

**The role of carbon dioxide in host-finding by mosquitoes (Diptera: Culicidae):
a review**

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Abstract

From a critical review of the literature, it is concluded that the role of carbon dioxide in host-seeking by mosquitoes comprises two distinct actions. Firstly, it acts as an 'attractant', orientation towards the host being mediated by kinesis and optomotor anemotaxis. When tested in the absence of moving air currents, orientation to the source is not possible and only the kinetic or 'activating' effect is manifested. Moreover, in the absence of other host factors, sustained flight takes place only in response to intermittent pulses of carbon dioxide; this response is not elicited in uniformly permeated airstreams. Secondly, carbon dioxide has a combined action with warm moist convection currents at close range and with odour factors at a distance from the host.

Introduction

In recent years, the chemical control of insect behaviour has been the subject of intensive studies (Wright, 1958; Bossert & Wilson, 1963; Farkas & Shorey, 1974; Kennedy, 1977a, 1977b). This work has greatly increased our understanding of the mechanisms involved in orientation to airborne chemical signals and, from it, a number of points have emerged that are relevant to the problem of host-seeking by blood-sucking insects. Firstly, a point source of a chemical forms an odour plume down the axis of the wind. Secondly, insects orient in response to the stimulus by flying upwind. Thirdly, the same chemical can have different effects on insects, depending on the distance from the source. Fourthly, because of turbulence and irregularities in air-flow, an olfactory stimulus cannot give precise information on the exact location of the source. On arrival in the vicinity of the source, that is to say when they fly out of the narrow upwind end of the odour plume, many insects settle, and the final stage of orientation is completed by walking.

The principal difference in the orientation of blood-sucking insects, compared with other insects, lies in their responses at close range. Since the final approach to the host by biting flies is normally made while the insect is on the wing, the exact location of the target is achieved either by visual cues or by flying down the warm moist convection currents rising from the body of the host (Daykin et al., 1965). On the other hand, their distant responses to olfactory stimuli can be regarded as closely similar to the pattern described for other insects. For instance, the responses of male *Plodia* moths in a wind tunnel were shown by Kennedy & Marsh (1974) to consist of the maintenance of upwind flight on entering a pheromone plume and of crosswind flight on leaving it. These movements were under the control of optomotor responses triggered by the apparent movement of the ground under the insect. Similar responses to ground pattern movement were shown for the mosquito *Aedes aegypti* (L.) by Kennedy (1940), and the theoretical implications of this for dispersing mosquitoes were discussed by Klassen & Hocking (1964).

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Carbon dioxide is the most important olfactory stimulus involved in host-finding by mosquitoes, yet its role is still poorly understood. Hocking (1971) remarked that "one of the most controversial materials...is carbon dioxide, which sometimes attracts, sometimes repels, and sometimes is inactive". Gillies (1974) suggested that the term 'field attractant' might be useful, while Khan (1977) expressed the consensus view that it acts as a locomotor stimulant. It is proposed here that the role of carbon dioxide in host-finding is that of a kairomone, acting like any other airborne chemical stimulus, but that it has important additional effects superimposed on this basic pattern.

Carbon dioxide levels in the environment

Atmospheric levels of carbon dioxide are normally in the range 0.03–0.04% (Richards, 1952), but in tropical forests, the output of carbon dioxide at night by vegetation may give rise to levels of 0.06–0.1%. Dow (pers. comm.) found that in Utah concentrations at night within the foliage of isolated trees were 0.011% carbon dioxide higher than in the open. Expired human breath contains about 4.5% carbon dioxide. Human or animal exhalations can, therefore, be dispersed and diluted by a factor of something like 100 before falling to background levels.

Excretion of carbon dioxide through the skin of the human body is of a very low order, 0.3–1.5% of that from the lungs (Tregear, 1966). Moreover, because of the total surface area of the body over which excretion takes place, the concentration at any one point on the surface is very low. Brouwer (1960) found no evidence to indicate that these small quantities played any part in the responses of mosquitoes. However, Kellogg's (1970) findings (see below) show that there are at least theoretical objections to this view.

