by Dr Cheke's estimates of age from pteridine concentrations and how closely both sets of results agree with earlier estimates for similar migrations (Johnson *et al.* 1985). I have always found Dr Johnson's earlier estimates of survival difficult to accept, although I have never questioned the fact that the flies were covering these distances. However, although the data showed the journeys took 30–60 days to accomplish, I found it hard to conceive that sufficient numbers of flies were surviving so long to provide such high biting rates at the furthest destinations. With this new corroborating evidence it seems that under the right conditions *S. damnosum* is a better survivor than some of us supposed, and certainly better than laboratory survival experiments show. I for one, will have to change my opinion of this fascinating little insect. This new evidence is very welcome.

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R. H. A. BAKER. Regarding the corroboration between fly longevity, as estimated by pteridine concentrations, and the time taken for waves of invading flies to travel 500 km from Sierra Leone to Mali, how can this information be used operationally? If longevity can be directly related to distance flown, a retrospective study could try to identify the source breeding sites of the invading flies. It is possible, however, that some flies would take a much shorter time to fly this distance than the 15–20 km per day suggested from comparisons of the waves of moving flies.

The value of data from satellites for forecasting outbreaks of locusts and other pests has been discussed by various speakers at this meeting, but satellite imagery could also be of benefit to OCP if it could provide information at the river or even breeding site level. At the beginning of the wet season, spraying helicopters could be targetted more accurately if it were possible to identify tributaries where there had been rain and which were likely to have started to flow. Ideally, it would be possible to detect the presence of flowing (white) water.

M. D. WILSON (*Department of Medical Entomology, School of Tropical Medicine, Liverpool, U.K.*). There is a lot of deforestation taking place in the lowland rainforest outside the Onchocerciasis Control Programme area of West Africa. Will this phenomenon result in the creation of habitats permanently suitable for colonization by the dangerous savanna vector species? This would have obvious implications for the future control strategy and boundary of the Programme.

R. H. A. BAKER. This is a very important point. In recent years, the savanna vector species have begun to colonize deforested parts of the Programme area and this situation can only deteriorate.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES