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Windborne Spread of Insect-Transmitted Diseases of Animals and Man

D. E. Pedgley

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Windborne spread of insect-transmitted diseases of animals and man

By D. E. Pedgley

Centre for Overseas Pest Research,† College House, Wrights Lane, London W8 5SJ, U.K.

There are many kinds of flying insects that transmit disease. Some are known to be able to travel up to several tens of kilometres, and for a few there is evidence of movements over hundreds of kilometres. Such long movements are wind-dominated, and they involve flying for hours, sometimes continuously. They are also rapid, and they need to be taken into account when forecasting disease spread. Both the monitoring and the controlling of outbreaks might then be improved.

1. Introduction

Spread of insect-transmitted animal and human diseases is brought about by movements of both hosts and vectors. Of the many kinds of insect vectors, those that are winged are almost all Diptera. Some, such as screw-worm flies, bot flies and warble flies, cause disease directly, by their maggots' feeding on living or diseased flesh. Others carry disease-causing organisms, and act either as simple mechanical vectors (such as house flies, blow flies and horse flies) or as intermediate hosts in which the disease organisms undergo some development and are passed on during a blood meal (such as mosquitoes, midges, sand flies, blackflies and tsetse). The disease organisms include viruses, bacteria, protozoa and filarial worms. Among the diseases of man are malaria, yellow fever, dengue fever, sleeping sickness, leishmaniasis and river blindness. Among the diseases of animals are African horse sickness, bluetongue, bovine ephemeral fever, Rift Valley fever and several forms of encephalitis.

Some of these vectors, such as mosquitoes, midges and sand flies, are weak fliers, with forward speeds in still air of the order of 0.5 m s^{-1}. Others are strong fliers, with air speeds of the order of 5 m s^{-1}. In still air, direction and distance of movement are limited by heading, and by air speed and flight duration, but in the presence of wind, both direction and distance can be altered. For example, a flying insect can reach any stationary goal, such as shelter, food, a mate or an egg-laying site, if its air speed is greater than the wind speed. Otherwise, the flying insect must be taken more or less downwind, and the distance moved is then determined largely by wind speed and flight duration.

Wind speed often increases with height above the ground, and there is usually a layer next to the ground within which wind speed is less than the insect's air speed; this has been called the insect's boundary layer (Taylor 1960, 1974). Within it the flying insect has a chance of reaching a stationary goal, but by flying above the layer the insect must be taken more or less downwind. Boundary layer depth varies with the weather and with the species and even between individuals of the same species (their age, sex, physiological state, etc.). Unevenness of the ground or of its vegetation cover will provide patches of shelter where the insect's boundary layer may be deepened. Slackening of the wind that often occurs at night also deepens the boundary layer, and those insects that use odours to help guide them to goals might be further

† Now the Tropical Development and Research Institute.

helped by the resulting weaker turbulence at night, and hence by the reduced diffusion in the odour plumes.

For good practical reasons, the movement of flying insects has been most often studied close to the ground, within or not far above the boundary layer. Flight at greater heights is difficult to examine and tends to be ignored. Johnson (1969), in his extensive review of insect migration and dispersal by flight, drew particular attention to the paucity of direct observations of this essentially windborne movement of flying insects above the boundary layer, sometimes over tens or hundreds of kilometres. There have been further observations since that review, but the evidence for such movements is still largely circumstantial. Direct evidence is provided by mark-and-recapture experiments in which individuals are tagged with dye, radioactive material or some other tracer, then released and caught again somewhere else, more or less downwind. One practical difficulty with such experiments is the need to mark many individuals, even millions, to have a chance of catching at least one some hundreds of kilometres away. Another is the need to have an extensive network of traps, difficult to service frequently. An interpretational difficulty is knowing whether the behaviour of marked individuals caught is typical of the marked individuals as a whole, or of the unmarked population. Recapture of a marked individual at least shows that downwind movements can occur, if wind speed at flight height is judged to be much greater than the insect's air speed. Further direct evidence is provided by relating the flight of individuals to winds at the time. Observations by eye are restricted in range, but those by radar are less restricted and they also provide a facility for studies at night.

Circumstantial evidence for long-distance windborne movement of flying insects can be derived from case studies in which insects that are known or inferred to have arrived at a particular time and place are back-tracked to known or likely sources by means of windfield maps and reasonable assumptions about flight behaviour. A flight taking no more than a few hours can often be back-tracked by eye from a single map, but one lasting up to a few days requires more careful calculation of the back-track to take account of changes in the windfield with time. The longer the flight time, the greater the errors in the calculated back-track: errors become unacceptably large after a few days. Even where back-tracks are not calculated, an association between insect arrivals and particular kinds of wind systems can be indicative of windborne movement, and so are sightings of flying insects far downwind of sources. In contrast to such studies of particular events, the seasonal redistribution of whole populations in relation to seasonal changes of windfields provides circumstantial evidence for long, windborne movements. Climbing to above the boundary layer at take-off, captures at heights of hundreds of metres above the ground, and the ability to fly many hours in the laboratory are further indications of long-distance flight. Although individually these pieces of circumstantial evidence may not be convincing, in combination for a given species the case can be strongly made. For many species it is likely that new evidence in favour of long-distance windborne movements is yet to be discovered. A review, with many examples, has been made by Pedgley (1982) for flying insects in general; the following is concerned with disease-carrying flies in particular.

