PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Reinfestations of the Southeasterrn Flank of the Onchocerciasis Control Programme Area by Windborne Vectors [and Discussion]

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Reinfestations of the southeastern flank of the Onchocerciasis Control Programme area by windborne vectors

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During the rainy season of 1980 the southeastern flank of the W.H.O. Onchocerciasis Control Programme was extended to include potential sources of *Simulium squamosum*, *S. damnosum s.s.* and *S. sirbanum*, vectors of onchocerciasis that were reinfesting the controlled zone in Togo. The experimental extension with a radius of 100 km from the reinvaded sites only partly reduced the scale of the reinfestations. To examine whether some *S. squamosum*, the principal species involved in Togo, were travelling more than 100 km, a larger experimental extension was treated in 1981, which further reduced the numbers reinvading. The results of these trials and data on the ages and species compositions of the reinfesting flies, their likely sources and the meteorological conditions in the area are discussed. It was concluded that *S. squamosum* may travel for 150 km or more in Togo and that *S. damnosum* and *S. sirbanum* travel similar distances in both Togo and Benin.

1. Introduction

The causative agent of the debilitating disease onchocerciasis is a nematode worm *Onchocerca volvulus* (Leuckart). The disease is known colloquially as 'river blindness' because its vectors breed in rivers, and impairment or loss of vision is a common consequence of infection. It is spread from person to person by adult blackflies, which rely for reproduction on the presence of fast-flowing sections of rivers, especially rapids, because their larvae cannot develop in slow-moving water. In West Africa the vectors are sibling species of the *Simulium damnosum* Theobald species complex.

In February 1975 the World Health Organization Onchocerciasis Control Programme (O.C.P.) began treating rivers in an area of 654000 km^2 encompassing parts of seven countries (Walsh *et al.* 1981*a*). Aerial applications of the larvicide temephos (commercial name Abate) were used and the applications were restricted to potential breeding sites of *S. damnosum sensu lato* (*s.l.*). Control of the vectors was largely successful within the main O.C.P. area (Walsh *et al.* 1979), but flies continued to appear on its periphery.

Only some members of the *S. damnosum* complex migrated into the west of the area (Garms *et al.* 1979), and so knowledge of the behaviour, ecology and epidemiological roles of the different sibling species is important. The siblings were described on the basis of the staining properties of chromosomes from larval salivary glands (Vajime & Dunbar 1975), and the breeding distributions of these 'cytospecies' are habitat-related. *S. damnosum sensu stricto* (*s.s.*) and *S. sirbanum* V & D are common in savannah regions, *S. squamosum* (Enderlein) is found

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in or close to mountains and hills in both forest and savannah zones, while *S. yahense* V & D is restricted to forests. Members of the *S. soubrense* V & D/*S. sanctipauli* V & D subgroup are found mostly in forested regions, but one form of this group inhabits savannahs in Togo and Benin (Meredith *et al.* 1983). Studies in the west of the O.C.P. demonstrated that the flies migrating in from outside the area were 'savannah' species *S. damnosum s.s.* and *S. sirbanum* (Garms *et al.* 1979). Sources of these flies were located 300 km or more to the southwest, and an extension of the O.C.P. area by 110000 km^2 to include the sources diminished the reinvasions