Detection of carbon dioxide by the mosquito

Willis & Roth (1952) concluded from amputation experiments on female *Ae. aegypti* that carbon dioxide receptors were located on the antennae. However, the failure of antennectomised mosquitoes to respond to stimulation could reflect either impaired flight capacity (Bässler, 1958) or the necessity for sensory inputs from the antennal nerve for the response to carbon dioxide to be mediated (Kellogg, 1970). The latter author showed by electrophysiological methods that none of the antennal sensilla tested responded to carbon dioxide. On the other hand, one of the neurones supplying the club-shaped pegs on the maxillary palps was sensitive to small, abrupt changes in carbon dioxide in the atmosphere. The restriction of this function to the palps was further demonstrated by Omer & Gillies (1971), who showed that palpectomised females of *Culex quinquefasciatus* Say (formerly *C. pipiens fatigans* Wiedemann) failed to respond to carbon dioxide in a wind tunnel although their response to other host stimuli remained.

The question of the threshold concentration of carbon dioxide at which mosquitoes respond is one that remains unanswered. Indeed, it is possible that it may be the wrong question to ask. Kellogg's (1970) recordings from palpal peg neurones showed electrical changes when the concentration of carbon dioxide was raised by as little as 0.01%. Larger steps in concentration gave greater electrical responses. Thus, from the point of view of mosquito orientation, it may be that the crucial factor is the change in concentration not the level. For instance, Smith et al. (1970) found that *Ae. aegypti* females that had been kept in a carbon dioxide-free atmosphere oriented to an olfactometer port through which room air passed, in preference to one with clean air. Similarly, Mayer & James (1969) found that the addition of as little as 0.05% carbon dioxide to room air elicited responses from *Ae. aegypti* in a wind tunnel. In both these experiments, the room air may have contained odour factors in addition to carbon dioxide.

These findings show that, as suggested by Wright & Kellogg (1962), mosquitoes respond to alterations of carbon dioxide concentration, regardless of the background

level, and that very small changes may influence their behaviour. The subject is clearly one on which much more precise information is required.

Behavioural responses

Activation

By activation is meant simply the induction of flight activity. It may be divided into two phases:

(a) *Take-off*. Daykin et al. (1965) showed that, in the absence of host stimuli, the rate of take-off by resting mosquitoes was essentially a random process. When mosquitoes were exposed to an airstream to which 0.2% carbon dioxide was added, the rate of take-off was greatly increased for a period of about two minutes before falling off again to a low level. Laarman (1955) and Burgess (1959) described similar activation by carbon dioxide in open cages. Khan & Maibach (1966) showed that, in a vertical tower with the stimulus injected near the base of the tower, carbon dioxide by itself induced flying but not probing.

(b) *Sustained flight*. In a tunnel 2.74m long down which an airstream uniformly permeated with carbon dioxide at a concentration of 0.2 or 0.05% was flowing, Mayer & James (1969) found that *Ae. aegypti* failed to progress more than a short distance up the tunnel. It is presumed that the mosquitoes settled again soon after take-off. Omer & Gillies (1971) and Omer (1979), using the same type of wind tunnel, had similar results with *C. quinquefasciatus* and *Anopheles arabiensis* Patton. However, when the carbon dioxide was presented as a pulsed stimulus, being added to the airstream at a rate of 20s on and 20s off, the mosquitoes moved rapidly up the tunnel towards the inlet. It is concluded that carbon dioxide stimulates sustained flight, provided the level of the stimulus is varying; in a moving airstream, this results in upwind displacement. These laboratory findings are in agreement with the results of releasing carbon dioxide in the field, where, owing to turbulence, the stimulus must be received intermittently.

Orientation to the host

In nature, the effectiveness of carbon dioxide in guiding mosquitoes towards baited traps is well-established (e.g. Brown, 1952; Reeves, 1951; and the review by Service, 1976). However, the behaviour of mosquitoes on arrival in the vicinity of the source may be highly erratic and their movements not directed with any precision to the source (Gillies & Snow, 1967). When emitted by a host, carbon dioxide is one link in the chain of the stimulus-response situation created by the presence of the host (Wright et al., 1965; Gillies & Wilkes, 1969). As Hocking (1971) put it, "an experimental study which starts in the middle of a chain will yield very different results from one which starts at the beginning". The abnormal behaviour at the site of an artificial source of carbon dioxide may simply reflect the absence of directive stimuli in the form of convection currents. This behaviour also seems to underlie the difficulties sometimes encountered in designing effective carbon dioxide-baited traps (e.g. Service, 1969; Cornet & Chateau, 1971; Schreck et al., 1972). The success of the trap designed by the last-named authors, which was made of transparent Plexiglas with a number of metal-ringed entry ports, could well have resulted from the visual targets presented by the ports.