2. Examples of windborne spread of disease-carrying flies

Among flies causing myiases – the feeding of maggots on the flesh of living animals – the species that has been most studied is the screw-worm fly, *Cochliomya hominivorax*, a cause of heavy cattle losses in some years. It infests the New World tropics, but because it is killed by frost its occurrence at higher latitudes depends on annual reinvasion. In the U.S.A. it is able to overwinter in the extreme southeast and southwest. By means of sterile-male releases, flies were eradicated from the southeast in 1959, and in the southwest by 1966; but because of reinvasion from Mexico, sterile-male releases are needed each year along the border (Williams *et al.* 1977). The reinvasion has not been demonstrated to be windborne, but it takes place in spring, when southerly winds are frequent. This species is a weak but persistent flier, at 2 km h^{-1} for about 2 h a day up to more than 2 weeks, consistent with moves of the order of 100 km per week in 10 km h^{-1} winds (Crystal 1977).

The house fly, *Musca domestica*, is a known or suspected carrier of a variety of disease organisms, taking them from refuse to human food and thereby spreading typhoid, dysentery and other diseases. Many mark-and-recapture experiments have shown that individuals can move some tens of kilometres in a few days. In those experiments where movement was related to winds at the time, both upwind and downwind tendencies were found. This species has also been seen flying over the sea 70 km from land (Greenberg 1973). In the laboratory, average flight durations of 1–2 h have been recorded, and a maximum of 8 h (Shepard *et al.* 1972), so movements of 100 km or more are possible in even only moderately strong winds.

The long-known importance of mosquitoes in the spread of several diseases, including malaria, yellow fever and dengue fever, has led to extensive study of flight. There have been many mark-and-recapture experiments but, as with house flies, few have examined the effects of wind. Marked individuals have been recaught some tens of kilometres from their release points. In wind speeds comparable with their air speeds, movement has been seen to be mostly downwind. Several species have been caught at altitudes up to 1500 m, more by night than by day, suggesting that active climbing dominates ascent rather than passive lifting in atmospheric updraughts, which would generally be stronger and deeper by day.

There have been some case studies of long-distance windborne movement. In 1927 clouds of *Aedes sollicitans* were seen arriving at a ship 175 km downwind of the east coast of the U.S.A. in southwest winds blowing from the probable source in the Dismal Swamp area of North Carolina (Curry 1939). During 1942, before the battle of El Alamein, there was an occasion when large numbers of *Anopheles pharoensis*, mostly females, invaded a military camp 50 km from the nearest possible breeding place and much further from any place where they are likely to have bred in sufficient numbers. This arrival was associated with deep easterly winds, to an altitude of at least 3 km, blowing from the Nile delta (Kirkpatrick 1957). From 6 to 8 August 1959 there were outbreaks of malaria at scattered settlements along the Israel coast in an area considered to have been disease-free for many years. The transmission date is likely to have been 24 July. On the previous night there had been exceptional southwest winds, and even rain. Subsequent surveys found breeding colonies of the same mosquito, *A. pharoenis*, the nearest source for which was again the Nile delta, nearly 300 km upwind. Further evidence implicating the delta as a source was the observed resistance to dieldrin of larvae in Israel. Such resistance would have been brought by parent females, because dieldrin resistance was already fully developed in parts of the delta (Garrett-Jones 1962). In 1953 there was an extensive invasion of *Aedes vexans* into Illinois. There could have been no local breeding, and the most likely source was in Wisconsin about 350 km to the northwest. On the day of the invasion, the wind turned to northwest behind a windshift line moving from Wisconsin to Illinois (Horsfall 1954).

The third of these mosquito case studies is an example of a movement inferred from a subsequent disease outbreak, rather than from a direct observation of arriving insects. Another example of this kind involves an outbreak of Rift Valley fever in Egypt during 1977, where

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the main vector is probably *Culex pipiens*. Sickness and death among livestock were first noticed in early August around Aswan, but the exact date is unknown. Sudan was the most likely source: the disease had been present in the north of the country in June 1976, and retrospective examination of sera collected in Egypt from 1972 to 1976 showed that virus was unlikely to have been present. Export of cattle and sheep from Sudan to Egypt had been banned in 1975 and 1976, and 1977 exports went by sea, not through Aswan. Moreover, animals trekked to Aswan would have taken too long to be carriers, and the chances of mosquitoes being carried in vehicles was small. The most likely cause of the outbreak was the arrival of infected insects from the south, and indeed there was an unusually long spell of southerly winds at Aswan from 28 July to 3 August, when the monsoon spread north from Sudan (Sellers *et al.* 1982).