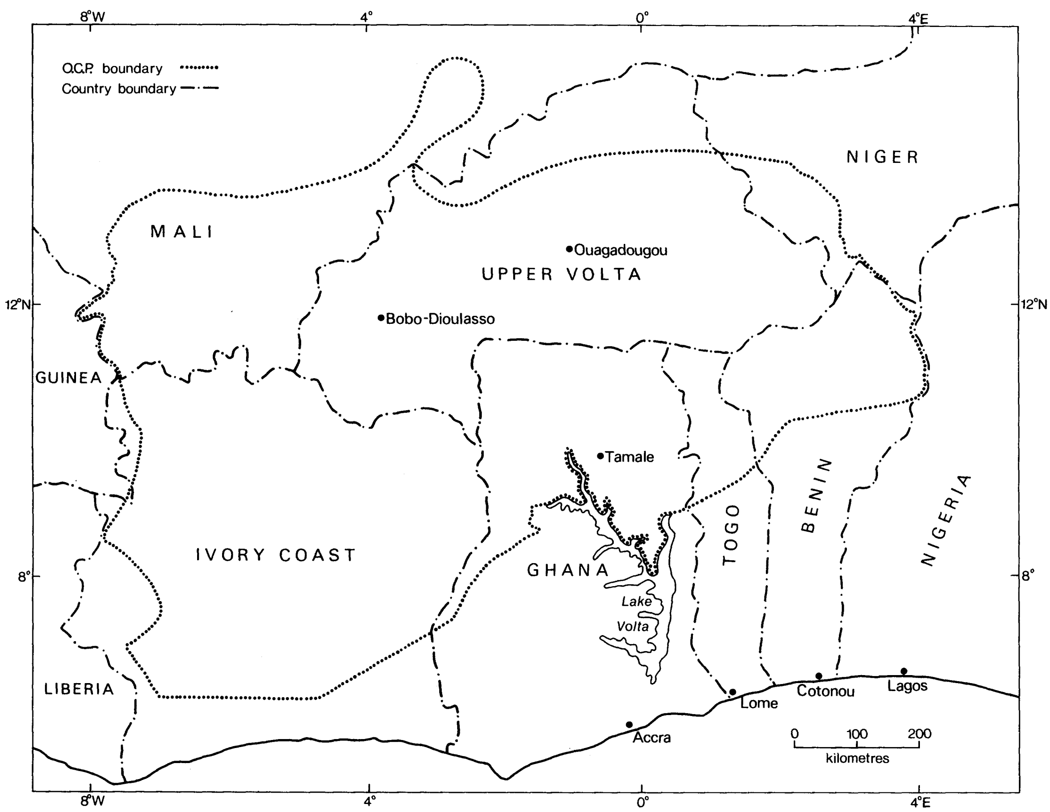

FIGURE 1. The Onchocerciasis Control Programme area in 1980.

to a negligible level (Walsh *et al.* 1981 *b*). These experiments strongly suggested that the flies were moving in the direction of the prevailing winds i.e. from the southwest to the northeast once the Inter-Tropical Convergence Zone (I.T.C.Z.) had passed north of the source areas. The extent of the O.C.P. area in 1980, which includes the western extension, is shown in figure 1.

The western part of the O.C.P. was not, however, the only region where flies were still occurring within the treated zone. The southeastern flank was also affected, but the character of the reinfestations in Togo and Benin was different. In 1979 the flies did not appear synchronously at different sites, and in Togo *S. squamosum* was the main component of the reinfesting populations when these were at their highest levels of 400 or more flies per day during June and July (Garms *et al.* 1982).

The areas in Togo and Benin most affected by reinfestations are illustrated in figure 2 and the known breeding sites of *S. damnosum s.s.*, *S. sirbanum* and *S. squamosum* south of the O.C.P. boundary are shown in figure 3. *S. squamosum* is abundant to the southwest and south of the boundary, but it is very rare or absent to the southeast. This pattern had been reflected in the species composition of the flies caught within the boundary in 1979, with *S. squamosum* predominating in catches at Mô bridge (site A in figure 2), being less common at Landa-Pozanda (B) and very rare in Benin (Garms *et al.* 1982). Members of the *S. soubrense*/*S. sanctipauli* species groups were very rarely caught within the O.C.P. boundaries, although they breed in much of the area further south.

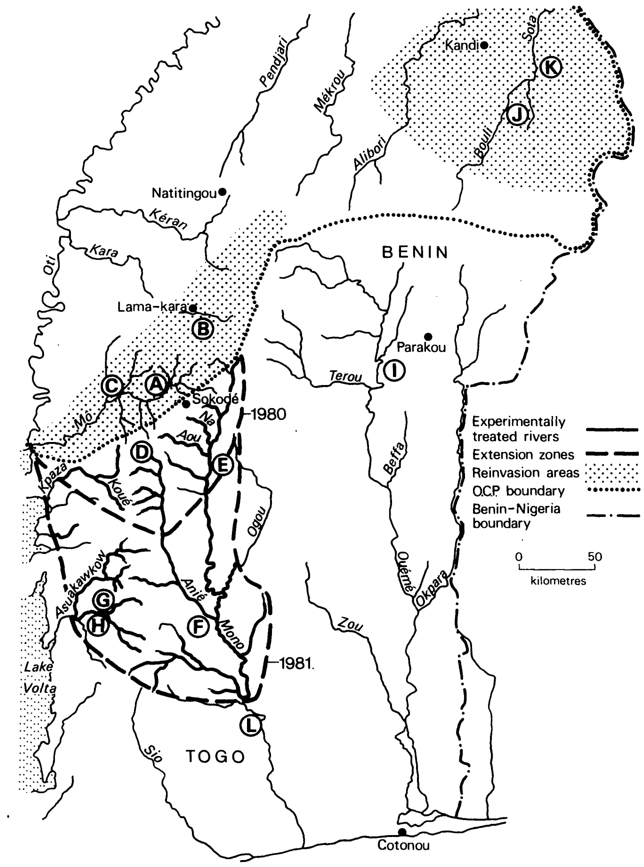

FIGURE 2. The study area in Ghana, Togo and Benin showing the zones subject to reinvasions, the rivers treated experimentally as part of extensions of the O.C.P. area in 1980 and in 1981, and the fly catching points. A, Mô bridge; B, Landa-Pozanda; C, Bagan; D, Fazao; E, Landa-Mono; F, Alamassou; G, Djodji; H, Ahamansu; I, Bétérou; J, Zougou; K, Gbassé; L, Tététou.

Because *S. squamosum* was breeding profusely to the south and southwest of the reinfested zone in Togo and because the studies in the west of the O.C.P. had suggested that *S. squamosum* seldom travelled far (Garms *et al.* 1979; Townson & Meredith 1979, Walsh *et al.* 1981 *a*), it was thought that a limited extension zone covering all *S. squamosum* breeding sites within 100 km of the heavily infested Mô valley might suffice to reduce the reinvasions to a satisfactory level. In this paper we present the results of experimental treatments carried out in 1980 to test this hypothesis and the results of subsequent trials in 1981. The experiments were primarily concerned with studying events in Togo, which contrasted not only with the western situation but also with that in Benin where the fly numbers were higher, with peaks in excess of 1000 flies per day, and *S. squamosum* was not involved. The Benin invaders, like those in the Ivory Coast, were *S. damnosum s.s.* and *S. sirbanum* (Garms *et al.* 1982).

