

ARTICLES

OUT FOR BLOOD; FLIGHT ORIENTATION UP-WIND IN
THE ABSENCE OF VISUAL CLUESFirst AMCA Memorial Lecture April 1979¹

J. D. GILLETT

Department of Entomology, London School of Hygiene & Tropical Medicine, Keppel Street
(Gower Street), London WC1E 7HT, U.K.

Mr. President, fellow members of the American Mosquito Control Association, Ladies and Gentlemen, you have heard the president's words about Dr. Don Rees. I did not have the honor of knowing him personally but I did know his work, or some of it, and always valued it highly. I am deeply conscious of the responsibility that falls on me in honoring such a distinguished name in the world of mosquitoology and indeed in entomology and in science generally. I am conscious, too, of the honor in being chosen to give this first AMCA memorial lecture. Let me start, then, by thanking the Association for allowing me to carry this responsibility. And let me thank you, Dr. Nielsen, Sir, for the generous introduction; you present me with quite a challenge.

Most entomologists must go out into the world to seek their chosen quarry, that is, the particular group of insects that especially interests them. We, however, have only to wait for our chosen insects to seek us out; for to the mosquito, or at least to those that are of special concern to us, we ourselves are the quarry. They come to us, at times in the most persistent fashion and in almost unbelievable numbers. It is about this aspect of the complex lives of mosquitoes that I wish to explore with you today for surely, as members of a mosquito control association, it is this activity of mosquitoes that is our main

concern. Without it these creatures, with their complex life histories, would be of no greater interest than, say, dragonflies or caddisworms (both of which, I may add, are exceedingly interesting). With it, however, with their persistent lust for our blood, they have ranked amongst those we honor as the highest in the land in deciding the course of history. Indeed they have often sealed the fate of these worthy gentlemen and their followers and at times done more to shape the course of history than all of them put together.

It is, of course, their role as transmitters of pathogens that destroy or incapacitate us that has given them this special power. Yet the misery and suffering they cause us at times, even when the transmission of disease is not involved, is enough to keep the AMCA pretty busy. When in 1955-56 my wife and I had the privilege of living in America when I was the fortunate recipient of a Rockefeller Foundation Fellowship, one of the things that struck us—one of the many things, I should say, was the efficient anti-mosquito screening that was a permanent feature of so many houses. It brought home to us that here is a country that takes its mosquitoes seriously, a country that has, if you like, been forced to take its mosquitoes seriously. Ladies and gentlemen, it is about the mosquito's success in forcing us to take them seriously that I want to talk today. Not their role as transmitters of disease but how they successfully seek us out, for without the one we would not have the other.

¹ Made possible by a travel grant provided by LECO, Inc. The member memorialized is Don Merrill Rees, 1901-1976.

People who have made a special study of this important subject have usually concentrated their efforts on one aspect or another. Some have concentrated on smell, some on color, others on moisture and carbon dioxide. A few have considered temperature, or more accurately warm air, that is air warmer than the surrounding ambient air. And a few have considered a combination of some of these, for example moisture and warmth. In all these studies, the investigator has taken certain attributes of the target, in other words, us, and looked to see which may be important in serving to guide the mosquito to its feedingplace.

Now it is abundantly clear when looking through this work that all these signposts are used at times by the mosquito that is out for blood. Smell, which is known to be extraordinarily efficient in guiding male moths to their mates, may well be one of the long-distance attractants indicating to female mosquitoes that they are on the right road. But as every driver knows it is one thing to be on the correct main highway to the city, quite another to know which way to turn on arrival at the outskirts of that city. It is no longer enough to know simply the number of the highway; other and more complex signals are needed. In the same way, the marauding insect may now respond to all the signals: warm moist air, movement, color and so on and probably to a combination of these. Moreover, to one species warmth may be the key stimulus, whereas to another, one of the many other signals that we unknowingly provide may prove to be the guiding light.

In my view we sometimes tend to oversimplify the picture. Indeed we have to in order to deal with one aspect at a time. But it seems probable that a mosquito uses many sources of information, not necessarily all at once, but perhaps in sequence, one after another. But even at any one moment there is no reason for thinking that its sources of information are limited to one kind. Mosquitoes are pretty sophisticated animals with inbuilt

behavior patterns that well adapt them to cope with the world about them.