In contrast to mosquitoes, little work has been done on the flight of midges, carriers of several viruses as well as parasitic worms, but the available information suggests a similar behaviour. Several case studies have shown that movements over hundreds of kilometres are possible. Thus bluetongue, primarily a disease of sheep, appeared in southwest Portugal at the start of July 1956. Several farms about 50 km apart were affected within a period less than the minimum for the sheep–midge–sheep cycle of 13 days, therefore suggesting a common source. If the principal vector, *Culicoides imicola*, had come to Portugal on the wind, as seems very likely, it would have been with southeasterly winds on 21 or 22 June, the only days that month when winds were not northeasterly or light and variable. These unusual southeasterly winds were due to the presence of a slow-moving cyclone off the coast of Morocco, which was the likely source of disease. Downwind flight over the sea would have taken about 10 h (Sellers *et al.* 1978). The same disease broke out simultaneously in northern and southeastern Cyprus in August 1977. Movement of sheep can be ruled out as the cause, so it is likely that midges brought the disease. A spell of northeast winds from 11 to 14 August fits the reported range of first outbreaks (20–25 August), and would have entailed cross-water flights of 5–20 h from possible sources in Turkey or Syria. In this example, surface winds were light and variable, and downwind movement would have taken place at altitudes above 500 m (Sellers *et al.* 1979). Bovine ephemeral fever is another virus disease, almost certainly transmitted by midges. There was a spectacular spread in Australia from Darwin in September 1967, southeastwards to Victoria by February 1968. During its later stages, this spread was 300 km per week over a 500 km front. It cannot have been due to stock movements, but it was in just the direction to be expected of windborne vectors (Murray 1970).

The stable fly, *Stomoxys calcitrans*, is a blood-sucking fly that bites both man and his livestock. There do not seem to have been any studies of long-distance movement of this species, but mark-and-recapture experiments have shown it can travel 8 km in less than 2 h (Eddy *et al.* 1962). Laboratory studies have shown that it can fly for an hour a day, and sometimes much more (Bailey *et al.* 1973), and winds are known to be able to bring it from inland to the ocean shore in eastern U.S.A. (Hansens 1951).

Blackflies are small biting flies that feed on blood. Mark-and-recapture experiments with three *Simulium* species that are carriers in Central America of the filarial worm, *Onchocerca volvulus*, causing river blindness, demonstrated movements of 15 km, but in variable winds (Dalmat 1955). In Canada, dense clouds of *S. arcticum* have attacked cattle up to 200 km from the nearest source (Rempel & Arnason 1947), and similar distances have been travelled by individual *S. damnosum* in Cameroon (Thompson 1976). The latter species has been much studied in West Africa, where it is the sole vector of *O. volvulus*. It breeds in fast-flowing water;

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hence it is seasonal in the northern part of West Africa, where rivers commonly cease flowing for a part of the year. Nevertheless, flies can reappear before flow restarts, when the nearest sources are 100 km away or more. There was for a time some controversy over whether this reappearance represented persistance or invasion (see, for example, Ovazza *et al.* 1967). The importance of invasion, however, has been highlighted dramatically by the World Health Organization Onchocerciasis Control Programme in the Volta basin and surrounding areas (Garms 1981). More than 700000 km^2 have been effectively cleared of breeding sites by aerial application of insecticide to the rivers, but there is reinvasion each year after the onset of monsoon southwest winds, with flies being caught several hundred kilometres from the nearest sources. Back-tracking by using windfield maps is difficult because the exact dates of arrival are unknown: they are not necessarily the same as capture dates because some time is likely to have been spent in egg-laying nearby. Also, windfields vary owing to the presence of rainstorms (Magor & Rosenberg 1980). Sources have been determined empirically by selective extension of the controlled area (Walsh *et al.* 1981). Understanding this reinvasion is made more difficult by the existence of several cytospecies within the *S. damnosum* complex, the forest forms of which are less mobile than the savannah forms – as might be expected where savannah rivers provide fewer and more temporary breeding sites. Attempts have been made to catch this species from an aircraft and from suction traps on the ground, but with almost no success (Johnson *et al.* 1982). Presumably cross-country flight is at very low densities, and may even extend to hundreds of metres above the ground.