Some of the reinfesting flies are known to carry infective larvae of *Onchocerca* sp. (Cheke *et al.*

1982; Omar & Garms 1981) and a detailed account of their epidemiological importance will appear elsewhere (Garms & Cheke 1983).

2. Methods

The numbers of *S. damnosum s.l.* at the fly-catching sites (figure 2) were monitored by vector collectors (Walsh *et al.* 1978) and those monitored daily from 07h00 to 18h00 during both 1980 and 1981 within the O.C.P. area were at Mô bridge (A) and Landa Pozanda (B) in Togo,

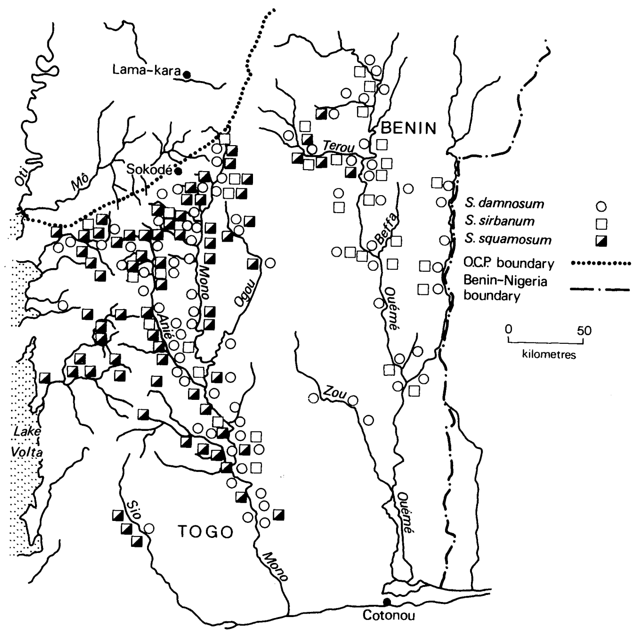

Figure 3. The known breeding distributions within the study area of *S. damnosum s.s.*, *S. sirbanum* and *S. squamosum*.

and at Gbassé (K) in Benin. Living samples from the catches were transported to Lama-Kara, where the flies' ovaries were examined to determine if they were nulliparous or parous (Lewis 1958), a measure of their physiological age. Each fly was then classed as belonging to one of the categories *damnosum/sirbanum*, *squamosum*, or *soubrense/sanctipauli*, by using morphological methods (Garms *et al.* 1982).

The efficacy of the control methods within the O.C.P. area was checked by routine searches by O.C.P. staff and by random spot-checks with the use of a Hughes 500C helicopter. The latter was also used to survey rivers outside the area to find potential sources and to map the breeding sites of each cytospecies. Mature larvae were collected in cold Carnoy's fluid for subsequent cytotaxonomic identifications by S. E. O. Meredith and G. Fiasorgbor.

In 1980 weekly experimental treatments in the area illustrated in figure 2, with the use of aerial applications of temephos, were carried out six times beginning on 17 June. The experimental area was chosen to include all *S. damnosum s.l.* breeding sites within 100 km of Mô bridge, in particular *S. squamosum* breeding sites such as the Kpaza, Koué and Anié rivers.

The directions and speeds of the winds at 10 m above ground level, and at 600, 900 and 1500 m above sea level, as well as the occurrences of any storms at Kandi in Benin throughout the period May–September 1980, were obtained from the meteorological station. Similar data were obtained from the station at Parakou, also in Benin, and from stations at Lama-Kara and Sokodé in Togo, but fewer readings were available from these stations.

Since the 1980 experimental treatments did not eliminate the reinfestations, the experimental area was extended in 1981 (figure 2) and six complete treatment cycles were carried out, each requiring 2.5 days, with the first beginning on 23 June and the last on 28 July. A seventh was begun on 4 August but was curtailed because many rivers became flooded.

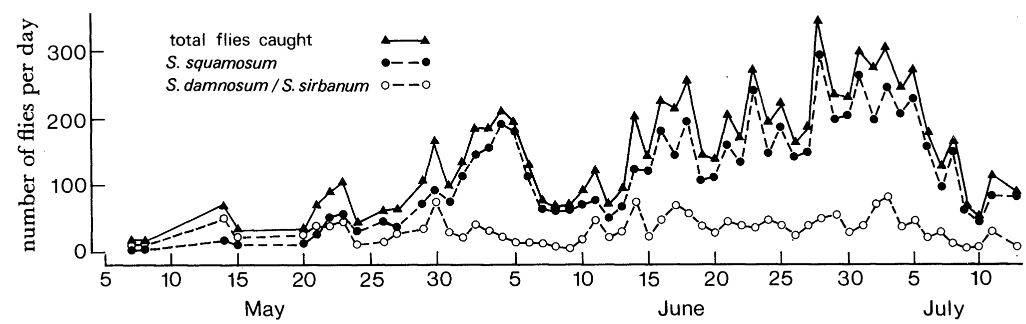

FIGURE 4. The numbers of flies caught and the species composition at Mô bridge, 7 May–13 July 1980.

