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Spiracular Responses of Aedes Mosquitoes¹ to Carbon Dioxide and Oxygen²

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ABSTRACT

Observations were made on the responses of the thoracic spiracles of adult Aedes aegypti (L.), and adult A. triseriatus (Say) to a constant CO2 pressure in serial concentrations of O2 in N2 and to the O2 in N2 series alone. Less than atmospheric pressures of O2 caused an increase in the frequency and duration of spiracular opening. Higher than atmospheric O2 tensions had no effect on frequency of spiracular opening, but reduced the duration of opening. Carbon dioxide effected full spiracular opening in proportion to the O2 concentration. The duration of spiracular opening, regardless of amplitude, was also proportional to the ratio of CO2 to O2. Responses of Aedes spiracles to hypoxia and CO2 decreased with increasing duration of exposure.

Since Hazelhoff (19264) first reported that spiracles of the cockroach opened in response to CO2, many efforts have been made to define the mechanism and find the site of action of this gas (Wigglesworth 1935; Case 1956, 1957a, b; Hoyle 1959, 1960, 1961; Schneiderman 1960; Van der Kloot 1963; Miller 1960, 1962). Several investigators have noted that CO2-induced spiracular opening was proportional to the O2 tension (Wigglesworth 1935, Case 1956, Schneiderman 1960, Miller 1962), and in fact graded spiracular opening was observed in locusts (Miller 1960), cockroaches (Hazelhoff 19264), and Musca and Callitroga adults (Case 1956) as a result of varying ratios of CO₂ to O2. In view of the dominant role CO2 and O2 play in control of spiracular opening and closing, it was considered desirable to measure their sensory effects in Aedes. Mosquitoes do not normally experience ambient concentrations of these gases as employed here. The assumption was made that the experimental gas regimes provided to the external environment would elicit the same spiracular responses as similar intratracheal gas tensions. Mosquitoes proved ideal subjects because their spiracles were easy to observe, exhibited graded opening, and did not become involved with possibly complicating ventilatory movements.

METHODS

The behavior of the thoracic spiracles of adult female mosquitoes was observed and recorded as previously outlined (Krafsur et al. 1970). Gas mixtures were prepared from cylinders of O2, N2, and CO2 and were measured with flowmeters. With the exception of CO2, gases were bubbled through water to give 85-95% RH. CO2 was used in small amounts and applied directly to the gas delivery tube. The total rate of gas flow was 5000 cc/min and temperatures were maintained at 21.1-22.7°C. Spiracular opening and closing was noted as follows: "Freq." refers to the number of openings per minute of observation.

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"toD" indicates the number of seconds per minute that spiracles were observed partially open, "toF" is the number of seconds per minute that spiracles were fully open, and "toT" is the total seconds per minute that spiracles were open regardless of amplitude. An account of the nature of thoracic spiracular opening is given in a previous communication (Krafsur et al. 1970).

RESULTS

A preliminary experiment was designed to test the hypothesis that spiracular response to CO2 was proportional to the oxygen tension. Spiracular behavior was compared among a group of A. triseriatus (Say) randomly exposed to atmospheres of the same relative proportions of CO2 to O2 but different absolute amounts of each. Control observations were made in atmospheres of 20% O₂ (air) or 100% O₂ (Table 1). As might be expected, spiracular opening was significantly more conservative in mosquitoes exposed to the higher O_2 tension (P < 0.05). However, this conservativeness was not reflected in amplitude of opening, but only in duration. In contrast, no differences in spiracular behavior were apparent in these same atmospheres when CO2 was injected in similar ratios. Thus, both amplitude and duration of spiracular response to CO₂ was directly proportional to the oxygen tension.

