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Effects of Wind on the Behaviour and Distribution of Mosquitoes and Blackflies

by

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ABSTRACT. — Flight activity of haematophagous insects can be greatly reduced by wind, but species inhabiting woods and other sheltered sites will be less affected than those living in more exposed areas. If flight is suppressed this may lead to reductions in blood-feeding and oviposition and thus a reduction in their reproductive capacity. Although wind usually inhibits flight it appears that newly emerged adults of some mosquito species are specially adapted to take-off and flight in windy weather, thus promoting dispersal and colonization of new areas. Dispersal of simuliids and mosquitoes can be very important in control programmes as they can create problems of recolonization. Because air turbulence and convection are usually greatest during the day, simuliids and day-flying mosquitoes are more likely to be swept into the upper air and carried long distances than mosquito species that are active at night.

INTRODUCTION

There are about 3,300 known mosquito species, several of which are vectors of malaria, filariasis and a multitude of arboviruses of man and wild and domesticated animals. There are about 1,200 species of simuliids, commonly called blackflies, a few of which are vectors of onchocerciasis, a debilitating filarial disease of man that can cause various degrees of blindness. They are also vectors of pathogens to animals including filarial parasites and *Leucocytozoon* species. Both groups of insects have a more or less worldwide distribution, occurring in tropical rain forests, savanna areas and high arctic regions. Apart from their importance as disease vectors, mosquitoes and blackflies can also be pests of economic importance, especially in northern temperate regions where they may bite in enormous numbers. In some localities outdoor activities at certain times of the year may have to cease due to the intolerably high biting densities of these pests.

Weather conditions such as temperature, precipitation, relative humidity and wind can greatly affect the abundance, ecology and behaviour of mosquitoes and blackflies (Service, 1978). Here, only the effects of wind on the behaviour of mosquitos and blackflies are considered

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DEFINITIONS OF DISPERSAL AND MIGRATION

When an insect is flying at a speed that exceeds the wind speed it is described as flying under its own control and within its boundary layer (Taylor, 1958), the depth of which will vary according to wind speed. It leaves this protective zone, either actively or involuntary, by ascending into areas of greater wind speed where it is passively transported by the wind. The first stages of descent are outside the control of the insect and are governed by changes in wind speed and ground topography resulting in the insect dropping more or less randomly back into its boundary layer. It can now either land or reorientate itself and fly by its own power within the boundary layer to seek out, depending on its physiological needs, hosts or oviposition sites.

Definitions and understanding of the terms insect dispersal and insect migration are confused. Dispersal is often used to describe short-range appetitive flights more or less within the home-territory of insects, for example mosquitoes and blackflies dispersing to obtain blood-meals and lay eggs. Migration is often considered to represent non-appetitive flight of insects from one habitat to another, that is long-range dispersal, and includes occasions on which the insect actively flies to other areas or is passively transported by the wind. Neither mosquitoes nor blackflies are strong fliers compared with butterflies and locusts, and it is likely that most long distance travel involves passive transport with the wind. Although they may not be capable of actively flying long distances, they may behave so as to make maximum use of the wind for a free ride. If, for example, insects are positively phototactic at some stage in their life this will probably cause them to fly upwards towards the sky and as a result be swept along on air currents, this could be called adaptive migratory behaviour. However, little is known about the flight behaviour of blackflies and mosquitoes and because of this I have called both short and long distance travel dispersal.

EFFECT OF WIND ON BITING BEHAVIOUR OF MOSQUITOES

In general the smaller the insect the more susceptible it is to wind and the more likely its normal behaviour will be modified. Mosquitoes bite their hosts at any time of the diel depending on species, but windspeeds greater than about 3 km/h often drastically reduce host seeking flights. Some species breed in woods and forests and are considerably protected from wind by the shelter of dense vegetation, especially those biting at ground level and ovipositing in ground collections of water, and which are normally flying very near the ground (Service, 1971). If windy weather inhibits host seeking flights, then it seems likely that fewer eggs will be laid by females during their lifespan and the next mosquito generation will be smaller. It might be expected that in general mosquitoes breeding in woods and forests will disperse relatively little, either within their habitats or into other areas, and will therefore tend to be genetically isolated, however, there is very little information on this.