3. REINFESTATIONS AND THE EFFECTS OF EXPERIMENTAL TREATMENTS IN 1980

(a) *Numbers and species of flies reinfesting Togo*

The proportion of *S. squamosum* in the catches at Mô bridge, which was about 30% in early May, increased steadily until mid-June and then remained at approximately 80%. *S. squamosum* was responsible for the main peaks in numbers, as the contribution of *S. damnosum*/*S. sirbanum* to the daily totals remained more or less constant (figure 4) even during the experiments. However, the proportion of *S. damnosum*/*S. sirbanum* in the catches at Landa-Pozanda was much higher than at Mô bridge: in May 84%, in June 54% and in July 50% were *S. damnosum*/*S. sirbanum*.

Before the experimental treatments fewer flies were caught than during the corresponding period in 1979, and this may have been because in 1980 there was less rain early in the season, especially during June, than in 1979 (table 1). Otherwise there were striking similarities between the events in the two years because (1) the species compositions were similar, (2) at Mô bridge the fly numbers increased abruptly and remained high, and (3) the pattern at Landa-Pozanda, where the numbers remained low, was unlike that at Mô bridge.

For the first three weeks after the start, on 17 June, of the experimental treatments the numbers at Mô bridge remained high (figure 5) and during this period there were some unsuccessful treatments within the experimental area. In particular there was still substantial breeding by *S. damnosum s.l.* in the Kpaza river at the end of June. After 5 July, fly numbers at Mô bridge declined from 200–300 per day to about 50. At Landa-Pozanda (figure 5) the pattern differed from that of 1979 and the only period when significant numbers were caught was at the end of June and the beginning of July: the maximum of 98 was recorded on 3 July.

These reductions can be attributed at least partly to the experimental treatments in the light of the following. In July the rivers in the experimental area were all flowing well, breeding

TABLE 1. MONTHLY RAINFALL TOTALS (MILLIMETRES)

	Sokode			Lama-Kara			Parakou			Kandi		
	1979	1980	1981	1979	1980	1981	1979	1980	1981	1979	1980	1981
April	84	87	64		39	110	107	101	64	61	39	44
May	121	138	117	228	168	167	158	126	158	52	152	121
June	229	99	186	190	127	192	233	111	129	153	200	164
July	217	263	272	265	167	188	195	165	57	174	93	
August	216	308	323	326	224	299	181	283	319	326	258	229
September	347	132	174		234	173	298	174	150	259	197	144
October	114	194	58		188		63	149	22	31	30	8

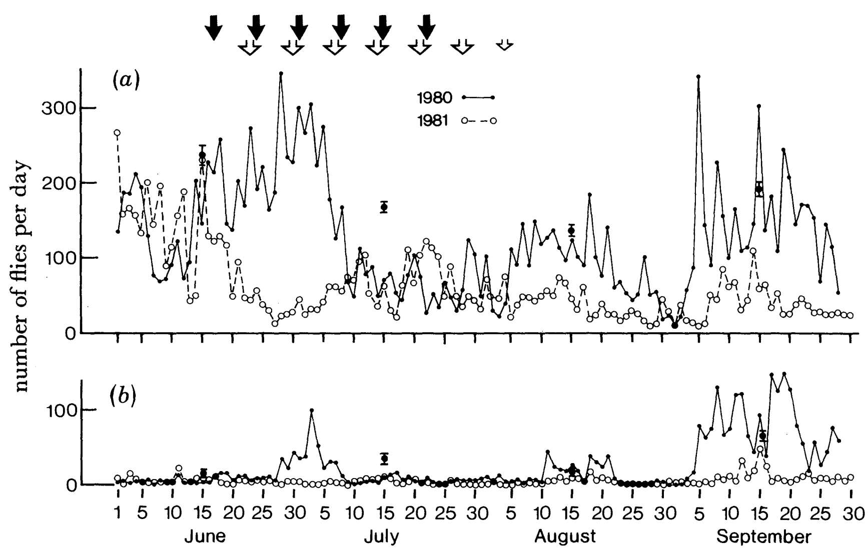

FIGURE 5. The numbers of flies caught at (*a*) Mô bridge and (*b*) Landa-Pozanda during June, July, August and September in 1980 and 1981. The mean numbers per month and their standard errors for 1979 are also shown, and the dates of the experimental treatments in each year are indicated.

conditions were suitable and there was no lack of breeding sites, so it is possible to discount natural causes, such as a deficiency of potential sources. Surveys on 18–19 July demonstrated that the treatments preceding these dates had been fully effective in the experimental area, thus eliminating it as a source. Despite some minor treatment failures within the O.C.P. these could not have accounted for the numbers of flies recorded, with the possible exception of a failure on a small tributary of the Mô in late July which could have been responsible for the increase in nulliparous flies at Mô bridge at that time (see §3*b*).