Removal of carbon dioxide from expired breath greatly reduces the numbers of mosquitoes attacking a host (Snow, 1970; Khan & Maibach, 1972). The distance downwind over which different emission rates of carbon dioxide influence the behaviour of flying mosquitoes has been estimated by Gillies & Wilkes (1969, 1970, 1972, 1974) and Schreck et al. (1972). Their conclusions are shown in Fig. 1.

In the field, therefore, carbon dioxide is unquestionably acting as an orienting stimulus.

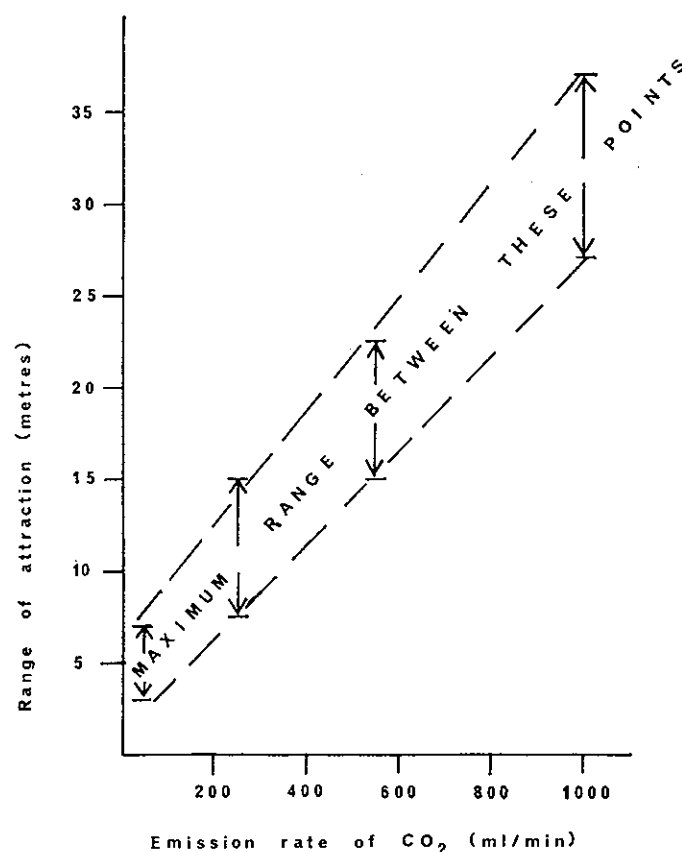


Fig. 1.—Results of field experiments on the range of effect of carbon dioxide on mosquitoes at varying emission rates. (The lower interrupted line represents the furthest trapping point at which a positive effect was obtained; the upper line represents the nearest trapping point at which no effect was recorded.) (Data from Gillies & Wilkes, 1969, 1970, 1974; Schreck et al., 1972.)

Combined effects with other stimuli

One of the most striking effects of carbon dioxide is to modify or augment the effects of other stimuli, which is often referred to as 'synergism'. Strictly speaking, this term should be reserved for instances where the response to two stimuli in combination is greater than to the sum of the two individual effects. In the case of carbon dioxide it appears that the combined action ranges from priming the response to a stimulus that by itself has no effect, through additive effects in combination with another stimulus, to a true synergism. Khan et al. (1966) and Khan & Maibach (1966) showed that, while *Ae. aegypti* females would orient to the convection currents rising from a moist warm body, this effect was enhanced when carbon dioxide was added to the environment. The experiments of Van Thiel & Weurman (1947) gave essentially similar results in *An. atroparvus* Van Thiel.

