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Tsetse movement in wind fields: possible epidemiological and entomological implications for trypanosomiasis and its control

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Summary

This paper presents evidence that tsetse flies (*Glossina*) can be dispersed by wind. This dispersal in West Africa is suggested to be along a south-west north-east axis. The implications of wind dispersal of *Glossina* for chemical and genetic control operations is discussed. Field experiments necessary to test this hypothesis are recommended. A study of human trypanosomiasis foci in West Africa has revealed that foci are orientated in roughly parallel lines in a south-west north-east direction. This directionality was significant when compared with 7 other compass points. It is proposed that foci could be populated by infected flies dispersed from the south west, where denser populations exist, on the prevailing winds in the late dry/early rainy season. The significance of these ideas in relation to the epidemiology of *Trypanosoma brucei rhodesiense* in Ethiopia and *T. evansi* are discussed.

Key words: trypanosomiasis; West Africa; *Glossina*; wind dispersal; epidemiology; *Trypanosoma*; vector control.

Introduction

It has been recognised that West African Trypanosomiasis (WAT) is associated with well defined residual foci where the prevalence of the disease is much higher than in surrounding areas (Lapeysonnie, 1969; Janssens, 1971). Several explanations have been suggested such as healthy human carriers; animal reservoirs; ecological and entomological factors leading to increased

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transmission and climatic changes over several years (Scott, 1961, 1970; Lapeysonnie, 1969; Janssens, 1971; Ford, 1971; Molyneux, 1973). It has also been suggested that foci were only activated when strains of parasites were brought in from outside. Janssens (1971) also cites the introduction of migrants, lower resistance due to malnutrition and alteration of trypanosome strains as alternative explanations. Frézil and Carnevale (1976) have suggested that the persistence of Central African foci could be due to the capacity of *Glossina* to live up to 6 months under favourable conditions. Some foci (Say, Niger; Sansanni-Mango and Dapango, N. Togo; Nola, Central African Empire) had seemingly been eradicated only for the disease to recur despite consistently negative case finding reports.

Distribution of human West African trypanosomiasis: the suggested role of wind dispersed Glossina

The suggestions we make derive from recent observations in the field and a search of available literature. We hope to furnish another view of the problem of WAT epidemiology which may have wider implications. We suggest that on the basis of the geographical distribution of the foci (de Raadt and Seed, 1977) and their apparent linear association (Fig. 1) along a south-west north-east axis that these foci are associated with advances of *Glossina* carried by winds associated with the Inter Tropical Convergence Zone (ITCZ). The residual foci could be associated with movement of infected *Glossina* with the prevailing winds. These foci may represent particularly favourable areas for wind dispersed flies, to settle, feed and transmit infection. Alternatively, because suitable habitats are hostile climatically at the end of the dry season when this invasion is likely to occur they initiate disease where intimate man-fly contact exists (Nash, 1978).

The persistence of residual foci (Fig. 1) could be related to a variety of factors but the sudden appearance of the disease through the agency of wind blown infected *Glossina* could explain its sudden resurgences when it has been apparently absent. The reason for focality could also be related to secondary phenomena such as the distribution of surveillance teams or depopulation in areas where Onchocerciasis is hyperendemic. Large areas exist (Fig. 1) where foci are absent and where settlement is known to be inhibited by Onchocerciasis.

Glossina are not renowned for their wind dispersal. Those responsible for locust and *Simulium* control (Rainey, 1974; Le Berre et al., 1978) have demonstrated, however, the importance of wind as a dispersal agency. It seems possible that *Glossina* could, from populations in southern zones be dispersed by wind to invade "residual foci". These foci are areas of relatively high population density where tsetse could easily find food; chains of foci can be associated with prevailing wind direction (Fig. 1 and Table 1) and the further north-east flies are dispersed the more intimate man-fly contact is likely to be. *Glossina* have been recorded many kilometres north of the known limit of permanent populations. Roubaud (1920) and Challier and Laveissière (1977) have reported *G. palpalis* and *G. tachinoides* at Dori, Upper Volta, which could have been dispersed on wind. A single fly could infect several individuals and be an excellent reservoir (Frézil and Carnevale, 1976).