Now in order, as it were, to make use of these various signals the insect must be capable of orienting its flight up-wind. The mere presence of olfactory particles, warm or moist air or a combination of the 2 or of CO₂ may arouse, but it is the following up of gradients of these that will lead eventually to the host. And the quickest way on to these gradients is, of course, to fly up-wind until contact is made with the specific stimulus. That is for the mosquito, already aroused into activity and air-borne, to orientate itself so as to fly against the wind.

Initial arousal comes at the same time each day and is triggered by the mosquito's own inborne rhythm—a rhythm of alternating periods of rest and activity that is characteristic of almost all living things and is basically independent of outside conditions although it may need some change outside to set the phase of the rhythm. But what the mosquito does during its active period depends on its own physiological state; a newly emerged insect may mate; a slightly older mosquito will seek a meal; while a gravid female will seek a place for oviposition. Our concern today is with the middle one of these activities—feeding. How does the aroused and hungry female, out for blood, find its way into wind. In my opinion, probably by one or both of two means and it is these that I want mainly to explore today.

Forty years ago, in a brilliantly conceived and executed series of experiments Kennedy (1939) showed that, in the case of *Aedes aegypti*, orientation up-wind was dependent on visual cues indicating drift. In other words, to quote the admirable summary made by Clements (1963) "upwind orientation is not an orientation to the wind itself . . . but results from compensatory movements made in response to visual stimuli. Flying mosquitoes adjust their speed so that the image of the background passes over their eyes at a constant speed." Since, as Kennedy showed, a flying mosquito will not tolerate images passing over its eyes

either from behind forwards, or laterally, it will adjust its flight direction and speed accordingly and these adjustments will automatically lead to an upwind orientation, that is, with a visual image of the background passing over the eyes from in front backwards.

This key work helped to solve a riddle that had long perplexed workers in this field. The impossibility of orientation by means of the mechanical effects of a current in a uniform medium seems self evident and was stressed both by Kennedy (*loc. cit.*) and by Fraenkel and Gunn (1940) a year later in their well known book. Nevertheless this important fact is not always remembered; we most of us spend the greater part of our lives with both legs firmly on the ground and our heads in the air, and wind direction presents no difficulty to us. Those of us who have to navigate in the air, however, may have, like Kennedy's mosquitoes, to fall back on visual cues to estimate the speed and direction of the wind.

How then, we may well ask, and one person in particular has asked, how then could I write, when I was discussing flight in my book on mosquitoes, and I quote, "Perhaps other mechanisms become unlocked, such as direct response to air movement, when the eyes are unable to play their part" (Gillett 1972). Clearly this statement goes against everything that I have just been saying. Allow me then to expand, first reminding you of the facts of life that led me to make this seemingly extraordinary statement and then introducing some new ideas on what this other mechanism might be.

Many, if not most, species of mosquito seek their blood meal at night, when visual cues will be at a minimum or even non-existent. But, ask the faithful, is it really ever totally dark? This is a good question and one we must tackle before we go any further. First, however, we must define what is dark to a mosquito. The only reliable information of which I am aware comes in studies made by Muirhead-Thomson (1940) on the behavior of *Anopheles minimus*, a very impor-

tant transmitter of malaria in Southeast Asia. In the first paper in that classic series he showed how ovipositing females could discriminate light and shade when illumination was equivalent to about a quarter of meteorological starlight, but this discrimination broke down somewhere between this level and the equivalent of one eighth starlight. This gives us something to go on, even though it is one species only. *An. minimus* is, however, a night feeding mosquito (Muirhead-Thomson 1941), unlike *Ae. aegypti* which usually shows a main biting preference for the last few hours before sundown.

Conditions in the equatorial tropics can be very different from those of more northerly climes. It is true that starlight is often a conspicuous feature of the tropical night, but tropical starlight can be very much reduced by thick cloud cover; the cumulo-nimbus clouds, so typical of the wet tropics can be many hundreds of meters in thickness. The base of these often spectacular cloud formations may be only 300 meters above the ground, but the tops may extend upwards to reach an altitude of 10,000 or even 12,000 meters (38,000 feet). A dense blanket of 11 kilometers (7 miles) in thickness is a very effective light filter indeed; it has been estimated that starlight can thus be reduced to a tenth of its normal value—say 2×10^{-5} lux (Blackall, personal communication).