The effect of carbon dioxide on non-specific odour factors is similar. Laarman (1958) compared the reactions of *An. atroparvus* in an open-cage olfactometer to an airstream containing (1) total emanations from a rabbit, (2) pure carbon dioxide at a rate

equivalent to the expired breath of the animal, and (3) emanations from the rabbit from which carbon dioxide had been removed. He found that rabbit odour plus carbon dioxide elicited the strongest reaction, the effect of carbon dioxide was intermediate, while odour alone caused the weakest response. Bos & Laarman (1975) obtained similar results in testing the effect of guinea-pig blood on *An. stephensi* Liston. Bar-Zeev et al. (1977) studied the responses of *Ae. aegypti* in a two-chamber olfactometer and again obtained similar results, 1% carbon dioxide in air at 60% RH being more attractive than emanations from the human arm alone but less so than carbon dioxide added to odour from the arm. McIver (1968) showed that the addition of carbon dioxide to extracted odour factors from mice greatly increased the numbers of *Ae. aegypti* responding. When females of *Ae. aegypti* were tested in a wind tunnel, Mayer & James (1969) found that they moved upwind when air, which had been blown over a human arm, was introduced into the airstream and that the addition of 0.05% carbon dioxide to this air increased the movement. Carbon dioxide by itself had no effect. Omer (1979) made similar observations on *C. quinquefasciatus* and *An. arabiensis*.

These experiments show very clearly the combined action of carbon dioxide and whole-body odours, both factors having an orientating effect of variable extent when presented singly and a greatly enhanced effect together. Tests with pure L-lactic acid gave similar results but with the difference that, in the absence of carbon dioxide, the lactic acid stimulus had no effect on mosquito activity (Acree et al., 1968; Smith et al., 1970). Similarly, Roessler (1961) and Carlson et al. (1973) found that the presence of carbon dioxide was necessary for a response by *Ae. aegypti* to all the single chemical factors tested and found active. Thus, for odour to be effective by itself, it appears that a multi-component chemical stimulus is necessary.

On the basis of the speed of response of *Ae. aegypti* to airstreams containing odour factors with and without the addition of carbon dioxide, Mayer & James (1970) concluded that the integration of the two stimuli occurred centrally. The same conclusion was reached by Davis & Sokolove (1976), who found that the electrical responses of lactic acid-sensitive receptors on the antennae were not altered by the simultaneous presentation of carbon dioxide.

Discussion

Let us examine the statement that carbon dioxide is an activator. Activation is simply the first stage of orientation to the source of a chemical stimulus. If the stimulus is presented in still air, orientation to the source cannot take place because of the lack of orientating cues (for example, ground pattern movement) for the insect to steer by. Consequently, experiments conducted in chambers without steady air-flow can only reveal the initial kinetic effect, and observers may receive the misleading impression that carbon dioxide has no effect beyond this. There is a further difficulty, however. Even if air movement is provided, as in a wind tunnel, sustained flight may not ensue as long as the atmosphere is uniformly permeated with the gas. In this type of experiment, it appears that mosquitoes will only orient to the wind when the gas is presented as an intermittent stimulus. This conclusion is mainly based on the experiments of Omer & Gillies (1971) and Omer (1979); its confirmation by other methods is desirable. This problem does not arise with the two-chamber olfactometers of Schreck et al. (1967) and of Bar-Zeev et al. (1977), since the insect will encounter turbulence and contrasting carbon dioxide levels at the ports of the olfactometer. The stimulus is thus presented in a more natural way, and orientation of the mosquitoes is facilitated.

We should also examine the statement that carbon dioxide in some circumstances acts as a repellent. Willis & Roth (1952) found that carbon dioxide emitted through the port of an olfactometer had an effect they described as repellent. As pointed out by Brouwer (1960), given the initial activating effect of carbon dioxide, their findings

are more simply explained by the tendency of mosquitoes to be in flight when in the vicinity of the carbon dioxide-emitting port and at rest round the control port. Müller (1968) came to the surprising conclusion that carbon dioxide was repellent in concentrations from 1 to 33% but attractive at 50%. From the author's statements, the latter effect was accompanied by narcotisation. His olfactometer consisted of a narrow Y-shaped glass tube, the stem being 8.6mm and the arms 6mm in diameter. Under these confined conditions, normal turning responses in flight would be greatly impeded, making interpretation of the results difficult.

