Ventilation in the adults of *Amblyomma hebraeum* and *A. marmoreum* (Acarina, Ixodidae), vectors of heartwater in Southern Africa

INTRODUCTION

The ability of ticks to survive for extended periods whilst the host has important implications for the transmission of diseases. Long off-host survival not only increases the chances of finding a suitable host but also may result in tick feeding and include an integument which can dramatically restrict transpirational water loss as well as the ability to actively absorb water vapour from unsaturated air (2).

Control of spiracular opening is also important in restricting water loss. Ticks possess only one pair of spiracles which in unfed adult ticks have been shown to open on an intermittent basis (2). These findings provide strong evidence for the occurrence of discontinuous ventilation in ticks (i.e. ventilation involving periodic bursts or emissions of CO₂ and intermittent uptake of O₂).

Discontinuous ventilation has been found to be widespread in insects and its chief selective advantage is believed to lie in a reduction of respiratory water loss as a result of the loss of water vapour being restricted to discrete cyclic events (5). In ticks, however, the existence of discontinuous ventilation awaits experimental confirmation.

In this paper we confirm the existence of discontinuous ventilation in two species of ticks by direct measurement of respiratory gas exchange; we compare the ventilatory patterns observed to those typical of insects and finally we discuss the significance of discontinuous ventilation with respect to the ability of ticks to survive for extended periods whilst off the host.

We investigated the dynamics of respiratory gas exchange in the unfed adult stages of the South African bont tick *Amblyomma hebraeum* Koch and the South African tortoise tick *Amblyomma marmoreum*. In Southern Africa, *A. hebraeum* is the main vector of the disease heartwater. *Amblyomma marmoreum* is also capable of transmitting the rickettsia but the significance of this species in the epidemiology of the disease heartwater remains unclear (9).

MATERIALS AND METHODS

Adult ticks (six-week-old) used in the experiments were from colonies maintained in the laboratory (25 °C, 85 % RH, ambient photoperiod).

Measurements of CO₂ emission were made at 25 °C using a flow through respirometry system described elsewhere (3). In brief, the system employed a Licor CO₂ analyser, respirometers of 3 ml volume, a computerized data acquisition system and flow rates of 50 100 ml min⁻¹ STPD. The incident air stream was scrubbed of H₂O and CO₂ by a Drierite/Ascacite column. Unfed ticks were
monitored for 8-16 h at a temporal resolution of 5-10 s. Respiratory quotients (RQ) were determined by a closed system technique (4).

RESULTS

Respiratory gas exchange in unfed adults of both species (fig. 1) was characterized by elevated and erratic CO₂ emission rates during activity and discontinuous ventilation during inactivity. Discontinuous ventilation consisted of short but clearly defined bursts of CO₂ emission (B phase) followed by much longer interburst phases where CO₂ emission was marginally above base line levels. Characteristics of discontinuous ventilation in *A. hebraeum* flat adults are summarized in table I and compared to those in *A. marmoreum*. For both species rates of burst CO₂ emission (burst VCO₂) and burst length were similar. Rate of interburst CO₂ emission in *A. marmoreum* accounted for approximately 11% of total CO₂ emission during each discontinuous ventilation cycle (DVC). In *A. hebraeum*, CO₂ emission during the interburst period was seldom distinguishable from base line levels and hence was not measured. The major difference in ventilatory characteristics between the two species was the duration of the DVC, approximately 2.5 h in *A. marmoreum* compared to 1.5 h in *A. hebraeum*.

Standard VCO₂ (sVCO₂) of unfed ticks was calculated from the mean VCO₂ of the animal whilst exhibiting regular discontinuous ventilation. Measurements of sVCO₂ were converted to sVO₂ after determination of respiratory quotients (RQ's). Unfed adult *A. hebraeum* had a considerably lower SMR than *A. marmoreum* (table I).

<table>
<thead>
<tr>
<th>TABLE 1</th>
<th>Characteristics of the discontinuous ventilatory cycle in the unfed adults of two species of ticks.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td><em>A. hebraeum</em></td>
</tr>
<tr>
<td>Mass (mg)</td>
<td>31.3 ± 9.9</td>
</tr>
<tr>
<td>N</td>
<td>12 (6 M, 6 F)</td>
</tr>
<tr>
<td>VCO₂ (µl h⁻¹)</td>
<td>0.416 ± 0.269</td>
</tr>
<tr>
<td>VCO₂ (µl mg⁻¹ h⁻¹)</td>
<td>0.0136 ± 0.0006</td>
</tr>
<tr>
<td>Burst VCO₂ (µl mg⁻¹ h⁻¹)</td>
<td>0.0262 ± 0.0104</td>
</tr>
<tr>
<td>Interburst VCO₂ (µl mg⁻¹)</td>
<td>-</td>
</tr>
<tr>
<td>Burst length (min)</td>
<td>5.16 ± 1.03</td>
</tr>
<tr>
<td>Burst frequency (h⁻¹)</td>
<td>0.74 ± 0.26</td>
</tr>
<tr>
<td>RQ</td>
<td>0.82</td>
</tr>
<tr>
<td>VO₂ (µl mg⁻¹ h⁻¹)</td>
<td>0.0158 ± 0.0097</td>
</tr>
</tbody>
</table>

1 Values taken from Table 3 (in 4).
** CO₂ emission indistinguishable from base line levels.

DISCUSSION

In brief, the ventilatory cycle in insects consists of three stages: A closed phase (C phase) in which the spiracles are closed thus preventing any gas exchange or respiratory water loss. This stage is followed by a flutter phase (F phase) during which slight opening of the spiracles, on an intermittent basis, allows a slow ingress of O₂ but little egress of CO₂ or water vapour. Finally, in the open or burst phase (B phase), the accumulation of CO₂ from respiring tissues triggers some or all of the spiracles to open widely resulting in the rapid release of CO₂ and water vapour to the outside (5).