It is true that cumulo-nimbus clouds are often associated with thunder and the seemingly total darkness is apt to be interrupted by vivid flashes of lightning, often (with repeated discharge) lasting a full second in duration. It is not known whether or not an insect flying in these conditions could, so to speak, make use of the light periods and cash in on Kennedy's cues. Cumulo-nimbus clouds are also often associated with turbulence, which at times can be violent, the typical pre-thunder squall of the tropics. But squally conditions usually last for only 20 min or so, at least in my experience. Then, of course, very heavy rain or even hail may follow. The period of very heavy

rain, however, also usually lasts for a short while and is followed by a longer period of steady but gentler precipitation. Mosquito activity may be very much reduced or absent during the squally prelude and during the very heavy precipitation that follows but it is known that mosquito activity tends to increase during the persistent rain that usually comes afterwards even when this, by more usual standards, is comparatively heavy (Gillett 1972). In any case comparatively thick dense cloud cover with a very low base occurs often enough without lightning discharge. Couple this cloud cover with the dense canopy of evergreen rain forest and we have what must be regarded as zero illumination for the mosquito.

Now, unless it can be shown that night feeding mosquitoes do not feed in such large numbers during these conditions (and I have already brought forward evidence that the reverse is in fact often the case), we must assume that mosquitoes are able to find their way to sources of blood in total darkness. At any rate we will make this assumption for the argument that I am about to put forward. I am going to make two other assumptions, one based on well established fact, the other on conjecture based on observation in the field.

Wind velocity (both direction and speed) is not uniform with height but exhibits characteristic changes as one approaches the surface of the earth. The drag produced by the surface results in an atmospheric boundary layer, the exact nature of which depends on temperature, moisture content and on the type of ground cover; there is a progressive removal of momentum by viscous drag, which is particularly marked just above the ground. Wind velocity at ground level itself is, of course, always zero. Wind profiles during the hours of darkness usually differ markedly from those during the day time in the same place, the atmospheric boundary layer (a.b.l.) tending to be much shallower at night (Deardoff 1976, Smith and Carson 1977 and Smith and Hunt 1978).

During the daytime the a.b.l. is unstable

owing to large temperature differences between the air and the ground. During the night, however, heat begins to be lost from the surface and there is a damping of turbulence; the a.b.l. becomes increasingly stable. Naturally the change from the daytime unstable to the nighttime stable conditions is not an all or nothing phenomenon, and the transitional state between the two regimes, when heat-loss from the surface is zero, is referred to by meteorologists as neutral conditions (Smith and Hunt 1978). The daytime unstable condition need not concern us here. The equation for the stable condition is:

$$U_z = U_* / 0.4 \log (Z/Z_0) + 5.2 (Z-Z_0) (0.4 \times 94700U_*^2)^{-1} \times H$$

where U_z = wind velocity at height Z
 U_* = measure of the mean low-level wind
 Z_0 = the roughness of the surface
 H = measure of rate of heat-loss by the surface

Under neutral conditions (which tend to be prolonged into the night when clouds cover the sky) and assuming a given wind speed at a given height, the equation may be simplified:

$$\frac{U_z}{U_r} = \frac{\log (Z/Z_0)}{\log (Z_r/Z_0)}$$

where U_r = wind velocity at reference height Z_r .

Mr. R. M. Blackall of the Meteorological Office in Britain, to whom I am greatly indebted for these equations, has used them to produce computer plotted curves showing wind profiles under various conditions. These are shown in Figures 1 and 2 for neutral and stable conditions respectively.

On looking at these nine wind profiles we can see that as nighttime stability sets in the slope of the curve diverges more from vertical but, and here is the important point, no matter how we vary the conditions in producing these profiles,

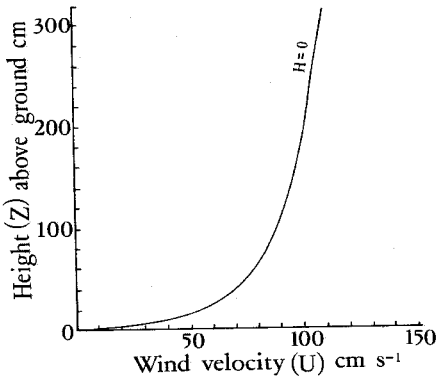


Fig. 1. Computer plotted wind profile curve (assuming a wind velocity of 100 cm per second at a height of 200 cm above the ground) under neutral conditions of the atmospheric boundary layer, as tend to occur just before nightfall or under heavy cloud cover at night, when heat loss (H) by the surface is zero.