Woodland species either feeding on birds, or mammals such as monkeys inhabiting the tree canopy, or ovipositing in water-filled tree-holes and leaf axils above ground level are more likely to become dispersed by winds than those restricted to low level flights. Mosquito species which breed in and inhabit open areas are also more likely to be prevented from seeking hosts and oviposition sites by windy weather than sylvan species, and therefore will more likely be passively transported to other areas.

In central Alaska Gjullin et al. (1961) found that winds of more than 3 km/h considerably reduced mosquito flights, and when they reached 8 km/h flying ceased, but in marked contrast arctic species breeding in tundra localities were not appreciably affected by winds of up to 8 km/h, the critical threshold appeared to be about 11 km/h. Similarly, in Wisconsin Grimstad and DeFoliart (1974) found that mosquito flight was inhibited by winds of about 8 km/h, whereas in subarctic Canada Haufe (1966) reported that only speeds of about 29 km/h or more reduced mosquito flight.

Apart from location, time of flight activities may be important. At sunset when surface temperatures start to fall, the layer of air directly above the ground is cooler than higher layers and the air near the ground becomes more stable and less turbulent at night than during the daytime. Mosquitoes that fly mainly during the day are, therefore, more likely to be swept into the upper air by turbulence and convection and dispersed considerable distances than species flying in more stable night air.

BITING BEHAVIOUR OF BLACKFLIES

There is considerably less information on the effects of winds on host seeking and oviposition flights of blackflies, than on mosquitoes. It appears, however, that at least in some species adults do not bite at their emergence sites but rest on nearby riverine vegetation for a short period before dispersing, sometimes for several kilometres. This behaviour may help explain why frequently very few or no radioactive adults are caught in dispersal studies in which blackflies are labelled as larvae with radio-chemicals and catches for adults are made near their emergence sites. It has been thought that this type of post-teneral dispersal of blackflies is due to them actively flying, and not just being passively transported by the wind, but there is relatively little evidence to support this hypothesis.

LONG-RANGE DISPERSAL OF MOSQUITOES

There are several records of mosquitoes being carried considerable distances by prevailing winds, as much as 177 km for *Aedes sollicitans* (Curry, 1939), but often for shorter distances (see Eyles, 1944 and Johnson, 1969 for reviews). It has often been considered that wind dispersal of mosquitoes is principally accidental but in Canada Klassen and Hocking (1964) showed that *Aedes cataphylla* seemed adapted to take-off in windy weather shortly after emergence, but not in later life. This and other species tend to fly up into the air at a steep angle (30-60°) after emergence until they reach about 12 m, after which flight levels out (Haeger, 1960). Recently emerged *Culex tarsalis* have also been observed to spiral up to heights of 37-46 m then level off, and when wind speeds were less than about 5-6 km/h to fly into the wind, presumably for hosts, but in greater windspeeds they became wind-borne (Bailey et al., 1965). It is not clear whether this type of behaviour is inadvertent or adaptive as it appears to be with *Aedes cataphylla.*

Army camps in the Egyptian desert have been reported as being invaded by enormous numbers of *Anopheles pharoensis* after midnight when winds were blowing strongly to the north-east; they were considered to be newly emerged females (Garrett-Jones, 1950; Kirkpatrick, 1957). *Aedes taeniorhynchus*, a common saltmarsh species in the USA, appears to be adapted to post-teneral undistracted flights with the wind which result in newly emerged individuals being dispersed considerable distances from their breeding places (Nielsen, 1958; Provost, 1953). There is some evidence that adults of this species exhibit "migratory behaviour" if their larvae have been overcrowded, and it is tempting to speculate that this is a mechanism to prevent populations exceeding the holding capacity of a habitat.