To conclude, although carbon dioxide may be described as an activator, the use of this term is misleading since it tends to obscure the fact that activation and anemotaxic orientation to the source are all part of the same process of 'attraction'. Moreover, in this respect, carbon dioxide and odour both operate in a similar way, a fact that was realised by Laarman (1958, 1959).

Conclusions

Carbon dioxide induces a directed response serving to guide the mosquito towards the host. The response is initially one of activation followed by upwind flight, the mosquito being steered by optomotor responses elicited by ground pattern movement. Thus, orientation to the host is the result of two behavioural responses, kinesis and optomotor anemotaxis, and in this sense carbon dioxide is acting as an attractant.

The orientating effect of carbon dioxide appears to be comparable to that of odour factors. However, there is one important difference. When tested in the laboratory, the odour stimulus is effective even when presented at a constant level, whereas carbon dioxide by itself causes directed responses only when the stimulus is pulsed. This difference is probably seldom manifested in nature, where the irregular and filamentous structure of the odour plume will normally ensure that the stimulus is received by the mosquito intermittently. It is also likely that host odour and carbon dioxide will be closely intermingled so that the two will be sensed simultaneously.

In terms of attractant effect, carbon dioxide is less powerful than the combined effect of all host factors, both at close range and at moderate distances from the host.

Carbon dioxide has an important combined effect, increasing the response to convection currents and perhaps visual factors close to the host and the response to odour factors at a distance.

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References

- ACREE, F., TURNER, R. B., GOUCK, H. K., BEROZA, M. & SMITH, N. (1968). L-lactic acid: a mosquito attractant isolated from humans.—*Science, N.Y.* **161**, 1346-1347.
- BAR-ZEEV, M., MAIBACH, H. I. & KHAN, A. A. (1977). Studies on the attraction of *Aedes aegypti* (Diptera: Culicidae) to man.—*J. med. Entomol.* **14**, 113-120.
- BÄSSLER, U. (1958). Versuche der Orientierung der Stechmücken: die Schwarmbildung und die Bedeutung des Johnstonschen Organs.—*Z. vergl. Physiol.* **41**, 300-330.
- BOS, H. J. & LAARMAN, J. J. (1975). Guinea pig, lysine, cadaverine and estradiol as attractants for the malaria mosquito *Anopheles stephensi*.—*Entomologia exp. appl.* **18**, 161-172.
- BOSSERT, W. H. & WILSON, E. O. (1963). The analysis of olfactory communication among animals.—*J. theor. Biol.* **5**, 443-469.
- BROUWER, R. (1960). Variations in human body odour as a cause of individual differences of attraction for malaria mosquitoes.—*Trop. geogr. Med.* **12**, 186-192.
- BROWN, A. W. A. (1952). Factors in the attractiveness of bodies for mosquitoes. *Trans. IXth Int. Congr. Ent.* **1**, 895-900.