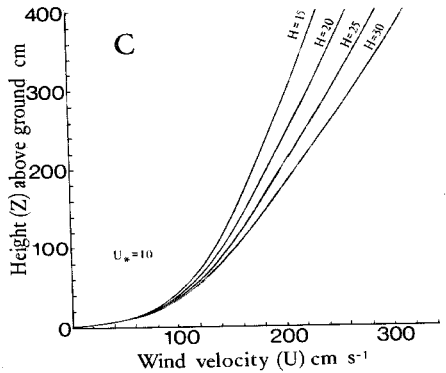
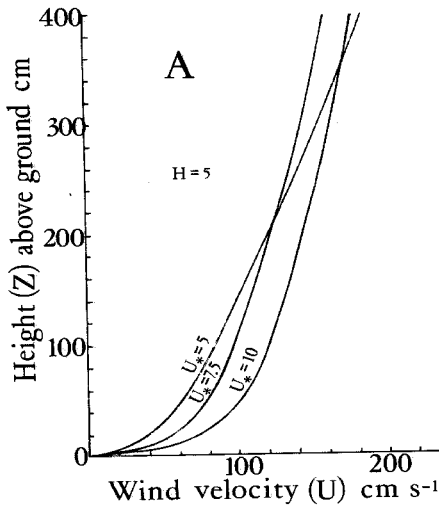
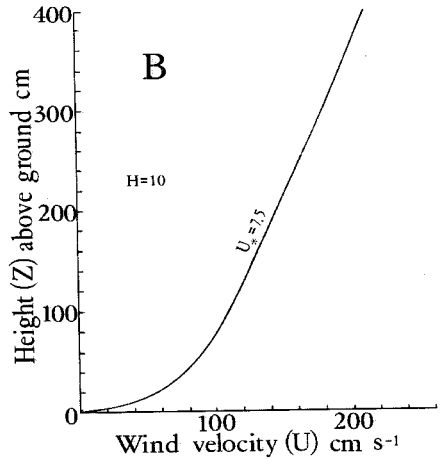


Fig. 2. Computer plotted wind profile curves under increasing degrees of stability of the atmospheric boundary layer as the night progresses. A—with constant low heat-loss (H) but with increasing mean low-level wind velocities

(U_*); B—with greater heat-loss but with low mean low-level wind velocity; C—the opposite of A) with constant mean low-level wind velocity but with increasing rates of heat-loss.

there is a characteristically sharp drop in wind velocity as we approach the ground. It must be remembered that the wind profiles are shaped by many variables such as the nature of the soil, type of ground cover, time of day, air temperature, moisture content, cloud cover and so on and that the profiles themselves will fluctuate with time. If, as may well be imagined, we are interested in conditions within, say, rain forest, or within a banana grove, further complications arise (Elston and Monteith 1975, Thom 1975). But the point remains that whatever the result of all these interacting factors the a.b.l. is there and it is through this layer, not above or below it, that the mosquito must make its approach. Our first assumption is, then, that wind velocity drops off sharply as we approach the substrate.

Now the Kennedy model assumes that flight is made on an even path at a constant height above the substrate. And inspection of some easily observable day-flying species such as *Ae. aegypti* shows that this can indeed be the case. On the other hand, I have myself noted on numerous occasions in the wild a quite different type of flight path. In my book I referred to the typical dipping and diving approach in species of *Hodgesia*. I have noted a similar hesitant approach in some other mosquitoes, always the same phenomenon: the insect flies forward and then suddenly drops, as far as one can see vertically, or almost vertically, only to rise again to about its former level. Alternatively it may suddenly rise and then drop. The extent of the drop or rise varies from a few centimeters to somewhere in the order of 20 or even 30 cm (1 foot). If we now make the assumption that this type of flight is characteristic of night-flying mosquitoes, at least during the exploratory phase before coming within range of specific stimuli from the host, we find that we have a perfect mechanism for the detection of wind direction without any need to fall back on visual cueing.