In contrast to these examples of long-range dispersal by newly emerged mosquitoes Garrett-Jones (1962) obtained evidence in Israel that relatively old females (infected with malaria parasites) of *Anopheles pharoensis* were transported for at least 280 km on prevailing winds. In the Gambia suction and light traps (0.69-9.15 m) showed that the numbers of *Anopheles melas* and *Culex thalassius* decreased with height, but that their age-composition increased with height, suggesting that older females tend to fly higher than younger ones and are therefore more prone to wind dispersal (Snow and Wilkes, 1977). In Canada, Davies (1957) observed that wind reduced flight activities of older blackflies more than newly emerged individuals which were better adapted to windborne dispersal, whereas in West Africa there is considerable evidence that it is mainly the older females of the *Simulium damnosum* complex that are regularly dispersed many hundreds of kilometres.

Many observations on flight distances have been made on saltwater mosquitoes because their nearest point of origin, usually coastal sites, can be readily identified. For example, saltwater species such as *Aedes vigilax* have been caught about 97 km inland (Hamlyn-Harris, 1933) and *Aedes sollicitans* has been recovered 177 km from its larval habitats. Curry (1939) appears to have been the first to have used synoptic weather charts to show the probable origin of this species. It should not be interpreted, however, that saltwater species necessarily disperse further than freshwater species, although they might be more adapted to dispersal than species breeding in more sheltered inland sites such as woods. *Aedes vexans*, a freshwater species has been recorded as being carried on a massive cold front 145-370 km in 24-48 h, and possibly even 740 km (Horsfall, 1954).

In Canada, Wellington (1944) observed that during windy weather females of an unidentified *Culex* mosquito flew up to a height of 6 m during temperature inversions and when ground temperatures were 20°C or more; males occurred both above and below this level. On calm nights and when ground temperatures were only 15°C only females flew at lower levels and only males flew in the warmer (18°C) higher air. When ground temperatures dropped to below 15°C males were not caught, and females flew at greater heights.

If ground terrain is more or less uniform, the overlying air masses tend to become relatively uniform in their horizontal distribution. The transition from one type of air mass to another is usually relatively abrupt and areas of low pressure frequency form with characteristic frontal systems. There are few records of mosquitoes being transported on frontal systems, but in the USA Horsfall (1954) recorded the rapid dispersal of *Aedes vexans* on a massive cold front. Unpublished observations in Canada have shown that cycling of mosquito activity over densely populated uniform terrain corresponded to alternating changes of air masses along the movement of the polar front (Haufe, 1963).

LONG-RANGE DISPERSAL OF BLACKFLIES

Blackflies have long been recognised as examples of haematophagous insects that are frequently dispersed relatively long distances. For example, large swarms of *Simulium arcticum* have often been encountered 80 km from larval habitats and a few adults have been caught 145 km away (Cameron, 1922). The once notorious *Simulium colombaschense* used to periodically disperse from its breeding sites on the River Danube and arrive in enormous numbers 80 km or more away (Baranov, 1934). In West Africa Ovazza, Renard and Balay (1965; 1967) noted that adults of the *Simulium damnosum* complex appeared in areas only after the Intertropical Convergence Zone (ITCZ) was to the north. Marr (1971) observed *Simulium damnosum* flying over bushes and trees in which other adults were resting, and suggested that winds, especially those associated with squall lines, were possibly important for dispersal.

The long-range dispersal of species of the *Simulium damnosum* complex has caused concern to those involved with the multinational Onchocerciasis Control Programme (OCP) in West Africa, which was launched in 1974 and will probably continue for 20 years. The programme aims at reducing to an acceptable level the transmission to man of onchocerciasis (river blindness) in the Volta River Basin (700.000 m^2) by repeatedly dosing all rivers and streams, which are larval habitats of *Simulium damnosum*, with the insecticide temephos (Abate). These measures have proved very successful in drastically reducing the vector population, but one of the main problems remains the periodic wet-season reinvasion of *Simulium damnosum* from the south-west to north-east, which often coincides with monsoon weather. Two species of the *Simulium damnosum* complex have been identified as immigrants, *Simulium damnosum* s.s. and *Simulium sirbanum,* both of which are savanna species.