Having demonstrated a sensory effect of O2 and CO₂ on spiracular opening and a relationship of CO₂induced opening to O2 tension, an attempt was made to define spiracular behavior as functions of (1) oxygen tension alone and (2) a graded series of ratios of these 2 gases. Extensive observations were made on A. triseriatus mosquitoes exposed to a constant 25 cc/min CO2 in atmospheres of 10, 15, 20, 30, 40, and 50% O_2 diluted with N_2 , or in pure O_2 . Oxygen, rather than CO2, was varied because large volumes of gas could be more accurately delivered than very small amounts. Individual insects were observed first in gas flow without CO2 for a 1-min observation period, and subsequently in O2 and N2 plus CO2 for the following 2 min. An accommodation period of from 2 to 3 min in the chosen O₂ tension was pro-

Table 1.—Spiracular behavior of A. triseriatus observed: A. in atmospheres of 20% O2 (20 mosquitoes) or 100% O₂ (20 mosquitoes), and B, the same mosquitoes in the same atmospheres plus a CO₂ concentration of 2.5% of the O₂ tension.

		Spiracular responses		
Treatment	na	Freq.±sE	toF±sE	toT±sE
		A		
100% O ₂	20	2.75 ± 0.39		26.1±3.9 *
20% O ₂	20	$2.90 \pm .54$		34.8±4.7 *
		B		
100% O2 + CO2	20	1.87± .24		48.2±2.3
$20\% O_2 + CO_2$	20	$2.20 \pm .36$	40.9 ± 4.1	49.2±2.3

a n = no. observations. P < 0.05.

vided. The data therefore reflected spiracular behavior in 7 O₂ tensions and 7 CO₂ to O₂ ratios. Three samples of 10 mosquitoes each were randomly examined in each O2 tension.

Fig. 1 illustrates spiracular responses to O₂ tensions of 10-100% in the absence of ambient CO₂. To first examine frequency of spiracular opening, it is clear that a logarithmic rate of decrease occurred with increasing O₂ concentration; this rate abruptly leveled off beyond 20% O2 with no further significant change. That remarkably similar frequency responses to O2 tensions above the 20% value occur in Aedes is in contrast to Wigglesworth's (1935) finding in Xenopsylla which showed that frequency of opening and closing continued to decrease in O2 values greater than 20%. Expressed as total time of opening (toT), the average time spiracles were open per minute of observation was inversely proportional to the O₂ tension. The average slope of the response was such that for each 10% increase in O2, a corresponding decrease of 2.6 sec/min was obtained in spiracular opening. The slope was greatest in the range of 20-30% O₂, where a decrease of 9.2 sec in spiracular opening was observed. Further 10% increases in O₂ concentration beyond the 50% level resulted in a slope of only 0.51 sec. Amplitude of spiracular opening (toF) as a function of O2 alone was of little importance because only twitchlike openings were observed in all but the lowest 2 O2 concentrations. Thus the relationship of spiracular behavior to higher than normal ambient O2 tensions was such that frequency was not immediately affected but duration of each opening decreased; in lower than normal ambient O₂ tensions both frequency and duration of opening were elevated.

Parameters representing spiracular behavior as functions of CO₂:O₂ ratios are given in Table 2 and Fig. 2. Comparison of the control values with those obtained in identical O₂ tensions plus CO₂ indicate that an average 11% increase in the mean time of spiracular opening (toT) occurred. However, the increase in toT was not constant for each O2 tension employed. In the range of 10-20% O2, addition of CO₂ effected a mean 14% increase in spiracular opening, while between 30 and 100% O2 an average 9% increase was observed. The average slope of spiracular response (toT) was 2.6 sec decrease/ minute for each 10% increase in O2. This value is quite similar to that obtained in the control observations. Thus, the average duration of spiracular openings per minute (toT) were more closely related to the O2 tension than to the ratio of CO2 to O2. On the other hand, values representing frequency of spiracular opening and amplitude of opening (toF) in O2 plus CO2 were not at all like those obtained in O2 alone. As a function of increasing O2 concentration (but decreasing proportion of CO2 to O2), frequency of spiracular opening increased up to the 40% O2 level, or 1.25% CO2 of O2. Further increases in O2 resulted in a decrease in frequency of opening. This decrease was insignificant (P > 0.10) and it may be stated that frequency of spiracular opening

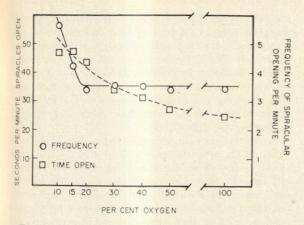


Fig. 1.—Frequency of spiracular opening and total time of opening in A. triseriatus as functions of O₂ concentration. Each point is the average of thirty 1-min observations.