Meteorology

The Inter Tropical Front is frequently used in the same context as the ITCZ which is a zone lying between the air masses of differing densities represented by the Tropical Continental Air which is associated with dry north-easterly or easterly winds and Tropical Maritime Air, associated with wet south-westerly winds (Harrison Church, 1970). The Tropical Maritime Air forms a wedge under the Tropical Continental Air which penetrates northwards as the Tropical Maritime Air becomes predominant. The areas between these air masses is the ITCZ. The zone itself is not associated with rain but the warm moist air behind the northerly moving front is associated with precipitation. "Line Squalls" are associated with changes of season and are represented by south-west to north-east thunder storms which are proceeded by one or two days of high temperature and humidities and calm air. South-westerly winds then blow and heavy rain early in the squall is followed by gentler rain falls later. Associated with the moist Maritime Air are prevailing south-westerly winds. The directionality of these winds is given by Harrison Church (1970). The prevailing wind direction for most of the year in West Africa is south westerly. Although during December-January a reversal due to the Harmattan takes place.

Entomological evidence

Insects other than Glossina

Extensive studies on biometeorology and insect migration have been carried out and Rainey (1974) has reviewed this topic. It seems curious that in view of the evidence available from other sources (Rainey, 1974; Le Berre et al. 1978; Duviard, 1977) that *Glossina* have not been considered in this context. Rainey (1974) remarks "a population of airborne insects must be envisaged as a biometeorological system whose effective study takes account not only of the aerodynamics, physiology and behaviour of the individual insects and the biological sources and sinks affecting the population but also of the dynamics of its atmospheric environment and the associated energy exchanges". We see no reason why *Glossina* should be regarded as an exception to this.

Evidence for movement of Glossina

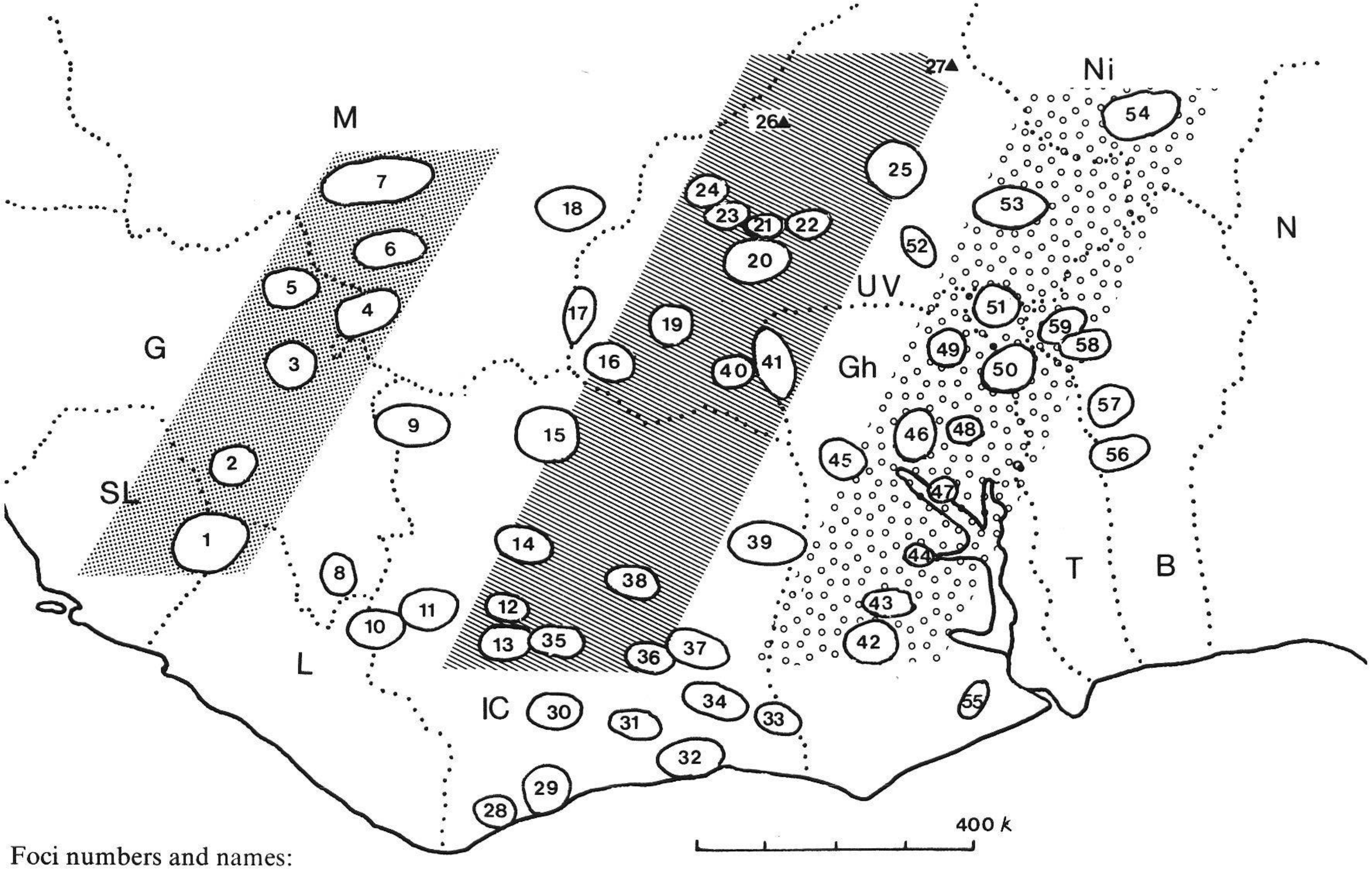
Glover (1961) reviewing West African studies on fly movements reported that Simpson (1918) found with *G. tachinoides* the greatest distance covered by