A continuous very low inter-burst emission of CO₂ does occur in ticks, similar to that described in insects during the constricted-spiracle (closed phase). However, unlike in insects there is no clearly defined increase in VCO₂ corresponding to the F phase occurring prior to the burst phase. This suggests that if an F phase exists in ticks, it must be characterized by extremely low rates of gaseous exchange because it cannot be clearly distinguished via diffusive loss of CO₂ through the spiracles.

It has recently been suggested (4) that ticks probably do not exhibit a fluttering-spiracle (F) phase of the kind observed in insects but instead may rely primarily on diffusive uptake of O₂ through the cuticle between burst phases. This diffusive uptake of O₂ through the cuticle appears sufficient for non-active respiration for prolonged periods, although regular release of CO₂ is still necessary. If this is the case then the standard metabolic rate of ticks can be expected to be very low compared to that of insects which are not thought to make significant use of cuticular O₂ ingress.
The allometric equation describing the relationship between insect body mass and standard metabolic rate is given below:

\[ MR = 11.3M^{0.67} \]  
(10)

where MR is metabolic rate (j-h⁻¹), and M is body mass (g).

The metabolic rates of the unfed stages of ticks are much lower than that predicted on the basis of body mass from data on insects. Metabolic rates of *A. hebraeum* and *A. marmoreum* are only 0.8 and 1.4 % (2.3 %) respectively of that predicted for insects of an equivalent body mass. Considering that metabolic rates of the unfed stages of ticks are much lower than that predicted for insects of a similar size, the role of cuticular diffusion may indeed play an important role in ixodid tick gas exchange. It should also be noted that unfed adult ixodids, due to dorso-ventral flattening, must have a large surface area to volume ratio compared to most insects of similar body size. Although this feature makes ticks more prone to desiccation, it would presumably increase their capacity for diffusive gas exchange across the integument. However, we still lack the required information on actual tick surface areas and cuticular \( O_2 \) permeabilities to test the hypothesis that cuticular diffusion may play an important role in ixodid respiratory gas exchange.

There is little doubt that the discontinuous ventilation in ticks is important in reducing respiratory water loss during the period between moultng and feeding. Previous workers have demonstrated dramatic increases in water loss in various species of ticks in which the spiracles have been forced to remain open by exposure to high \( CO_2 \) concentrations (1,2).

Since respiratory water loss is minimal during spiracle closure (interburst phase), but high when the spiracles are open (burst phase), one can postulate that burst frequencies in any particular species of tick may give some indication as to its ability to reduce respiratory water loss. During regular discontinuous ventilation cycles, the burst frequency of *A. hebraeum* was on average once every 1.5 h which is much higher than the burst frequencies of once every 2.5 h found for *A. marmoreum*. Such low rates of spiracular opening in *A. marmoreum* would suggest that this species can more effectively reduce respiratory water loss than *A. hebraeum*.

**CONCLUSION**

Previous reviews of the physiological ecology of ticks have emphasized that survival between blood meals is a function of maintaining a balance between energy and water use with the maintenance of water homeostasis being considered the most critical survival factor (7). Furthermore it has been suggested that integumental permeability to water flux may be of greater value to maintenance of water balance of ixodid ticks than the critical equilibrium activity (2). In the light of our findings, we suggest that ventilatory patterns in ticks and the role they play in reducing respiratory water loss should be given more attention when trying to interpret survival potential and habitat associations of ixodid ticks. The two species under consideration in this study, *A. hebraeum* and *A. marmoreum*, are largely sympatric in their distribution in Southern Africa although *A. marmoreum* is found in drier areas than *A. hebraeum* (8). The apparent superior ability of *A. marmoreum* to reduce respiratory water loss may be of significance in explaining its tolerance to drier habitats than *A. hebraeum*.

**REFERENCES**


The objective of this study was to establish the major features of respiratory gas exchange in unfed adults of the ticks *Amblyomma hebraeum* and *A. marmoreum*, both vectors of heartwater in Southern Africa. Carbon dioxide emission of ticks was measured at 25 °C using flow-through respirometry in order to determine standard metabolic rate (SMR) and the temporal pattern of gaseous emission. For both species, SMR was extremely low and approximately 100 fold less than that predicted for an insect of equivalent body mass. Ventilation in inactive ticks was discontinuous and characterized by periodic bursts of CO₂ emissions during spiracular opening. The main selective advantage of this type of ventilation is believed to lie in a reduction of respiratory water loss. It is suggested that future research into water balance physiology of ticks should address the role of ventilatory patterns in determining off-host survival and habitat associations.

**Key words**: Heartwater - Tick - *Amblyomma hebraeum* - *Amblyomma marmoreum* - Gas exchange - Water metabolism.