No *S. squamosum* were found among survivors within the O.C.P., only *S. damnosum s.s.* and *S. sirbanum*. The only known breeding sites of *S. squamosum* that could have been potential sources of the continuing infestations were the upper Terou in Benin and areas outside the experimental zone including massive breeding sites such as the Asuakawkow system, which was the only likely candidate as a source because the numbers of *S. squamosum* breeding in the other areas were low.

(*b*) *Ages of flies reinfesting Togo*

After the start of the experimental treatments, the proportions of parous flies in the catches at Mô bridge increased from 78.3% in May and 80.5% in the first three weeks of June to 88.2% at the end of June and to 94.1% for the period 1–15 July. Subsequently for the period 16–31 July they decreased to 83.7%, a decrease attributable to an increase in nulliparous flies around 14 July caused by breeding in a small tributary of the Mô, which is within 0.5 km of Mô bridge. Inadvertently this river was not treated until two weeks after it had begun to flow. There was another, unaccounted for, increase in nulliparous flies at the end of July.

There was no difference between the daily parous rates for all flies at Mô bridge for the period before the experimental treatments (1–20 June) and the same period in 1979 (Mann–Whitney rank sum test, $P = 0.64$), but the parous rates during the experimental period (21 June–14 July) were significantly higher than for the corresponding time in 1979 ($P = 0.0004$). However, within 1980 there was no difference between parous rates for the period 18 May–20 June and 1–15 July ($P = 0.39$), which was also true if the results for *S. squamosum* alone are compared for the same periods ($P = 0.16$). Nevertheless although for the period 20 May–20 June inclusive there was no difference between the parous rates for *S. damnosum*/*S. sirbanum* and those for *S. squamosum* ($P = 0.82$), during the trials (21 June–13 July) the proportion of parous *S. squamosum* was significantly higher than that of parous *S. damnosum*/*S. sirbanum* ($P = 0.03$).

At Landa-Pozanda there was no discernible change because the flies were nearly all parous before the experimental treatments started. At the beginning of July when the numbers increased to 98 flies, the parous rate remained high (99%), which was evidence that the increase was not due to local (undetected) breeding but was part of a reinvasion. Parous rates at Bagan, Fazao and Landa-Mono did not change significantly after the start of the experimental treatments, but at Bagan they were higher in July than during July 1979.

(*c*) *Numbers, species and ages of flies reinfesting Benin*

The numbers of flies caught at Gbassé (figure 6) increased gradually until 10 June but thereafter there was a sharp increase, which continued until late June with peaks of nearly 700 flies. After this the numbers remained high, with some exceptionally high catches, similar to the pattern recorded in 1979. All the flies examined from catches at Gbassé and Zougou were *S. damnosum*/*S. sirbanum*. Few samples were examined for physiological age but out of 116 from a sample caught on 5 July 86% were parous.

(*d*) *Meteorological conditions associated with the* 1980 *reinfestations*

The strongest winds at all the stations were usually at 600 or 900 m above sea level, and because the 600 m data are most likely to reflect the conditions experienced by migrating *S. damnosum s.l.* (Magor & Rosenberg 1980) these were analysed in most detail. Summaries of the directions and speeds of the winds recorded 600 m above sea level at 00h00, 06h00, 12h00 and 18h00 daily at Kandi are illustrated (figure 7), and the results for Parakou and Sokodé were similar, but the winds over the Benin stations were stronger than those recorded over Sokodé, reproducing a result also found in 1979 (Garms *et al.* 1982). Winds at all the stations were predominantly southwesterly or southerly and strongest at 00h00 and 06h00.

The possible effects of the experimental treatments precluded interpretation of the information on the occurrence of storms in Togo but at Gbassé, in Benin, this consideration was of less

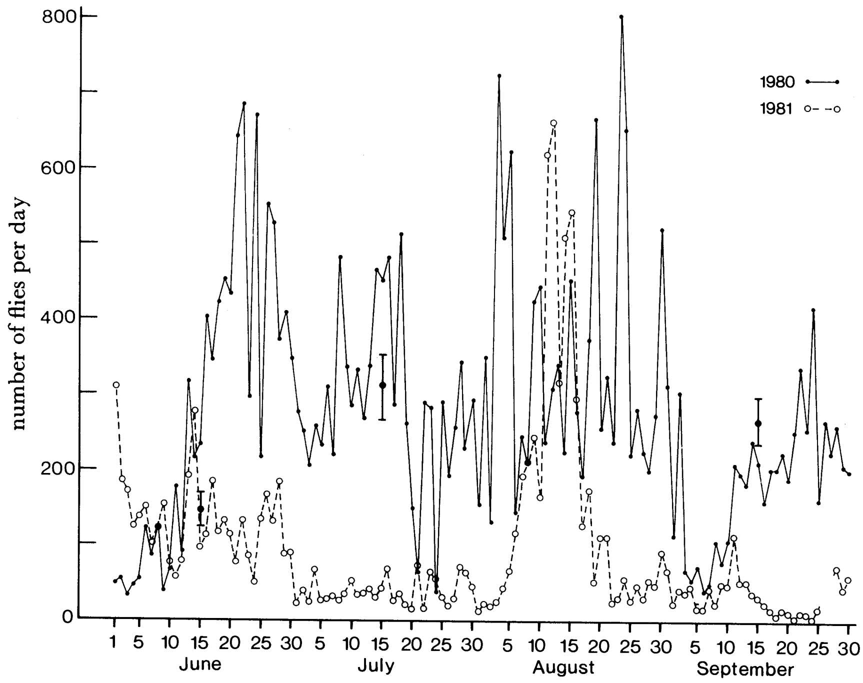

FIGURE 6. The numbers of flies caught at Gbassé during June, July, August and September in 1980 and 1981, together with mean numbers per month in 1979 and their standard errors.