(and hence closing) is directly related to the relative concentration of CO_2 to O_2 .

Amplitude of spiracular opening was the 1 feature of spiracular behavior clearly showing a dose-dependent response to the ratio of CO₂ to O₂ (Fig. 2). The rate of increase in toF was greatest between 2.5 and 1.25% CO₂ of the O₂ concentration, and here the slope amounted to an 11.4% increase in duration of toF per 0.25% increase in CO2 to O2. Beyond these values rates of change in toF were attenuated. It is therefore apparent, in light of Hassan's (1944) finding that spiracular opening is the result of relaxation of the spiracular closer muscle, that CO2 first effects a greater degree of muscle relaxation and secondly extends the period of relaxation beyond that determined by the normal frequency of motor impulses to the muscle. Support for the latter contention may be found in Table 2, which suggests that an inverse relationship exists between frequency of spiracular opening and proportional time of spiracular opening; the relationship is particularly clear if full spiracular opening (toF) is compared with frequency. It would be interesting to know if, in fact, the spiracular responses to the ratios of ambient CO2 to O2 applied here reflect responses occurring to similar intratracheal gas tensions. This point will be taken up later.

Table 2.—Spiracular responses in A. triseriatus to varying levels of O₂ and N₂ with a constant level of CO₂ at 0.5% of the total atmosphere.

Atmosphere		Spiracular responses		
% O ₂	% CO ₂ of O ₂	Freq.±se	toT±se	
10	5.00	1.50±0.48	55.6±1.76	
15	3.33	$1.70\pm .33$	54.4±1.58	
20	2.50	2.11± .36	52.7±1.62	
30	1.66	$3.23 \pm .31$	39.3 ± 2.30	
10	1.25	3.68± .34	38.9 ± 1.34	
50	1.00	$3.35 \pm .22$	31.0 ± 2.46	
100	0.50	$3.05\pm .29$	32.1 ± 2.89	

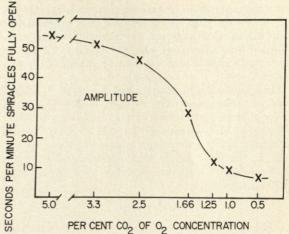
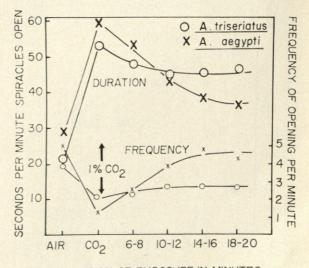


Fig. 2.—Amplitude of spiracular opening in A. triseriatus as a function of the CO₂:O₂ ratio. Each point is the average of 30 two-min observations.

In this study only the initial sensory effects of CO₂ and O₂ on spiracular behavior were measured, because it was necessary to gather an adequate number of samples rather than to make extensive observations on a limited number of insects. It was therefore desirable to investigate spiracular response to CO₂ as a function of duration of exposure. A limited series of observations were made on 6 A. triseriatus and 6 A. aegypti (L.) mosquitoes, observed first in air for 1 min and subsequently in air plus 1% CO₂ for 20 min. Observations were recorded for 2-min periods with 2-min intervals between. Five such periods of observation were made over a 20-min period for each mosquito. The results (Fig. 3) clearly indicate that spiracular response to CO₂ became attenuated with



DURATION OF EXPOSURE IN MINUTES

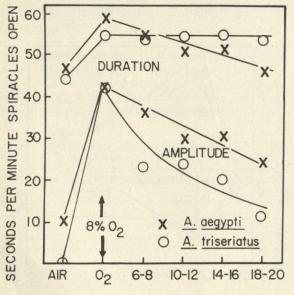
Fig. 3.—Spiracular responses of A. aegypti and A. triseriatus to 1% CO₂ in air as a function of duration of exposure. Each point represents 6 observations.

increasing duration of exposure; thus, spiracular behavior in the presence of ambient CO₂ progressively approaches that observed in "normal" atmospheres. Similar responses were obtained by Case (1956) in Callitroga and Musca exposed to several CO₂ tensions.

