

SHORT COMMUNICATION

RESPIRATION BENEATH DESERT SAND: CARBON DIOXIDE  
DIFFUSION AND RESPIRATORY PATTERNS IN A  
TENEBRIONID BEETLE

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The massive dune sea of the southern Namib Desert is approximately 800 km in length and some 140 km wide. These dunes are among the highest in the world and, in spite of very sparse vegetation cover, they support a surprising variety of reptiles and arthropods (Koch, 1961; Louw & Seely, 1982). A feature of the arthropod fauna is the high species diversity of flightless tenebrionid beetles. These beetles do not construct burrows, but swim through the sand as if it were a fluid medium. For a description of the physical properties of dune sand see Lancaster (1981). Among the tenebrionids, *Onymacris unguicularis* is of special interest because it engages in fog-basking on the crests of the dunes when intermittent condensing fog occurs in the desert (Hamilton & Seely, 1976). This beetle occurs almost exclusively on the high slip-faces of the dunes, where it feeds on wind-blown plant detritus. To escape extremely high surface temperatures during midday and very low temperatures at night, *O. unguicularis* submerges beneath the sand to a depth of 5–10 cm for as much as 18 h per day (Seely, Mitchell & Louw, 1985). The present study assesses the respiratory consequences of such submergence by measuring the diffusion rate of carbon dioxide through a 5-cm layer of sand and the respiratory patterns, carbon dioxide production, and oxygen consumption of the beetles.

*Onymacris unguicularis* were collected on the slip-faces of sand dunes 10 km west of Gobabeb, Namibia. They were transported by air, together with a large sample of slip-face sand, to our laboratory in Cape Town, where they were maintained on a diet of lettuce and rolled oats in a photothermal gradient. In order to measure respiratory patterns, the beetles (mean mass  $0.737 \pm 0.120$  g; mean  $\pm$  S.D.) were individually placed in a cylindrical Perspex respirometer (diameter 6 cm; total volume 136 ml). Dry medical air was led into the upper portion of the respirometer at a flow rate of  $200 \text{ ml min}^{-1}$ , while the exit port, also at the top of the respirometer, was connected via a flow meter to an infra-red CO<sub>2</sub> analyser (Analytical Development Co., 225-MK3). The electrical output from the CO<sub>2</sub> analyser was connected to a chart recorder which allowed resolution to an accuracy of 3 p.p.m. CO<sub>2</sub>. The analyser was

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calibrated using certified span gases. During experiments the metasternum of each beetle was lightly glued to the bottom of the respirometer. This allowed free movement of the appendages and normal ventilatory movements, but prevented the insect from moving to the surface of the sand when sand was added to the respirometer. Respiratory patterns and CO<sub>2</sub> production were measured while the beetles were submerged beneath 5 cm of sand and also without any sand present. The respirometer was housed in a temperature-controlled chamber ( $\pm 1^\circ\text{C}$ ) and experiments were run at 25 and 35°C. Carbon dioxide production and respiratory patterns for each of the four treatments were recorded over 4–6 h. The sand and temperature treatments were organized in such a way that the natural circadian rhythm of the beetle would not influence the respiratory patterns and metabolic rate.

In order to estimate the rate at which CO<sub>2</sub> diffuses through the slip-face sand, we filled the respirometer with 5 cm of dune sand and then injected 100  $\mu\text{l}$  of CO<sub>2</sub> with a Hamilton syringe through an injection port at the base of the sand column. The time taken from injection to the deflection on the CO<sub>2</sub> analyser was measured with a stopwatch (0.1 s) when the respirometer contained sand and when it did not. The difference between these figures was interpreted as the time taken for the CO<sub>2</sub> bolus to diffuse through the 5-cm sand column. This experiment was carried out at both 25 and 35°C and replicated seven times.

In view of the unreliability of CO<sub>2</sub> production as a measure of aerobic metabolic rate (Schmidt-Nielsen, 1983), we also determined the resting metabolic rate of the beetles by measuring their oxygen consumption with an Applied Electrochemistry S-3A oxygen analyser, using a similar flow-through system. The output of the analyser was connected to a BBC microcomputer, and the techniques and calculations employed were identical to those described by Bartholomew, Lighton & Louw (1985). Measurements were made at 25°C, over periods of at least 6 h.