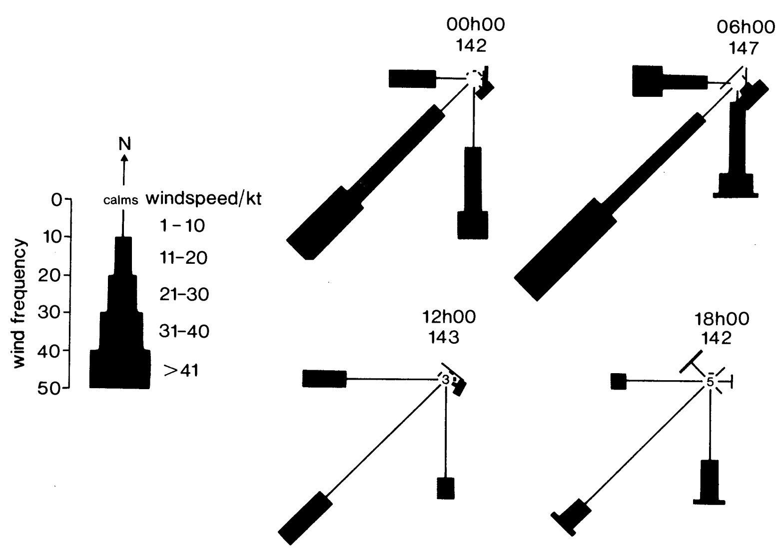

FIGURE 7. The frequencies during the period May–September 1980 inclusive of winds of different directions and speeds (1 knot (kt) ≈ 1.85 km h^{-1}) recorded at 00h00, 06h00, 12h00 and 18h00 at 600 m above sea level over Kandi and an explanatory diagram of the scales used. The numbers of observations made at each of the four times are also given and the figures in the centres of the diagrams refer to the numbers of times the winds were recorded as calm.

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importance. The possibility of flies coming into Benin from Nigeria has been raised (Garms *et al.* 1982) on the premise that the flies may travel in association with squall lines, which tend to move from east to west over West Africa during rainy seasons. During the period June to September inclusive, 78 thunderstorms were recorded at Kandi; these were not associated with any clear trends in the numbers of flies caught at Gbassé, but by considering only the storms with wind speeds in excess of 10 m s^{-1}, defined as squalls, a trend is apparent. For this analysis it was assumed that the numbers of flies caught on the same days as when the squalls occurred might have been affected by the squalls themselves (which often interrupted the catches), so the numbers caught at Gbassé on the day before each squall were compared with the numbers on the day after the squall. By this criterion, 13 squalls were followed by decreases and 4 by increases, a significant difference ($\chi^2 = 4.76$, $P < 0.05$); and if the magnitudes of the changes in numbers are taken into account the difference is also significant (Wilcoxon signed-ranks test, $P < 0.025$). Thus the evidence is contrary to the hypothesis of westward movements in association with squalls and suggests that such storms tend to interrupt the flow of flies into the O.C.P. The conclusion that the flies were coming into the O.C.P. with the prevailing winds, independent of isolated events such as storms, is supported by the patterns of gradual increases over a series of days which were noted at several sites (figures 5 and 6), and may reflect phenomena such as variations in the numbers of flies emerging from the sources.

4. Reinfestations and the effects of experimental treatments in 1981

(*a*) *Togo*

The experimental treatments performed in 1980 reduced the fly numbers within the O.C.P. area but failed to bring them down to a negligible level (see §3). A major source of *S. squamosum* beyond the 1980 experimental area was the Asuakawkow river system, so it was decided to treat this and other *S. squamosum* sites in Togo, together with some in eastern Ghana, during the 1981 rainy season.

The 1981 experiment was marred by more treatment failures, summarized below, than had occurred in the previous year. Larvae and pupae of *S. damnosum s.l.* were found on several occasions in the Kpaza system and in a tributary of the Asuakawkow, areas where the mountainous terrain posed difficulties for the control teams. No failures were observed in the Anié system except near Alamassou, where the first two treatments failed. Results were also good in the main courses of the Asuakawkow but the experimental treatments of the Mono were never satisfactory. Larvae of *S. damnosum s.l.* were found in the lower course of this river within the extension at almost all sites examined in July and early August. Most of the survivors were *S. damnosum s.s.*, few *S. soubrense*/*S. sanctipauli* being found. Some failures in the Mô were detected in June but later in the season there was no evidence of breeding: most of the Mô's tributaries were dry in June but some failures were detected in them later, in mid-July, which may have contributed to the increases in fly numbers and decreases in proportions of parous flies at Mô bridge at that time (see below).