- BURGESS, L. (1959). Probing behaviour of *Aedes aegypti* (L.) in response to heat and moisture.—*Nature, Lond.* 184, 1968–1969.
- CARLSON, D. A., SMITH, N., GOUCK, H. K. & GODWIN, D. R. (1973). Yellowfever mosquitoes: compounds related to lactic acid that attract females. *J. econ. Ent.* 66, 329–331.
- CORNET, M. & CHATEAU, R. (1971). Intérêt du gaz carbonique dans les enquêtes sur les vecteurs sylvatiques du virus amaril. Note préliminaire. *Cah. ORSTOM, Ent. méd. Parasit.* 9, 301–305.
- DAVIS, E. E. & SOKOLOVE, P. G. (1976). Lactic acid-sensitive receptors on the antennae of the mosquito, *Aedes aegypti*.—*J. comp. Physiol., A* 105, 43–54.
- DAYKIN, P. N., KELLOGG, F. E. & WRIGHT, R. H. (1965). Host-finding and repulsion of *Aedes aegypti*.—*Can. Ent.* 97, 239–263.
- FARKAS, S. R. & SHOREY, H. H. (1974). Mechanisms of orientation to a distant pheromone source.—pp. 81–95 in Birch, M. C. (Ed.). *Pheromones*.—495 pp. Amsterdam, North-Holland Publishing Co.
- GILLIES, M. T. (1974). Methods for assessing the density and survival of blood-sucking Diptera.—*A. Rev. Ent.* 19, 345–362.
- GILLIES, M. T. & SNOW, W. F. (1967). A CO₂-baited sticky trap for mosquitoes. *Trans. R. Soc. trop. Med. Hyg.* 61, 20.
- GILLIES, M. T. & WILKES, T. J. (1969). A comparison of the range of attraction of animal baits and of carbon dioxide for some West African mosquitoes.—*Bull. ent. Res.* 59, 441–456.
- GILLIES, M. T. & WILKES, T. J. (1970). The range of attraction of single baits for some West African mosquitoes.—*Bull. ent. Res.* 60, 225–235.
- GILLIES, M. T. & WILKES, T. J. (1972). The range of attraction of animal baits and carbon dioxide for mosquitoes. Studies in a freshwater area of West Africa.—*Bull. ent. Res.* 61, 389–404.
- GILLIES, M. T. & WILKES, T. J. (1974). The range of attraction of birds as baits for some West African mosquitoes (Diptera, Culicidae).—*Bull. ent. Res.* 63, 573–581.
- HOCKING, B. (1971). Blood-sucking behavior of terrestrial arthropods.—*A. Rev. Ent.* 16, 1–26.
- KELLOGG, F. E. (1970). Water vapour and carbon dioxide receptors in *Aedes aegypti*.—*J. Insect Physiol.* 16, 99–108.
- KENNEDY, J. S. (1940). The visual responses of flying mosquitoes.—*Proc. zool. Soc. Lond. (A)* 109, 221–242.
- KENNEDY, J. S. (1977a). Olfactory responses to distant plants and other odor sources.—pp. 67–91 in Shorey, H. H. & McKelvey, J. J., Jr (Eds.). *Chemical control of insect behavior. Theory and application*.—414 pp. New York, John Wiley.
- KENNEDY, J. S. (1977b). Behaviorally discriminating assays of attractants and repellents.—pp. 215–229 in Shorey, H. H. & McKelvey, J. J., Jr (Eds.). *Chemical control of insect behavior. Theory and application*.—414 pp. New York, John Wiley.
- KENNEDY, J. S. & MARSH, D. (1974). Pheromone-regulated anemotaxis in flying moths.—*Science, N.Y.* 184, 999–1001.
- KHAN, A. A. (1977). Mosquito attractants and repellents.—pp. 305–325 in Shorey, H. H. & McKelvey, J. J., Jr (Eds.). *Chemical control of insect behavior. Theory and application*. 414 pp. New York, John Wiley.
- KHAN, A. A. & MAIBACH, H. I. (1966). Quantitation of effect of several stimuli on landing and probing by *Aedes aegypti*.—*J. econ. Ent.* 59, 902–905.
- KHAN, A. A. & MAIBACH, H. I. (1972). Effect of human breath on mosquito attraction to man.—*Mosquito News* 32, 11–15.
- KHAN, A. A., MAIBACH, H. I., STRAUSS, W. G. & FENLEY, W. R. (1966). Quantitation of effect of several stimuli on the approach of *Aedes aegypti*.—*J. econ. Ent.* 59, 690–694.
- KLASSEN, W. & HOCKING, B. (1964). The influence of a deep river valley system on the dispersal of *Aedes* mosquitos.—*Bull. ent. Res.* 55, 289–304.
- LAARMAN, J. J. (1955). The host-seeking behaviour of the malaria mosquito *Anopheles maculipennis atroparvus*.—*Acta Leidensia* 25, 1–144.
- LAARMAN, J. J. (1958). The host-seeking behaviour of anopheline mosquitoes.—*Trop. geogr. Med.* 10, 293–305.
- LAARMAN, J. J. (1959). Host-seeking behaviour of malaria mosquitoes.—*Proc. XVth Int. Congr. Zool.* 1958, 648–649.