Table 1. Distribution of residual foci of WAT in relation to prevailing South Westerly winds. All foci are taken from map of de Raadt and Seed (1977) which is compiled from various sources

Presumed focal sources in forest or peri-forest zones	Extensions from presumed source foci and distance between foci centres (in km)
Bwedu (SL)	→ 110 → Kissidougou (G) → 170 → Kankan (G) ↗ 120 → Siguira (G) → 150 ↘ / ↘ 150 → Yanfolila (M) → 105 ↗ Ouélessébougou (M) → 80 → → Bamako (M)
Man (IC)	→ 115 → i) Séguéla (IC) → 200 → Korhogo (IC) → 130 → Niangoloko (UV) → 90 → Sidéradougou (UV) → 190 → → Boromo (UV) → 90 → Koudougou/Sabou (UV) → 160 → Kaya (UV) → 160 → Dori (UV)
Danané (IC)	→ 320 → ii) Boundiali (IC) → 225 → Orodora (UV) → 230 ↘ Dédougou (UV) → 170 → Ouahigouya (UV)
Nzérékoré (L)	→ 260 → iii) Odienné (IC) → 300 → Koutiala (M) → 405 ↗ Dédougou (UV)
Daloa	→ 140 → Séguéla (IC) → 200 → Korhogo (IC) → 130 → Niangoloko (UV) as above
Bouaflé	→ 110 → Bouaké (IC) ↗ 360 → Gaoua (UV) → 260 → Manga (UV) ↘ 400 → Wa (Gh)
Kumasi (Gh)	→ 50 → Mampong (Gh) → 90 → Ateburu (Gh) → 110 → Salaga (Gh) ↗ 100 → Yendi (Gh) → 120 ↘ / ↘ 105 → Tamale → 135 ↗ → → Gambaga (Gh) → 180 → Sannsani-Mango (T) → 60 → Dapango (T) → 140 → → Fada-N'Gourma (UV) → 240 → Say (Ni)
Bida (N)	→ 225 → Kaduna (N) → 75 → Zaria (N) → 140 → Gamadan (N)
Tiv-Wukari (N)	→ 400 → Biu (N)

SL = Sierra Leone; G = Guinea; IC = Ivory Coast; UV = Upper Volta; M = Mali; L = Liberia; Gh = Ghana; T = Togo; Ni = Niger; N = Nigeria

Fig. 1. Map showing documented foci of West African trypanosomiasis redrawn and modified from de Raadt and Seed (1977). Points 26 and 27 (Ouahigouya and Dori) are added to foci of map of de Raadt and Seed. Different shaded areas represent possible associated foci, in south-west north-east orientation.