Most of the immigrants are first identified as relatively old females, that have already fed at least once and some are infected with filarial worms of *Onchocerca volvulus*, the causative agent of river blindness. There is considerable evidence that large numbers of these flies have originated 200-250 km away, and some adults have probably travelled as far as 300-400 km, but it is not known whether they have arrived in one flight or have "stopped over" en route. Reinvasions of *Simulium damnosum* into the Volta River basin area which occurred in April 1962, June 1962 and March 1975 occurred at sites near areas affected by winds associated with the ITCZ and / or smaller scale localised storms including squall lines (Magor, Rosenberg and Pedgley, 1975). It had been thought that high and low biting rates by blackflies in the control area occurred more or less simultaneously at several different localities, and that maximum biting rates were encountered 1-4 days after north or north-westerly winds, while low catches occurred after calm periods. However, a more critical examination of the data suggests that such a clear-cut association may not be as great as formerly supposed, and that surges of invasion by immigrants, reflected in variations in the numbers biting are probably caused primarily by longer-term population changes at their source (C. G. Johnson, personal communication, 1977). To try to monitor and to quantify the reinvading aerial population Dr. Johnson placed several suction traps at a height of 13 m and well away from rivers in the control area in 1977. Over a 6-month period only a single *Simulium damnosum* was caught, although about 3,000 of several other blackfly species were collected. It appears that *Simulium damnosum* are arriving in the control area along a very broad front so that although their numbers may be quite large, their actual aerial density is very low. Despite the importance of reinvasions of *Simulium damnosum* in the area of the control programme and various investigations into the problem, it is proving exceedingly difficult to discover both the origin of the invading blackflies and how they arrive. It is unlikely that much clarification will be obtained unless an extensive entomological sampling programme, in collaboration with biometeorological studies, is established, but the cost of such an operation may be prohibitive.

CONCLUSIONS

Despite extensive investigations on the behaviour and biology of mosquitoes and blackflies, there is still very little information on either their short-range flights or how and when they disperse long distances. Efficient control programmes which have eliminated or drastically reduced local breeding populations of vectors have often shown, through reinvasion phenomena, that medium and long range dispersal of vectors appears to be much more frequent and normal than previously realised. This aspect of their behaviour clearly has important relevance to control measures.

REFERENCES

BAILEY, S. F., ELIASON, D. A. and HOFFMANN, B. L. (1965): Flight and dispersal of the mosquito *Culex tarsalis* Coquilett in the Sacramento valley of California. Hilgardia, 37: 73-113.

BARANOV, N. (1934): Golubăcka mušica u godini 1934. (In Siberian). (*Simulium reptans columbaczense* in the year 1934). Vet. Arh., 4: 48 pp. (Rev. appl. Ent (B), 22: 203-204).

CAMERON, A. E. (1922): The morphology and biology of a Canadian cattle-infesting black fly, *Simulium simile*, Mall. (Diptera, Simuliidae). Bull. Dep. Agric. Canad., N.S. no. 5 (*Ent. Bull.* 20) 26 pp.

CURRY, D. P. (1939): A documented record of a long flight of *Aedes sollicitans*. Proc. New Jersey Mosq. Exterm. Ass., 26: 228 pp.

DAVIES, L. (1957): S study of the age of females of *Simulium ornatum* Mg. (Diptera) attracted to cattle. Bull. ent. Res., 48: 535-552.

EYLES, D. E. (1944): A critical review of the literature relating to the flight and dispersion habits of anopheline mosquitoes. Publ. Hlth. Bull., (Wash.), no. 287: 39 pp.

GARRETT-JONES, C. (1950): A dispersion of mosquitoes by wind. Nature (*Lond.*), 165: 285.

GARRETT-JONES, C. (1962): The possibility of active long-distance migrations by *Anopheles pharoensis* Theobald. Bull. Wld. Hlth. Org., 27: 299-302.

GJULLIN, C. M., SAILER, R. I., STONE, A. and TRAVIS, B. V. (1961): The Mosquitoes of Alaska. U.S. Dept. Agric. Hand., Washington, DC., no. 182: 98 pp.

GRIMSTAD, P. R. and DEFOLIART, G. R. (1974): Mosquito nectar feeding in Wisconsin in relation to twilight and micro-climate. J. med. Ent., 11: 691-698.