- MAYER, M. S. & JAMES, J. D. (1969). Attraction of *Aedes aegypti* (L.): responses to human arms, carbon dioxide, and air currents in a new type of olfactometer.—*Bull. ent. Res.* **58**, 629–642.
- MAYER, M. S. & JAMES, J. D. (1970). Attraction of *Aedes aegypti*. II. Velocity of reaction to host with and without additional carbon dioxide.—*Entomologia exp. appl.* **13**, 47–53.
- MCIVER, S. B. (1968). Host preferences and discrimination by the mosquitoes *Aedes aegypti* and *Culex tarsalis* (Diptera: Culicidae).—*J. med. Entomol.* **5**, 422–428.
- MÜLLER, W. (1968). Die Distanz- und kontakt-Orientierung der Stechmücken (*Aedes aegypti*) (Wirtsfindung, Stechverhalten und Blutmahlzeit).—*Z. vergl. Physiol.* **58**, 241–303.
- OMER, S. M. (1979). Responses of females of *Anopheles arabiensis* and *Culex pipiens fatigans* to air currents, carbon dioxide and human hands in a flight-tunnel.—*Entomologia exp. appl.* **26**, 142–151.
- OMER, S. M. & GILLIES, M. T. (1971). Loss of response to carbon dioxide in palpectomized female mosquitoes.—*Entomologia exp. appl.* **14**, 251–252.
- REEVES, W. C. (1951). Field studies on carbon dioxide as a possible host simulant to mosquitoes.—*Proc. Soc. exp. Biol. Med.* **77**, 64–66.
- RICHARDS, P. W. (1952). The tropical rain forest.—450 pp. Cambridge University Press.
- ROESSLER, P. (1961). Versuche zur geruchlichen Anlockung weiblicher Stechmücken (*Aedes aegypti* L., Culicidae).—*Z. vergl. Physiol.* **44**, 184–231.
- SCHRECK, C. E., GOUCK, H. K. & POSEY, K. H. (1972). The range of effectiveness and trapping efficiency of a plexiglass mosquito trap baited with carbon dioxide.—*Mosquito News* **32**, 496–501.
- SCHRECK, C. E., GOUCK, H. K. & SMITH, N. (1967). An improved olfactometer for use in studying mosquito attractants and repellents.—*J. econ. Ent.* **60**, 1188–1190.
- SERVICE, M. W. (1969). The use of traps in sampling mosquito populations.—*Entomologia exp. appl.* **12**, 403–412.
- SERVICE, M. W. (1976). Mosquito ecology. Field sampling methods.—583 pp. London, Applied Science Publishers Ltd.
- SMITH, C. N., SMITH, N., GOUCK, H. K., WEIDHAAS, D. E., GILBERT, I. H., MAYER, M. S., SMITTLE, B. J. & HOFBAUER, A. (1970). L-lactic acid as a factor in the attraction of *Aedes aegypti* (Diptera: Culicidae) to human hosts.—*Ann. ent. Soc. Am.* **63**, 760–770.
- SNOW, W. F. (1970). The effect of a reduction in expired carbon dioxide on the attractiveness of human subjects to mosquitoes.—*Bull. ent. Res.* **60**, 43–48.
- TREGGAR, R. T. (1966). Physical functions of skin.—185 pp. London, Academic Press.
- VAN THIEL, P. H. & WEURMAN, C. (1947). L'attraction exercée sur *Anopheles maculipennis atroparvus* par l'acide carbonique dans l'appareil de choix II.—*Acta trop.* **4**, 1–9.
- WILLIS, E. R. & ROTH, L. M. (1952). Reactions of *Aedes aegypti* (L.) to carbon dioxide.—*J. exp. Zool.* **121**, 149–179.
- WRIGHT, R. H. (1958). The olfactory guidance of flying insects.—*Can. Ent.* **90**, 81–89.
- WRIGHT, R. H., DAYKIN, P. N. & KELLOGG, F. E. (1965). Reaction of flying mosquitoes to various stimuli.—*Proc. XIIth Int. Congr. Ent.* **1964**, 281–282.
- WRIGHT, R. H. & KELLOGG, F. E. (1962). Response of *Aedes aegypti* to moist convection currents.—*Nature, Lond.* **194**, 402–403.

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