Foci numbers and names:

1 Bwedu
2 Kissidougou
3 Kankan
4 Yanfolila
5 Siguira
6 Ouélessébougou
7 Bamako
8 Nzérékoré
9 Odienné
10 Danané
11 Man
12 Vavoua
13 Daloa
14 Séguéla
15 Boundiali
16 Banfora
17 Orodora
18 Koutiala
19 Sidéradougou
20 Boromo
21 Koudougou
22 Sabou
23 Tchériba
24 Dédougou
25 Kaya
26 Ouahigouya
27 Dori
28 San Pedro
29 Sassandra
30 Gagnoa
31 Tiassalé
32 Abidjan
33 Adzopé
34 Agboville
35 Bouaflé
36 Dimbokro
37 Abengourou
38 Bouaké
39 Bondoukou
40 Gaoua
41 Wa
42 Kumasi
43 Mampong
44 Ateburu
45 Damongo
46 Tamale
47 Salaga
48 Yendi
49 Gambaga
50 Sannsani-Mango
51 Dapango
52 Manga
53 Fada-N'Gourma
54 Say
55 Koforidua
56 Bassila
57 Diougou
58 Kétapo
59 Natitingou

a single fly was 7 miles. These flies were believed to have followed canoes. Nash (1948) reported that *G. tachinoides* would "make no effort to spread into woodland Savannah». Glover (1961) suggested that flies carried long distances were a possible means of reinfecting old cleared areas and he reported that in the Gboko clearing scheme *G. tachinoides* suddenly appeared in high density to be followed by its equally sudden disappearance. Roubaud (1920), however, believed that larger scale migration routes of *Glossina* species occurred in West Africa and that such migrations were determined by increased humidity. He observed an increase in *Glossina* populations at the beginning of the rains and found flies in localities where they had not been present in the dry season. Roubaud proposed that wind was an important factor in dispersal of tsetse and considered that the Harmattan was responsible for the retreat of the flies from more northern zones during the dry season. The Harmattan would be clearly beneficial to the survival of the fly populations. The possibility of tsetse migrations are, however, refuted by Swynnerton (1936) and Buxton (1955). The record of *G. tachinoides* in south western Arabia quoted by Buxton (1955) could, however, be explained by wind dispersal. The sole reference to the effect of wind on tsetse in Buxton (1955) are to the results of Vanderplank (1948) who believed the activity of the insect might be reduced when the velocity of the wind exceeds a particular value. The possibilities of the effect of wind on tsetse dispersal are not considered by Bursell (1970) nor by Glasgow (1970) in their reviews on dispersal and the *Glossina* community.

Evidence from recent insecticide trials

The entomological results of spray trials in the Komoe Valley of Upper Volta presented by Baldry et al. (in prep.) and Van Wettere et al. (1978), suggests that at certain times of year large scale fly movements associated with wind take place probably over wide areas. Van Wettere et al. (1978) in small scale field trials of aerosol applications of insecticides by helicopter to the riverine habitats of *G. tachinoides* along the Komoe river in Upper Volta observed that there was an increase in *G. tachinoides* in two areas which had been treated with 2.6 g/ha Fenthion (OMS-2) and 4.3 g/ha Permethrin (NRDC 143; OMS 1821). These applications were made during the time the Inter Tropical Convergence Zone (ITCZ) is usually at the longitude of the Komoe Valley (Magor et al., 1975; Duviard, 1977) and associated with which flies could have reinvaded the treated areas. Earlier applications of these insecticides at half the above doses were shown to be capable of markedly reducing *G. tachinoides* populations. A satisfactory explanation of these results was not provided by Van Wettere et al. (1978). The results of Baldry et al. (in prep.) who when working in the area exactly a year later observed a simultaneous massive increase of *G. tachinoides* in three different experimental blocks which had been sprayed with residual doses of endosulfan (OMS 570) at 100 and 200 g/ha and decamethrin (NRDC 161; OMS 1998) at 12.5 g/ha. The male and female