All gas volumes were corrected to standard temperature and pressure. Results have been expressed as means  $\pm$  S.D. and statistical significance was determined by Student's *t*-tests.

*Onymacris unguicularis* has fused elytra and its abdominal spiracles open into an enclosed subelytral cavity. Expired gases from these spiracles are therefore released to the atmosphere only when the respiratory cleft above the anus, the single aperture from the subelytral cavity, is periodically opened (Ahearn, 1970). The respiratory patterns displayed by *O. unguicularis* (Fig. 1) show that CO<sub>2</sub> is released in intermittent bursts. The time intervals between successive bursts were temperature-dependent (Table 1) and were significantly reduced from  $26.7 \pm 6.7$  min at 25°C to  $9.9 \pm 2.1$  min at 35°C ( $P < 0.001$ ). Covering the beetles with a 5-cm layer of sand significantly increased the time intervals between respiratory bursts at both temperatures ( $P < 0.05$ ). Again, there was a highly significant difference between the two temperatures ( $P < 0.001$ ; Table 1). Also, the presence of sand slightly reduced the sharpness of the peaks recorded on the chart recorder (Fig. 1).

When a 100- $\mu\text{l}$  bolus of CO<sub>2</sub> was injected into the base of the sand column contained in the respirometer, the mean time before it was recorded by the CO<sub>2</sub> sensor was  $15.6 \pm 0.7$  s ( $N = 7$ ) at 25°C. In the absence of the sand,  $9.4 \pm 0.5$  s

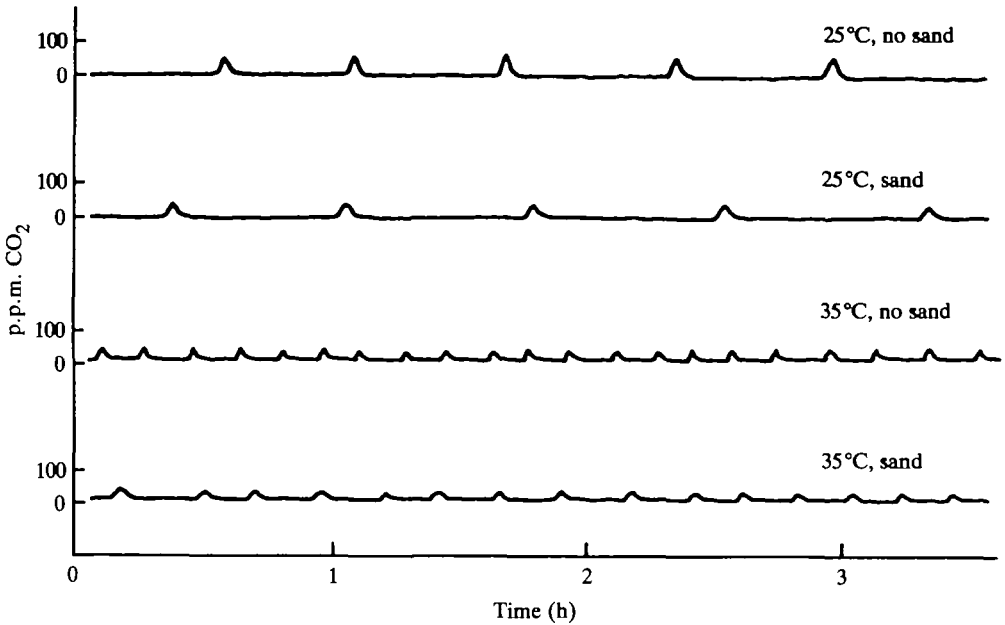


Fig. 1. Respiratory patterns of *Onymacris unguicularis*. Carbon dioxide production in p.p.m. shown for temperatures of 25 and 35°C, with and without a covering of sand.