In a 2nd series of observations, 5 each of A. aegypti and A. triseriatus were exposed to 8% O_2 in N_2 after first being observed in air. Responses to lower than normal O_2 tension, like that to CO_2 , became attenuated with increasing duration of exposure (Fig. 4). It therefore seems that accommodation results upon extended exposure to other than normal CO_2 and O_2 tensions.

DISCUSSION

The extraordinary sensitivity of Aedes spiracles to rather low tensions of CO2 gas is in contrast to the amounts required to elicit spiracular opening in other insects. In house flies, Musca domestica L., ca. 6% CO2 was necessary for full spiracular opening, while in Schistocerca, 5% failed to elicit a complete spiracular response under most conditions (Hoyle 1960). Saturniid pupae in diapause required CO₂ concentrations greater than 5% (Schneiderman 1960). Beyond the ambient and intratracheal O2 tensions, the critical concentration of CO2 necessary to elicit opening of the spiracle has been shown to vary with diet (Wigglesworth 1935), age and water balance (Bursell 1957), ionic balance of the insect (Hoyle 1961, Miller 1964), and probably anything affecting the general metabolism. The present observations may only indicate that the respiratory rate of Aedes is simply higher than the other forms cited above. There



DURATION OF EXPOSURE IN MINUTES

Fig. 4.—Spiracular responses of A, aegypti and A, triseriatus to 8% O_2 as a function of duration of exposure. Each point represents 5 observations.

are other possibilities, however far-fetched they may presently seem. CO₂ in very low concentrations has a function in the host-seeking behavior of mosquitoes (Clements 1963). Perhaps a reflex action is excited by CO₂, resulting in preflight behavior and a sudden elevation in metabolism. It is interesting that, perhaps similarly, dragonflies possess a central inhibitory reflex responsible for complete spiracular opening during flight (Miller 1962).

Aedes thoracic spiracles behaved as those of Xenopsylla in O₂ pressures of less than atmospheric; that is, they showed an increased frequency of opening and closing. However, the duration of each opening was comparatively unaffected in Aedes, but in the flea duration was shortened with decreasing O2 tension. In greater than atmospheric O₂ pressures, the frequency of spiracular opening in Aedes was unaffected, but the duration of opening was attenuated; in the flea, frequency of opening was reduced but duration of each opening increased (Wigglesworth 1935). Abnormal O₂ tensions had no predictable effect on frequency of spiracular opening in saturniid pupae in diapause (Schneiderman 1960). It is remarkable that so little effect of O2 tensions above 40% was observed in Aedes mosquitoes. Clearly, lack of O2 had an obvious and immediate effect upon spiracular behavior, but the converse was not so apparent.

By providing a constant amount of CO₂ and varying the proportions of O2 and N2, responses were obtained that differed strikingly from those in the same O2: N2 mixtures alone. Furthermore, spiracular behavior was clearly related to the ratio of CO2 to O2 in that the more CO₂ relative to O₂ pressure, the greater the reduction in number of spiracular openings, the greater the duration of opening, and most obvious of all, the greater duration spiracles were fully open. It may be significant that Aedes showed predominately increased duration of complete opening with increasing effective CO2 tension (Fig. 2) while Musca showed increased amplitude of opening, i.e., "graded opening" (Case 1956). Although graded (partial) openings of the spiracles do occur in Aedes, our observations indicated that usually, opening was either narrow, short, and twitchlike, or the complete or nearly complete opening as previously described (Krafsur et al. 1970). Spiracular opening in Aedes is not an all-or-none phenomenon.

It may be useful to interpret the observations presented here in the light of recent knowledge concerning the mechanism of spiracular responses to CO₂ and O₂. Relaxation of the spiracle closer muscle with consequent opening of the spiracle was first thought to be the result of an accumulation of acid metabolites formed by metabolically produced CO₂ (Wigglesworth 1935). Case (1957a) advanced the view that acids simply forced CO₂ from solution in the tissues and hemolymph; consequently, it was the gas in the extracellular environment rather than the acid that caused a spiracular response.