G. tachinoides population in all blocks had been reduced by well over 90% of its pre-spray level but during the first week of March a sudden increase in *G. tachinoides* including old females) was observed throughout the blocks indicating a mass movement of flies on a broad front from the unsprayed areas to the south west. Meteorological studies in this area confirm wind direction from the south west at this time of year (Magor et al., 1975; Le Berre et al., 1978). Kernaghan (1961) also observed the sudden appearance of *G. tachinoides* in a treated zone in Nigeria.

Simulium and Dysdercus movements in West Africa

Studies on the movements of *Simulium* have recently been described by Magor et al. (1975) and Le Berre et al. (1978). Previous to these Ovazza et al. (1965) noted that *S. damnosum* reappeared in an area only when the ITCZ was to the north of it. Magor et al. (1975) showed that during the period 9th–13th March, 1975, ITCZ was at the longitude of the R. Komoe and moved from just below 10° N. to above 15° N. – a distance of over 600 km in 4 days. *S. damnosum* reinvasions were associated with zones of wind convergence – Magor et al. (1975) state that *S. damnosum* reinvasion of south western Upper Volta is associated with downwind displacement analogous with the observations of Rainey (1969, 1974). Le Berre et al. (1978) conclude "that the direction of reinvasion is, in the region under consideration, from South-West to North-East; this coincides with the direction of the monsoon wind" and "that a large number of females are able to fly 200–250 km without it being possible to say if they make the journey in stages or in one flight. Some females are able to cover 300 to 400 km".

Duviard (1977) has studied a Cotton Stainer *Dysdercus voelkeri* at Ferkéssedougou and other areas in North Ivory Coast. At Ferkéssedougou migratory activity stopped during the dry season (December–January) but built up again in February. Zone B and C of the ITCZ (see Duviard's Fig. 6 p. 196) showed the highest convective activity 300–600 km south of the ITCZ. This convective activity was at a rate of 25–30 km/h. During periods of 3–15 days, the ITCZ varied from 5°–8° N. latitude (= 900 km). Diurnal oscillations of the ITCZ were 50–250 km in 24 h, with instant speed movements of more than 50 km/h. Seasonal displacements of *D. voelkeri* were at longitude 4° E. 900 km and at longitude 8° W. 1250 km. *D. voelkeri* was predominantly transported by south-westerly winds blowing regularly during the hours of dawn to midnight, reinforced at low elevation by the low level jet stream. These events explained the sudden migration occurring at the end of the dry season. Duviard's data explain the movement of *G. tachinoides* in a NE direction at the end of the dry season and support Roubaud (1920) that *G. palpalis* and *G. tachinoides* disperse south with the Harmattan. We propose that the *Glossina* belt north of the rain forest is fluid shifting SW–NE and vice versa in relation to the ITCZ and prevailing winds associated with it. The ITCZ is always proceeded by an increase in humidity. This could stimulate flies to disperse from riverine situations before its arrival. When it does arrive, flies would be in more open vegetation and therefore more likely to be affected by air movements; the vertical movement of *G. p. palpalis* to the top of the canopy in riverine vegetation during the night (Scholz et al. 1976) would also aid dispersal.

Epidemiological evidence

Trypanosomiasis outbreaks close to limit of tsetse distribution

There is no satisfactory explanation for outbreaks of WAT north of the limit of *Glossina* distribution. Laveissière (1977) has found cases in a leprosarium in Ouahigouya, Upper Volta, where no *Glossina* were found. The nearest known *G. tachinoides* record being 80 km south west or 60 km south according to the map of Challier and Laveissière (1977). An infected wind dispersed fly could have been responsible for these cases as Ouahigouya lies in a direct north easterly direction from the known foci (Fig. 1). In these situations mechanical coital or congenital infection are usually evoked.