A non-gravid female mosquito, activated into flight at night-time by its internal rhythm, finds itself airborne

under a very heavy cloud cover. Now, unless it is already within range of smell, warm moist air or CO₂ or perhaps light emanating from a potential host, it will have no way whatever of gauging wind direction as long as it adopts a constant height flight-path. It will help if we first draw the simplest picture. Let us suppose, as suggested by Bragg (personal communication) that the insect's own air speed is equal and opposite to that of the wind. It will of course be hovering. But now let us suppose that the insect drops suddenly to a lower level; if it was initially flying fairly close to the ground it will immediately be subjected both to apparent wind from behind and an acceleration forwards. How much of one and how much of the other will depend on how fast it managed to descend. If, for example, it was flying in the dark at 30 cm s⁻¹ against a wind of 30 cm s⁻¹ and it dropped almost instantaneously to a level where the wind velocity was only 20 cm s⁻¹, then the mosquito must sense a 10 cm s⁻¹ wind from behind. In fact the drop cannot be instantaneous, and thus the apparent hind wind will be less than 10 cm s⁻¹; and at the same time the insect will experience a positive acceleration. Conversely, if the insect suddenly rises it will experience a sudden head-wind and a negative acceleration. In either case it need take no turning action as its orientation is correct, that is up-wind.

Now let us suppose that the insect is initially flying downwind at 30 cm s⁻¹ in a wind of 30 cm s⁻¹. Its wind speed will still be 30 cm s⁻¹ but its land speed will be 60 cm s⁻¹, although in the absence of visual signals it would have no way of telling this. But, now suppose it drops suddenly to a level where the wind velocity is 20 cm s⁻¹, it will immediately sense a 10 cm s⁻¹ head wind (or something approaching this) accompanied by a negative acceleration. If it is to fly up-wind it must then make a turn through 180°. Similarly, if the original orientation was across the wind and it changed its height suddenly it would sense the wind from one side or the other, accompanied by an asymmetric

acceleration, and turn appropriately. The simplest program would be for the mosquito to turn away from the apparent wind when it moved downwards and into the apparent wind when it moved upwards. This simple rule would guarantee orientation up-wind from whatever position the mosquito started its flight.

We have, then a very simple mechanism that will allow a mosquito to orient itself up-wind in zero illumination, as long as the information provided falls within the limits of the insect's own powers of resolution and analysis. Let us first consider the detection of acceleration. If the insect changes its level with a vertical component of velocity V and by an amount H , it will take H/V time to make the change. By so doing it will move into a region of different wind velocity (lower if it moves downwards, higher if it moves upwards). If the wind velocity gradient with height is G then the insect will suffer a velocity change GH . Since, as we have seen, this change takes time H/V , the average acceleration will be $A = \frac{GH}{(H/V)} = GV$.

Let us suppose, for example that the wind velocity gradient G into which it moves is $50 \text{ (cm s}^{-1}\text{)/100 cm}$ and that the mosquito changes level with a vertical component V of 50 cm s^{-1} downwards. Its average acceleration will be $0.5 \times 50 = 25 \text{ cm s}^{-2}$. This is equal to about 1/40 gravitational acceleration; whether this can be recorded through the antennae or whether it is recorded, say, through pressure gradients set up in the haemolymph, as suggested by Warren (personal communication), is now, perhaps, up to some of you to find out. It seems possible that the halteres, which are known to be capable of detecting the small forces set up by flight yaw also serve to detect these changes which, as we have seen, will equal about one fortieth the body weight of the insect (if, in fact the diving velocity is greater, say nearer 100 cm s^{-1} , then the force necessary will be about 1/20 body weight). We already have evidence that mosquitoes can fly at speeds of over 200

cm s^{-1} (Hocking 1953), while Nielsen and Nielsen (1953) observed swarming *Aedes cantans* maintaining station in a wind of 800 cm s^{-1} .

When we come to consider the detection of wind direction we are on much firmer ground. The antennae, with the Johnston's organ placed at the base of each, and the individually innervated hairs scattered along each antennal shaft, would appear to be eminently suited for this purpose. Indeed, Bässler (1958) has already shown how the antennae are used for the correction of roll or list during flight. He showed further that unilateral stimulation of the antennae by a jet of air resulted in an increase of strength in the wing-beat on the opposite side. Unfortunately he then went on to argue that such unilateral stimulation would not occur in nature. But, on the assumption that night flying mosquitoes make exploratory dips in flight, unilateral stimulation is exactly what we would expect to find. Clements (1963) in discussing Bässler's results suggests that the antennae "may be important for maintaining equilibrium during flight, functioning through the effect on Johnston's organ of flagellar displacement." This may well be so. But what I now suggest is that this function of the antennae also serves to provide information that allows the insect to correct its course according to wind direction. Since the antennae are held out at an angle during flight they are ideally positioned for recording wind differences from whatever direction they come.