Biting densities at Mô bridge started to increase during May, developing a pattern similar to those of the two previous years, but the catches returned to low levels at the time of the experimental treatments (figure 5) and none of the high peaks, which were observed in 1979 and 1980 and were considered to be typical or reinvasion activities, occurred. Nevertheless the results were not satisfactory, especially during the second half of July when daily catches were in excess of 100 on several occasions. In June 93% of the flies were parous but in July only 73% and in August only 79%, so it is likely that flies from the unsuccessfully treated rivers were contributing to the numbers rather than only flies migrating from outside the boundaries of the experimental zone.

At Landa-Pozanda the numbers remained very low throughout the experimental treatments (figure 5). Except for a period during 12–16 July when some nulliparous flies appeared, all the flies examined from Landa-Pozanda in July were parous. During June 93% had been parous and in August 92% were.

Table 2. Mean numbers of *S. damnosum s.l.* caught per day at sites in Togo during July in 1979, 1980 and 1981

site	reference for figure 2	1979	1980	1981
Mô bridge	A	171	110	62
Landa-Pozanda	B	35	14	3
Bagan	C	166	113	100
Fazao	D	216	43	39
Landa-Mono	E	202	140	107
Alamassou	F	287	292	147
Djodji	G	559	431	17
Tététou	L	386	465	610

Although the experimental treatments did not eliminate biting fly populations these were markedly reduced throughout the treated area in Togo (see figure 2 and table 2) in contrast to outside the zone where at Tététou, for instance, more flies were caught per day in July 1981 than during that month in both 1980 and 1979.

The species compositions at Bagan, Mô bridge and Landa-Pozanda were similar to those recorded in 1979 and 1980. Most flies at Bagan and Mô bridge were *S. squamosum* and more than half of those caught at Landa-Pozanda were *S. damnosum*/*S. sirbanum*.

(*b*) *Benin*

After very high numbers in Benin at the end of May, daily catches decreased to a lower level of 100–200 per day at Gbassé in June and became very low in July. Towards mid-August daily catches increased but then declined again at the end of August and stayed low in September (figure 6).

All of the 194 flies examined from samples caught at Gbassé throughout the period May–September were *S. damnosum*/*S. sirbanum*. In samples caught at Zougou during August and September 166 *S. damnosum*/*S. sirbanum* were identified, but 2 *S. soubrense*/*S. sanctipauli* were also noted.

5. Discussion

The importance of *S. squamosum* as the major constituent of the fly populations reinfesting the Mô valley in Togo and the increasing predominance of *S. damnosum*/*S. sirbanum* at sites further east, as shown by Garms *et al.* (1982) for the 1979 season, was confirmed. However, the results were more equivocal with respect to the origins of the reinfesting flies because treating potential *S. squamosum* sources succeeded in markedly reducing their numbers but did not prevent substantial reinfestations from continuing.

Although the 1980 results suggested that *S. squamosum* were coming from beyond the boundaries of the first experimental zone and the 1981 extension further reduced the numbers and also the meteorological data are consistent with northward or northeastward movements, some doubts remained in 1981 because of a few treatment failures in the experimental zone, which included some sources of *S. squamosum*. In addition the environmental conditions in 1981 differed from those in the two preceding years: many rivers, including sections of the Anié and Mono that had been highly productive of *S. damnosum s.l.* in May and June of 1979, remained dry during these months in 1981 and it is difficult to eliminate the possible effects of such environmental factors on the fly numbers when comparing the results of different years. Nevertheless it seems likely that many *S. squamosum* had reinfested the Mô valley from sources up to 150 km distant, especially because much of the 1981 reinvasion activity could be attributed to treatment failures close to the catching points with correspondingly high proportions of nulliparous flies. Furthermore the reinfesting populations took longer to recover in 1981 than in 1980, although the environmental conditions in August and September were similar in those years (table 1), suggesting that the reinfesting populations are partly dependent on the productivity of the extra sites treated in 1981.

In 1980 all larvae identified from sites of treatment failures within the routine O.C.P. area were either *S. damnosum s.s.* or *S. sirbanum*, and such failures may have been responsible for much of the continuing reinfestations by these species during the trials because their numbers at Mô bridge were not reduced proportionally as much as those of *S. squamosum* (figure 4) and the proportions of parous *S. damnosum*/*S. sirbanum* became significantly less than the proportions of *S. squamosum*.

A possible, but unlikely, source of *S. squamosum* in both years was the Terou in Benin. This river was never treated but neither was it very productive of *S. damonosum s.l.* until late in the season in both years, and *S. squamosum* was in the minority in its breeding sites. Similarly the Ogou did not begin to flow until late in both seasons. Other possible sources of *S. squamosum* outside the experimental zone included breeding sites west of the Volta Lake such as the Tain and the Tanfi rivers in Ghana, where *S. squamosum* were recorded by Vajime & Quillévéré (1978), but they are unlikely to have been involved in view of the distances concerned (200–300 km) and the lack of flies at catching stations intermediate between them and the Mô valley.