Thomson (1969) reports the case of Gamadan near Kano, Nigeria, with an infection rate of 0.4% in 1966 which rose to over 1% in 1967 and 1968 until the very limited tsetse habitat in Mango plantations was sprayed with DDT. A few cases were found between October 1968 and 1970. However, in October 1970 a routine survey revealed a total of 24 new cases in the village whose infection was certainly acquired after the spraying campaign. These cases could have arisen either through infected tsetse being brought in by transportation on vehicles or by wind; uninfected tsetse brought in by either of the above methods could have remained sufficiently long to become infected from a previously undetected case. This is unlikely as there were very few, if any, such people and a non-teneral fly would have little chance of becoming infected and no permanent fly population existed for repeated surveys failed to find flies.

Serological and zymological evidence

Gray (1972) surveyed the distribution of antigens of *T. b. gambiense* in Nigeria, and grouped together the Nigerian isolates into two sub-strains on the basis of their ability to produce 3 antigens which had a restricted geographical distribution. Gray (1972) shows sub-strain A isolates are derived from the Benue Valley and are found as far north as Biu and they progress in a south-west north-east direction. The focus furthest west associated with sub-strain A being on the south-eastern edge of the Jos Plateau at Kwang. Sub-strain B which did not possess these antigens were all isolated from areas further west or on the Plateau itself. Godfrey and Kilgour (1976) have confirmed Gray's characterisation of Nigerian isolates into two groups by isozyme typing.

Gray (1972) remarks that his results substantiated the expansion of the disease in the Benue Valley. We propose that this was the result of wind dispersal. Gray was surprised to find the Bida isolate was sub-strain B and was related to those found on the western edge of the Plateau and further north and west. Wind dispersal of *Glossina* carrying sub-strain B from the Bida area would have given rise to this geographical pattern. The views of Duggan (1962) on the primordial endemic foci in Nigeria may need revision on the basis of the work of Gray (1972) and Godfrey and Kilgour (1976) and our interpretation of the results.

Insecticidal campaigns and human trypanosomiasis

A possible criticism of our ideas in relation to Nigeria is that WAT or *Glossina* should recur where insecticide control has taken place. However, in many areas there has been a natural decline in WAT before the eradication campaign (Thomson, 1969) and the campaign itself has also been accompanied by reduced surveillance for the disease followed by extensive habitat modification. Any flies subsequently present would be in low density and perhaps would not be detected with available techniques. It is not known, however, if such sprayed areas have been routinely surveyed for WAT but Gamadan and Ouahigouya are outbreaks which can be associated with perhaps individual infected flies.

WAT was not a serious problem in the Hadeja Valley project whose objective was to make available the fertile alluvial plain for agricultural use. However, a vigorous outbreak occurred 45 miles north east of Hadeja on the Katagum river until controlled by a ground spray campaign in 1964–1965.

Residual foci in West Africa

Scott (1961) has reported on a series of outbreaks of WAT in Ghana and discussed the residual foci. He suggested climatic changes occurred allowing closer man-fly (*G. palpalis*) contact to explain the south east Mamprussi outbreak, and that the Mid-White Volta and West Wa epidemics "had resulted from the introduction of a strain of trypanosome from an epidemic already established". The maps of Scott (1961) (Map 1, p. 124; Map 3, p. 130) show a predominantly south-west north-east trend in the persistent foci and if extended towards Togo, (see de Raadt and Seed, 1977) the Sansanni-Mango and Dapango foci lie in their path. Wind dispersal could provide an explanation for the persistence of these foci which were subject to pentamidisation and extensive surveys by French authorities (Lapeysonnie, 1969). We suggest that parallel lines of foci in West Africa exist, these are a) Guinea – Mali; b) Ivory Coast – Upper Volta; c) Ghana – N. Togo – Upper Volta – Niger; d) Bida – Kaduna – Kano; e) Benue Valley foci – Biu. Details of distances and possible interactive foci are given in Table 1 and Fig. 1.