HAEGER, J. S. (1960): Behaviour preceding migration in the salt-marsh mosquito, *Aedes taeniorhynchus*. Mosquito News, 20: 136-147.

HAMLYN-HARRIS, R. (1933): Some ecological factors involved in the dispersal of mosquitos in Queensland. Bull. ent. Res., 24: 229-232.

HAUFE, W. O. (1963): Entomological biometeorology. Int. J. Biometeor., 7: 129-136.

HAUFE, W. O. (1966): Synoptic correlation of weather with mosquito activity. Biometeorology, Part II. S. W. Tromp and W. H. Weihe (ed.), Pergamon Press, Oxford, 523-540.

HORSFALL, W. R. (1954): A migration of *Aedes vexans* Meigen. J. econ. Ent., 47: 544.

JOHNSON, C. G. (1969): Migration and Dispersal of Insects by Flight. Methuen, London, 763 pp.

KIRKPATRICK, T. W. (1957): Insect Life on the Tropics. Longman and Green, London, 311 pp.

KLASSEN, W. and HOCKING, B. (1964): The influence of a deep river valley system on the dispersal of *Aedes* mosquitos. Bull. ent. Res., 55: 289-304.

MAGOR, J. I., ROSENBERG, L. J. and PEDGLEY, D. E. (1975): Windborne movement of *Simulium damnosum*. Final report of the WGO-COPR Studies in 1975, COPR 39/3/3: 12 p. (mimeographed).

MARR, J. D. M. (1971): Observations on resting *Simulium damnosum* (Theobald) at a dam site in Northern Ghana. WHO/ONCHO/71.85: 12 pp. (mimeographed).

NAYAR, J. K. and SAUERMANN, D. M. (1969): Flight behaviour and phase polymorphism in the mosquito *Aedes taeniorhynchus*. Entomologia exp. appl., 12: 365-375.

NIELSEN, E. T. (1958): The initial stage of migration in saltmarsh mosquitoes. Bull. Ent. Res., 49: 305-315.

OVAZZA, M., OVAZZA L. and BALAY, G. (1965): Etude des populations de *Simulium damnosum* Theobald, 1903 (Diptera: Simuliidae) en zones de gîtes non permanents. II. Variations saisonnières se produisant dans les populations adultes et préimaginales. Discussion des différentes hypothèses qui peuvent expliquer le maintien de l'espèce dans les régions sèches. Bull. Soc. Path. exot., 58: 1118-1154.

OVAZZA, M., RENARD, J. and BALAY, G. (1967): Etude des populations de *Simulium damnosum* Theobald, 1903 (*Diptera, Simuliidae*) en zones de gîtes non permanents. III. Corrélation possible entre certains phénomènes météorologiques et la réapparition des femelles en début de saison des pluies. Bull. Soc. Path. exot., 60: 79-95.

PROVOST, M. W. (1953): Motives behind mosquito flights. Mosquito News, 13: 106-109.

QUARTERMAN, K. D., JENSEN, J. A., MATHIS, W. and SMITH, W. W. (1955): Flight dispersal of rice field mosquitoes in Arkansas. J. econ. Ent., 48: 30-32.

SERVICE, M. W. (1971): Flight periodicities and vertical distribution of *Aedes cantans* (Mg.), *Ae. geniculatus* (Ol.), *Anopheles plumbeus* Steph. and *Culex pipiens* L. (Dipt., Culicidae) in southern England. Bull. ent. Res., 60: 639-651.

SERVICE, M. W. (1978): The effect of weather on mosquito activity. In: Weather and Parasitic Animal Disease. T. E. Gibson (ed.) Tech. Note no. 159: World Meteor. Org., 151-166.

SNOW, W. F. and WILKES, T. J. (1977): Age composition and vertical distribution of mosquito populations in the Gambia, West Africa. J. med. Ent., 13: 507-513.

TAYLOR, L. R. (1958): Aphid dispersal and diurnal periodicity. Proc. Linn. Soc. Lond., 169: 17-73.

WELLINGTON, W. G. (1944): The effect of ground temperature inversions upon the flight activities of *Culex* sp. (Diptera: Culicidae). Canad. Ent., 76: 223.