Further efforts disclosed that the isolated spiracular apparatus of *Hyalophora* pupae spontaneously con-

tracted in the absence of any innervation; further, CO2 effected relaxation in this myogenic muscle and O₂ reduced the sensitivity of it to CO₂ (Beckel and Schneiderman 1957). In the American cockroach (Case 1957b) and the desert locust Schistocerca (Hoyle 1959, 1960), the occlusor muscle contracts in response to a steady stream of motor impulses from the central nervous system. Abrupt cessation of motor impulses leads to muscle relaxation and spiracular opening. CO2 apparently does not affect the frequency of impulses to the muscle, however, for Hoyle (1960) demonstrated that despite continuous motor nervous excitation, CO₂ caused relaxation of the closer muscle. Hoyle's investigations suggested that CO2 acted directly on the neuromuscular junction effecting a reduction in twitch tension and junction potential. Thus CO₂ reduced the response of the spiracular muscle to central control, and this reduction explains the peripheral action of the gas noted in earlier studies. Support for the work just cited was given by Miller (1962). In 4 species of adult dragonflies, CO₂ had a peripheral and direct effect upon the closer muscle; hypoxia acted via the central nervous system, reducing the frequency of motor impulses to the spiracle and thus heightening its sensitivity to CO2. In the rather special case of the spircaular apparatus of saturniid pupae, Van der Kloot (1963) provided evidence that CO2 hyperpolarized the closer muscle and this slowed or eliminated spontaneous activity. Again, CO2 acted directly upon the muscle and not through the central nervous system.

If the frequency of spiracular opening in Aedes is a reflection of the rather complicated electrical events taking place at the spiracle occlusor muscle, then Miller's contention that hypoxia reduces motor impulse frequency would adequately explain the effects of O2 at less than atmospheric pressures. Here it may be postulated that the closer muscle is more prone to depolarization, thus bringing about an increase in frequency of opening. However, less easy to rationalize are the effects of hyperoxic conditions on the frequency of spiracular opening in Aedes, for here the latter was unaffected. Under hyperoxic conditions it might be expected that metabolically produced CO2 would be physiologically less effective in inducing spiracular opening but this hypothesis was not borne out when a constant pressure of CO2 was maintained in the face of increasing O2 tensions above 20%.

Hoyle's (1960) proposal that CO₂ acts directly upon neuromuscular events in causing spiracular opening is consistent with the data presented in this report. Even in the lowest effective concentrations (i.e., in relation to the O₂ pressure) this gas exerted immediate reductions in the frequency of opening and closing.

In Musca and Callitroga, the reaction time of single spiracles to CO2 gas was directly proportional to its concentration (Case 1956). The oriental rat flea, Xenopsylla cheopis (Rothschild), judged by Wigglesworth's figures, gave similar reactions. In the present series of observations no systematic records were

kept of this reaction but it can be stated that even in the lowest effective CO2 tensions, response times were essentially immediate although exceptions did occur. In particular, if a spiracle were in the toD position, application of CO2 effected immediate opening; if the spiracle were closed, the effect of CO₂ was often not apparent until the next rhythmical opening was due.

The responses of Aedes spiracles to ambient CO₂ and to hypoxia were reduced with increasing duration of exposure. Similar results were obtained in the house fly (Case 1956) with regard to CO₂. If the effect of hypoxia in Aedes is to increase sensitivity to metabolically produced CO2, then the present observations may indicate that accommodation to low O₂ is in reality accommodation to CO₂. It has been suggested that the attenuated response seen in Musca is adaptation rather than fatigue (Case 1956). Desiccation was invoked to explain similar phenomena in tsetse flies (Bursell 1957), but whatever the mechanism involved, accommodation to sudden increases in CO₂ pressure would surely serve to act as a brake on spiracular transpiration of water.