Statistical analysis of foci

A trend analysis was carried out to test this hypothesis and considered the area delimited by the foci Bwedu, Sierra Leone (8.22 N: 10.21 W) and Bamako, Mali (12.40 N: 7.59 W) in the West and Bassila, Benin (9.01 N: 1.46 E) and Say, Niger (13.08 N: 2.20 E) in the East; the focal points of these residual foci being identified from the map of de Raadt and Seed (1977). The tropical rain forest and coastal belt were excluded as it was considered that the effect of wind on fly dispersal would be of less consequence than in the Savannah. Fifty-nine foci were analysed west of Nigeria and east of a line from Bwedu to Bamako. A set of parallel lines equivalent to 120 km apart was lain on the map and was rotated around a hypothetical mid point of the area (75 km west of Gaoua). This grid distance was chosen as the smallest to permit a chi square test on the eight compass points and allows between five and eight strips of territory in the roughly rectangular area under analysis depending on compass direction. A chi square test was applied to the resulting distribution of foci with the expected values adjusted according to area. The results of the chi square test (with degrees of freedom [d.f.] values) obtained for eight compass points analysed were:

	Chi square	*d.f.*
S – N	12.1	7
SSW – NNE	7.4	5
SW – NE	14.5	5
WSW – ENE	7.5	4
W – E	5.5	4
WNW – ESE	1.8	5
NW – SE	10.8	6
NNW – SSE	3.1	6

This reveals a significant orientation in only one case SW – NE (Chi square = 14.5, 5 degrees of freedom). Although the subjectivity necessary to carry out such a test is large, a trend in this direction appears to exist.

Epidemiology of T. (Trypanozoon) brucei rhodesiense

Baker at al. (1970) have discussed the origins of the Ethiopian outbreak of *Rhodesiense* trypanosomiasis and concluded that the disease had been recently introduced. Onyango (1969) suggested game movement from Uganda was a possible source of infection and Baker et al. (1970) reported a large game population was present. Although Uganda was the closest source of the disease *Trypanozoon* in game could have become infective to man without the introduction of parasites from Uganda (Van Miervenne et al., 1976). Flies, however, could have been blown into the Gambela area on prevailing south westerly winds from Uganda and it is known from locust studies that suitable winds occur in the region (Rainey, 1974).

Epidemiology of T. (T) evansi

Hoare's (1957) theory on the origin of *Trypanosoma evansi*, the parasite of camels and equines, outside the tsetse zone is widely accepted. This suggests camels come into contact with *Glossina* in the Northern Guinea Savannah Zone where they become infected with *Trypanozoon* parasites. On their return north the parasites are spread amongst camels and equines by mechanical transmission. Our theory would suggest an alternative origin of *T. evansi* in Saharan Africa. Infected wind dispersed *Glossina* could be blown north of the limits of permanent tsetse distribution and there infect camels. Hoare's (1957) theory is still valid but both explanations for the origin of *T. evansi* are acceptable.

Discussion

Entomological and epidemiological evidence has been presented which supports the hypothesis that *Glossina* can be dispersed by wind. We propose that flies are dispersed along a south-west north-east axis with the prevailing winds. It has not before been considered that movement of tsetse occurs in this way but should we be correct, it will have great significance for chemical and genetic control operations. Much field work will need to be done to test this hypothesis but large scale trapping of marked flies and their subsequent recapture could be carried out in chosen areas at appropriate times.

The implications for chemical and genetic control must be reassessed on the basis of the observations already made in Upper Volta by Baldry et al. (in prep.). In particular the length of any barriers currently being used for genetic control experiments by the release of sterile male flies.

We suggest also an explanation of the persistent foci of West African sleeping sickness. No suitable explanation is available which accounts for the observed facts as described by Janssens (1971). These foci have one order of magnitude higher prevalence than the surrounding areas and although the disease appears to be under control cases suddenly recur. We suggest that wind dispersed tsetse play a part in the resurgence of sleeping sickness. There is evidence of a directional relationship between known foci in a south-west north-east direction from both cartographic and statistical analysis. We would, however, not wish to rule out the migratory movements of man and/or his animals which in the past have been considered as possible sources of the disease and mechanisms for its spread as well as fly dispersal by transportation. The geographical distribution of these foci could also be secondarily related to depopulation through onchocerciasis; areas of high population density; more intimate man-fly contact in some areas through partial habitat destruction; and distribution of surveillance teams. All these are factors which could influence the patterns of the disease.

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