Because breeding sites of *S. damnosum s.s.* are ubiquitous in the area studied we have not been able to locate sources for this species, additional to where control failures were detected, and, besides, the flies may emanate from many different source areas. Similarly it is difficult to suggest likely source areas for the reinvasions by *S. damnosum*/*S. sirbanum* in Benin where this species pair predominated among the migrant flies, but breeding sites of these species were abundant in the Ouémé river system, especially in the Ouémé itself and the Okpara. The relatively low numbers of flies recorded at Gbassé from the end of June until the end of July in 1981 were unlikely to be a result of the experimental treatments in Togo during that period, although it is possible because *S. damnosum s.s.* usually breed extensively in the Mono, but was probably attributable to the low water levels in the Ouémé basin at that time.

Although the prevailing winds were from the south or southwest, many storms came from the east and if these were bringing flies with them then dramatic changes in the species compositions of the flies at sites in Togo might have been expected to have been associated with them because eastern sources, with their predominance of *S. damnosum s.s.*, contrasted with sources to the south and southwest where *S. squamosum* was dominant. Thus any westward movements associated with winds or storms from the east would have been expected to have increased the proportion of *S. damnosum s.s.* in the catches at Togolese sites within the O.C.P., but no such increases in association with storms were noted. Similarly there is no conclusive evidence for westward movements in Benin and, indeed, the squalls there, which tend to come from the east, were followed by decreases in fly numbers. However, the high frequency of strong winds at 600 m from the south and southwest are consistent with the hypothesis (Garms *et al.* 1982) that *S. damnosum s.l.* can migrate into the O.C.P. in Togo and Benin with such winds. The Kandi data suggest that, for long-distance northeastward movements of hundreds of kilometres, *S. damnosum s.l.* would be well adapted if they flew during the night or the early morning. The weaker winds common in the evenings and during the day might permit the flies to make controlled flights at these times for blood-seeking and ovipositing and also, perhaps, for gaining height before migrating. Once above the boundary layer (Taylor 1958, 1974) they are likely to be swept away by the stronger winds, which could take them 300 km in a night.

In conclusion it seems that *S. squamosum* populations in Togo are capable of travelling northward and to the northeast for up to 150 km in association with the prevailing winds and that *S. damnosum*/*S. sirbanum* can also travel for similar or longer distances in both Togo and Benin. However, despite the potential infectivity of reinvading *S. damnosum s.l.* the epidemiological data for *O. volvulus* infections within the O.C.P. area have continued to be very encouraging and it is thought that this is because the reinvading flies have tended to remain close to the rivers where they reoccur, without spreading to outlying areas as they used to do before the control programme began (Walsh *et al.* 1981*a*).

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Discussion

R. F. Sellers (*Animal Virus Research Institute, Pirbright, U.K.*). Is there a difference between the pattern of flight of insects by day and the pattern by night?

R. A. Cheke. *S. damnosum s.l.* only bite during daylight hours, but not enough is known about their nocturnal behaviour to give a satisfactory answer. *S. damnosum s.l.* have been caught at light traps beside breeding sites (Marr 1971; Service 1977, 1979; Walsh 1978), and Cooter (1982) has shown in the laboratory that *S. ornatum* Mg can fly at night as well as during the day. The possibilities for nocturnal migrations by blackflies should be investigated further, especially in view of the differences between day and night time winds.

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D. E. Pedgley. Winds in the lowest few hundred metres of the atmosphere over the O.C.P. area tend to accelerate during the night, except close to the ground. This is a well recognized character of many land areas subject to both monsoons and trade winds. Long-distance flights above the boundary layer would therefore be favoured at night.

R. C. Rainey, F.R.S. (*formerly Centre for Overseas Pest Research, U.K.*). I should like first to congratulate Dr Cheke and Dr Garms on their further instalment of this magnificent story, and then to emphasize the value of the unique evidence on the long-distance flights of the blackfly that this material provides. The near-completeness with which every breeding site among the rapids of the meticulously monitored rivers of the Project area of these seven countries has been kept free of larvae has meant that trickles of blackflies still intruding into this cleared area could be attributed, beyond all reasonable doubt, to reinvasion from known uncontrolled breeding areas beyond its perimeter. One would very much like to see what might be learned from case studies of individual trickles in relation to the corresponding day-to-day winds and weather, which are by no means entirely uniform. As a more general comment, it is not so many years since one accepted without hesitation the dictum that 'vectors are not migrants', which this *Simulium* story so clearly contradicts.

R. A. Cheke. Case studies of the winds and weather associated with particular events are difficult because we cannot be sure whether flies captured on a certain date have arrived at the site in question on the same day as they were caught, the day before or perhaps up to three days before. Partly because invading populations of ovipositing flies are younger than populations caught by vector collectors (Cheke *et al.* 1982) we suspect that the flies arrive gravid, lay eggs on the first evening after their arrival and seek bloodmeals on the following day. However, this may not be so, and flies in a mixture of different physiological states may be travelling together. Magor & Rosenberg (1980) investigated the meteorological conditions associated with discrete reinvasions and we have provided day-to-day wind data (Garms *et al.* 1982) but until more is known about the flies' behaviour the results of such studies are difficult to interpret.

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