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Variations in the Anatomy of Typhlodromus occidentalis (Acarina: Phytoseiidae)1

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ABSTRACT

The anatomy of *Typhlodromus occidentalis* Nesbitt is highly variable. Specimens found in Utah have unusually long dorsal setae and thus resemble *T. longipilus* Nesbitt rather than *T. occidentalis*. The peritremes are extremely short and typical of *T. occidentalis*, not *T. longipilus*. Within Utah, some of these phytoseiid mites have characteristics which appear to be genetically determined and

which become the normal anatomy of mites found in particular orchard populations. Female mites in some Utah orchards have 4 pairs of ventrianal setae, while 3 pairs predominate in other populations. The prominence of the ventrianal pores also seems to follow population lines. Deformities in the ventrianal plate and losses of single setae occur irregularly.

During recent years, there has been an accumulation of published information concerning integrated control of orchard mites and the biology of the major predators. In several parts of western United States the phytoseiid mite, Typhlodromus occidentalis Nesbitt, is considered to be the most valuable of these predators (Anderson and Morgan 1956, Lee and Davis 1968, Hoyt 1969). In spite of the agreement by most workers concerning the value of T. occidentalis as a predator, there is considerable doubt regarding its range of anatomical variation. Nesbitt (1951) described T. occidentalis and T. longipilus as distinct species. This distinction has been recognized by several workers (Chant 1959, Muma 1963), but questioned by others (Schuster and Pritchard 1963). In addition to disagreement among taxonomists, there have been some discrepancies in reports on the biology of T. occidentalis and the specific role it plays in the biological control of phytophagous mites.

The main character used by acarologists to separate T. occidentalis from T. longipilus is the relation of setal length to distance between setae on the dorsum of the mite. In T. occidentalis the setae are shorter than the distance separating a seta from the one posterior to it, while in T. longipilus, they are distinctly longer than this distance. Only a few additional features have been used as secondary characters to separate these 2 nominate species. The peritremes of both species are shorter than other Typhlodromus representatives; however they are distinctly shorter in T. occidentalis than in T. longipilus. Schuster and Pritchard (1963) in California reported a complete intergradation between these 2 species when a separation was attempted using dorsal setae and peritremes. Chant (1959), from work in Canada, and Muma (1963), in Florida, did not discuss this intergradation and considered the 2 species to be distinct.

The shape of the ventrianal plate, and the number and arrangement of the ventrianal setae, are valuable

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characters in the taxonomy of the genus Typhlodromus. These characters cannot be used to separate T. occidentalis from T. longipilus, but they constitute a basic part of the description. In the original description, Nesbitt (1951) stated that females of T. occidentalis had only 3 pairs of ventrianal setae. Both Chant (1959) and Schuster and Pritchard (1963) stated that 4 pairs of setae are normal, but some individuals have 3 pairs. Muma (1963) said either 3 or 4 pairs is common. In addition to the setation, there is frequently a pair of preanal pores on the ventrianal plate of phytoseiid mites. Muma (1963) described these pores as faint on T. occidentalis, whereas the other authors neither described them nor showed them in the drawings.

There are normally either 1 or 2 pairs of small metapodal platelets on the ventral surface of female phytoseiid mites near the ventrianal plate. Muma (1963) and Schuster and Pritchard (1963) recorded 2 pairs of metapodal platelets, while Chant (1959) stated that there is only 1 pair in *T. occidentalis*.

An attempt has been made to use several other characters, such as: spermatheca, amount of serration of the bristles, and teeth on the chelicerae. In general, these characters have been either too variable or too difficult to measure properly.

The present study originated from observations related to biological studies involving *T. occidentalis* in integrated control. Detailed records were kept of phytoseiid populations from apple orchards in Utah, and ca. 2000 slides were prepared. The orchards, all in nothern Utah, were located at Provo, Orem, Midvale, North Salt Lake City, and Perry. Certain characters did not occur with equal frequency in each orchard. Utah specimens did not agree with the major descriptions of either *T. occidentalis* or *T. longipilus*. Detailed measurements and observations were made of characters used in taxonomy from mites selected at random from 5 of the 7 orchards. Phytoseiid populations from several other orchards were ob-

served but not included in this study.

¹ Agricultural Experiment Station Project 431. Received for publication July 15, 1969.