Tsetse need shade for shelter and for development of pupae in the soil. Nevertheless, they do fly into the open in search of blood meals, and can cross clearings at least a few kilometres wide. Evidence from reinvasion of cleared areas, from decline in numbers next to strips treated with insecticide, from slowness of mixing between nearby populations and from mark-and-recapture experiments suggests that movements are commonly of the order of a few hundred metres a week (Glasgow 1963; Bursell 1970). In the absence of a host, flight seems to be ranging, and movements are well explained by quantitative models in which flight is assumed to be in steps with randomly changing directions (Rogers 1977), especially when step length, death rate and the probability of being caught are varied with age according to known biology (Hargrove 1981). Nevertheless, Roubaud (1920) has associated the reappearance of flies during the rainy season, at places in West Africa where they had been absent in the dry season, to the seasonal wind change. Moreover, rapid and simultaneous increase in catches of *Glossina tachinoides* along 80 km of recently sprayed River Komoë in Upper Volta, at about the time of onset of monsoon southwest winds, suggests that this riverine species had invaded on the wind (Baldry *et al.* 1981). The nearest upwind source would have been at least 30 km away.

Of the flying, disease-spreading insects that are not Diptera, mention may be made of the blood-feeding triatomid bugs, *Triatoma infestans* and *Rhodnius prolixus*, two of the vectors of Chagas' disease, or American trypanosomiasis. Laboratory measurements with balances have shown that flights up to a few hours' duration are possible (Gringorten & Friend 1979; Ward & Baker 1982). Such persistent flights, if they occurred in the field, would have clear implications for spread of disease. Initial infestation of new houses is by adults that must have reached there by flying (Schofield 1979), but there is no evidence yet as to any influence of wind on flight.

3. Discussion

Mark-and-recapture experiments have shown that individual flies, of a variety of kinds known to transmit disease, can move up to some tens of kilometres within days, or a week or two, apparently without wind assistance. The outward spread in all directions from a release point, as judged by the small fraction recovered (often less than 1 %, and perhaps unrepresentative of the majority of those released) may be due to searching flight, by at least part of the population, for particular goals within the boundary layer. Others might actively fly above the boundary layer, there to be taken more or less downwind for distances largely determined by wind speed and flight duration, and which can add up to hundreds of kilometres during a lifetime. The chances of demonstrating the existence of such flights by mark-and-recapture, let alone their frequency of occurrence or importance to survival of the species, are very small.

The evidence gathered so far suggests that much of the flight of disease-transmitting flies is goal-seeking. With tsetse and stable flies, and possibly also horse flies and sand flies, there is no convincing evidence yet of long-distance movements. Indeed, the realistic theoretical model for tsetse, based on known flight ability, may be applicable, in appropriate form, to other species. Simple descriptive models, empirically relating catch size to time and distance from the release point (see, for example, Freeman 1977), also imply a considerable random element in the movement. This does not mean, however, that there will not be occasions when goal-seeking flies get into barren areas devoid of goals, where strong winds could dominate flight. One can imagine, for example, tsetse being taken across lakes by squalls, or from the edges of forest into open country. It is also possible that part of a population, even only a small part, has a stage in its life cycle when flight is not goal-seeking (see Johnson 1969). More laboratory studies of flight duration and speed in relation to age, sexual maturation, and feeding could give evidence for or against the possibility of long flights, and field observations of take-off could give complementary evidence for or against active climbing to above the boundary layer.

With some species there is more or less convincing evidence, although admittedly circumstantial, that windborne flights by disease vectors over tens or hundreds of kilometres do occur. Similar flights by moths, beetles and many other kinds of insects also occur, some by pests of considerable agricultural importance. Are such long fights accidental, in the sense that goal-seeking individuals find themselves over barren country and obliged to fly, even for 20 h or more until they can find shelter or drop to the ground? Or are such flights purposeful? Some of the quoted movements by house flies, mosquitoes and midges were over sea or desert, but that was not so for the *Aedes* invasion of Illinois, nor for the screw-worm fly invasion of southwestern U.S.A., nor for the inferred midge movement in Australia. Well documented case studies of long-distance fly movements are still too few to judge how significant they are to species survival, but they are of considerable significance to disease epidemiology. Infected vectors may carry disease organisms hundreds of kilometres in a few days or hours. Even uninfected vectors that reinvade a cleared area may resume transmission of disease organisms still present in the animal hosts. At least the risk should be recognized that disease may be spread not only by many well known means but also by infected carriers being brought on the wind from known or likely sources that may be far away. More work needs to be done on when, where and how often such spread takes place. This can be by laboratory and field experiments on population dynamics, and by analysis or reanalysis of outbreak reports, particularly those that were apparently inexplicable. As with most insect pests, too little is known about the large-scale ecology of many disease-transmitting flies for it to be possible to predict movements with confidence, and thereby to improve monitoring and control strategies.

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