The Kennedy model presupposes that flight must be near the ground (or other substrate) for the insect to be able to detect visual images passing over the eye at the optimal rate and direction. And field observations of flight near to the ground have been interpreted as supporting this view. Kalmus and Hocking (1960) showed that *Aedes* approached for a feed at ankle level, and Haddow (1956) observed that day-feeding *Eretmapodites* also approached the host and fed close to the ground. But Laarman (1959) studied anophelines, most of which are active at

night time. Since these could not be directly observed, he trapped them by means of rotating nets at different heights above the ground. He showed that the nightly search for blood was also made less than 60 cm above ground level. This too has been used as evidence for orientation by visual cueing, on the assumption that darkness was not absolute. But all these observations, particularly those of Laarman, could equally well be brought forward in support of my hypothesis, for the effect of viscous drag of the air is greatest just above ground level, as the figures amply demonstrate.

Incidentally another very important point arises if we take the a.b.l. into consideration when discussing wind direction in relation to direction of flight. Not only do wind speeds fall below the free-stream value found above the layer to reach zero at ground level, but wind direction also changes with height. The amount of this change varies, but in stable conditions over land the wind may be backed by some 30° or more (Smith and Hunt 1978). It follows, therefore, that in studies of this kind, wind direction must be measured at the flight-level itself and not by reference to a weather vane or other instrument placed higher up.

Am I dismissing the former views about visual cueing? No, far from it. What I am suggesting is that there appears to me to be ample scope for an alternative mechanism to come into play on those occasions when thick dense cloud cover, augmented perhaps by a continuous forest canopy preclude the harnessing of visual cues. A highly sophisticated group such as the mosquitoes is likely to have alternative pathways to success at its disposal; if one fails or is not available then it will fall back on another. I am suggesting that vertical exploration of the atmospheric boundary layer close to the ground may well provide just such an alternative pathway when visual signals are absent.

Vertical sampling of the atmospheric boundary layer just above ground level may, in fact, be the more usual mechanism. The night-time a.b.l. starts to de-

velop an hour or so before sunset, only a few meters in depth at first but deepening as night becomes established. Now many species of mosquitoes show a single peak of feeding activity in the period just before or shortly after sundown. Could it perhaps be that this preference is a result of natural selection for a period of the day that provides optimum conditions for finding the quarry? Some species of *Anopheles* exhibit a build-up of activity as the night progresses to reach a peak shortly before dawn. Is it merely coincidence that the wind profiles show an increase in divergence from vertical as stability increases during the night? Many species of *Anopheles* fly close to the ground. Indeed, it used to be said that risk of malaria was significantly lowered by sleeping upstairs. Is it merely coincidence that the greatest change in the wind velocity gradient occurs less than a meter from the ground? Much has been written over the past 35 years on the meteorological factors that influence biting cycles, but hitherto, as far as I am aware, none has taken into account the diurnal changes in the atmospheric boundary layer.

We come back then to my seemingly outrageous statement about other mechanisms being unlocked when sight is no longer possible. I knew then that flight to the target was not always level; I knew then that wind velocity was not uniform with height, and both of these were at the back of my mind at that time. What I did not know was the remarkable change in the wind velocity gradient just above the ground and how this changed just before nightfall, and continued to change as the night progressed. Nor had I formulated any exact mechanism that could enable the mosquito to make use of these changes; this came about in the years that followed and I am greatly indebted to Dr. S. L. Bragg, Vice-Chancellor of Brunel University and formerly aeronautical engineer at Rolls Royce and to Dr. J. W. Warren, senior lecturer in physics also at Brunel University for their interest in and very valuable discussion of these prob-

lems. I am especially grateful to Mr. R. A. Blackall of the Meteorological Office in Britain for the time he spent in 1977 in preparing the computer plotted curves that are the backbone of the hypothesis. Naturally, I had hoped to put these ideas to the test myself, perhaps using infra red photography to demonstrate the actual flight path in darkness. My hope is now that perhaps one of you will take up this challenge. But, unless we blacken the eyes of normal day-flying species inside a cage, it will have to be done on species showing a nocturnal feeding cycle. Ladies and Gentlemen, I rest my case.

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ABBREVIATIONS OF GENERIC NAMES

Authors are generally following J. F. Reinert's suggestions for the abbreviation of names of genera of Culicidae. A partial list appears in *Mosquito News* 36(3):376. The name needs to be spelled out only the first time it appears in an article.