Table 1. *Respiration in Onymacris unguicularis: time intervals between successive bursts of CO<sub>2</sub> and total CO<sub>2</sub> production*

	Time between successive CO <sub>2</sub> bursts (min)			CO <sub>2</sub> production ( $\mu\text{g}^{-1}\text{h}^{-1}$ )		
	Mean	S.D.	N	Mean	S.D.	N
25°C, without sand	26.7	6.7	11	30	10	8
25°C, under sand	35.5	10.5	11	24	7	10
35°C, without sand	9.9	2.1	9	99	24	9
35°C, under sand	12.5	2.3	9	84	23	9

elapsed from the time of injection to the first response of the CO<sub>2</sub> analyser. The mean time, therefore, for the CO<sub>2</sub> bolus to percolate through the 5-cm sand column was 6 s. This experiment was repeated at 35°C but no significant difference was found between the two temperatures ( $P > 0.05$ ).

Measurements of mass-specific oxygen consumption showed that the resting metabolic rate of *O. unguicularis* was equivalent to  $44 \pm 9 \mu\text{l O}_2\text{g}^{-1}\text{h}^{-1}$  ( $N = 6$ ) at 25°C. The cyclical pattern observed for CO<sub>2</sub> production was also apparent in the O<sub>2</sub> consumption trace, and intervals between the peaks of O<sub>2</sub> uptake were sometimes as long as 45–60 min.

The results show that this tenebrionid beetle has an extraordinarily low metabolic rate, which would be of obvious survival value in a desert environment where food and water supplies are unpredictable. The metabolic rate of *O. unguicularis* is lower

than those previously recorded for four similar tenebrionid species from the same habitat by Bartholomew *et al.* (1985) (e.g.  $122 \mu\text{lg}^{-1}\text{h}^{-1}$  for *Onymacris plana* at  $22^\circ\text{C}$ ). The intervals between cyclical peaks of  $\text{CO}_2$  release and  $\text{O}_2$  uptake measured in the present study were also much longer than those recorded by Bartholomew *et al.* (1985). We suggest that these differences may be due to the shorter measurement time and different conditions employed in the latter study.

In conclusion, our results have confirmed those of Bartholomew *et al.* (1985) by showing that respiration in tenebrionid beetles is cyclical, with periodic bursts of  $\text{O}_2$  uptake and  $\text{CO}_2$  discharge. The earlier findings of Punt, Parser & Kuchlein (1957) showed this pattern in carabid beetles. Our results have demonstrated that periods of apnoea between respiratory peaks in *O. unguicularis* can be remarkably long (up to 60 min). We found that when the beetles were buried beneath the sand, and therefore in a more secure environment, the periods of apnoea were prolonged and the metabolic rate as judged by  $\text{CO}_2$  production was slightly but not significantly lowered ( $P > 0.05$ ; Table 1), probably because of the longer intervals between  $\text{CO}_2$  bursts. Temperature effects on the above parameters were as expected. Under the conditions used for determinations of  $\text{O}_2$  consumption ( $25^\circ\text{C}$  without sand),  $\text{CO}_2$  production was  $30 \pm 10 \mu\text{lg}^{-1}\text{h}^{-1}$ , and the respiratory quotient of 0.68 indicates that the beetles were catabolizing fat. The mass-specific aerobic metabolic rate was much lower than would be predicted from the size of the beetles (Bartholomew & Casey, 1977; Bartholomew *et al.* 1985).

Carbon dioxide diffused very rapidly through a 5-cm column of slip-face dune sand. This is the depth at which the beetles are commonly found and where they frequently encounter temperatures between 25 and  $35^\circ\text{C}$  (Seely *et al.* 1985). It is not surprising, therefore, that the beetles were able to respire normally beneath the sand and that respiratory patterns with and without sand were broadly similar. The intermittent respiration pattern *via* the subelytral cavity, with long periods of apnoea, also contributes to minimizing respiratory water loss in these desert tenebrionids (Nicolson, Louw & Edney, 1984). Together with the extremely low metabolic rate, this is of adaptive importance in a hot, arid environment.

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