Is the subsurface environment of the Namib Desert dunes a thermal haven for chthonic beetles?

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Tenebrionid beetles inhabiting the dunes of the Namib Desert spend most of their lives buried below the sand surface. When they surface, which is not necessarily daily, it is often for only a few minutes or hours. Is the decision to bury or emerge determined by thermal benefits or optimization of water vapour pressure relationships or other factors? We evaluated this question by measuring temperature and relative humidity above and below the sand in dunes near Gobabeb continuously over 24 h, and calculating the vapour pressure difference between a hypothetical beetle and its surroundings. When beetles emerged, temperatures were available such that buried beetles could have attained their preferred body temperature, of 36 to 40°C, and avoided solar radiation. Desiccation stress on the beetles was also greater above surface during the day when they emerged, and greater below surface at night, when they were buried. We conclude that it is neither the need to attain preferred body temperature nor the need to prevent desiccation that induces the beetles to emerge or bury.

Skemerkewers wat in die duine van die Namibwoestyn woon bring die grootste gedeelte van hulle lewens onder die sand se oppervlak deur. Wanneer hulle uitkom is dit gewoonlik slegs vir 'n paar uur per dag. Om vas te stel of die besluit om in te grawe of uit te kom deur temperatuur of waterdampdruk bepaal word, het ons die temperatuur en die relatiewe voggehalte bo en onder die sand by verskillende plekke in die Namib-duinesee naby Gobabeb pal oor 'n tydperk van 24 h gemeet. Dit het ons in staat gestel om die waterdampdrukverskil tussen 'n hipotetiese kewer en sy omgewing te bepaal. Teen die tyd van die dag wanneer die kewers uitkom was die temperatuur ondergrond reeds so dat hulle hul gewenste liggaamstemperatuur van 36° tot 40°C reeds ondergronds kon bereik en so die intense sonstraling kon vermy het. Eweneens was die stres van uitdroging op die kewers groter bo-op die oppervlak wanneer hulle uitgekom het en ook onder die oppervlakte in die aand wanneer hulle begrawe lê. Ons het tot die slotsom gekom dat dit nie die noodsaaklikheid is om 'n gewenste liggaamstemperatuur te kan bereik, wat bepaal of die kewers opkom, nóg die noodsaaklikheid om uitdroging te verhoed wat hulle laat ingrawe nie.

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Namib Desert sand dunes support a heterogeneous endemic fauna with tenebrionid beetles being the most conspicuous element (Koch 1962). Many animal species living in the dunes make extensive use of the subsurface environment. A number are in intimate contact with the sand because, although they bury beneath the surface, they do not construct burrows (Coineau, Lancaster, Prodon & Seely 1982; Koch 1961; Robinson & Seely 1980; Seely 1983). The climate of the Namib, a coastal desert, is moderate relative to some other deserts (e.g. Koch 1962; Besler 1972). Nevertheless, the extremes of the climate are highly stressful, and much research has been directed towards describing adaptations which allow the tenebrionids and other dune animals to cope with this stress (e.g. Edney 1971; Hamilton 1975; McClain, Seely, Hadley & Gray 1984). Emphasis in most early research has been on surface activity, presumably because of the animals' high visibility while on the surface, as well as their presence on the surface for feeding, drinking and reproductive behaviour (Seely 1983). Actually, burying animals spend much more time below the surface than on it (Seely 1983). Burying is usually interpreted, implicitly or explicitly, as necessary retreat from hostile conditions above ground.

Robinson & Seely (1980) have pointed out that temperature and humidity fluctuate less and provide conditions more amenable to life processes beneath the sand surface than above. Subsurface environments thus may contribute positively to the overall fitness of dune animals, including tenebrionids (Seely 1983). Diurnal Namib tenebrionids and other animals often are not on the surface when apparently 'suitable' environmental conditions occur there. Therefore we have attempted to ascertain, using measurements of surface and subsurface temperature and humidity at representative dune sites, whether tenebrionids bury and emerge in order to select particular environmental conditions.

Materials and methods

Measurements were made at six sites approximately equally spaced across the central Namib dune sea (Figure 1), between 2 March and 16 April 1982. We present data from two of the sites in this paper to illustrate conditions representing the extremes of the prevailing conditions. These two sites, 30 km apart, were visited on 25 – 26 March (Site 1) and 1 – 2 April

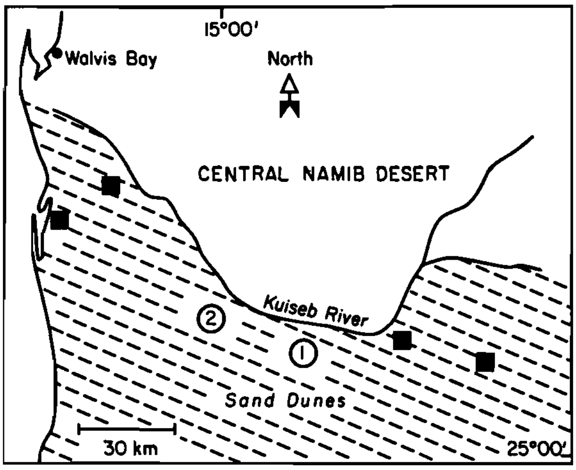

Figure 1 Map of the central Namib Desert dunes with study sites indicated.

(Site 2); Site 1 but not Site 2 recently had received a shower of rain of unknown magnitude, a relatively unpredictable event in this area (Pietruszka & Seely 1985). Subsurface temperatures were measured using an array of nine copper-constantan thermocouples mounted on a thermally inert rod, which was pushed into the dune sand to a depth of 300 mm. The temperature probe was located on level sand on an upper dune slope below the slipface, several metres distant from the nearest vegetation, and was allowed to equilibrate for a minimum of 10 h before recording commenced. The thermocouples were connected to a portable thermocouple thermometer (Bailey Bat-4) and calibrated to a precision of 0,2°C by water immersion before attachment to the probe.

The relative humidity of the sand pore space was measured using a piercing humidity probe (Vaisala HMP 15 with HM 1 14 RH indicator). The probe was pushed into the sand to a depth which located the centre of the 30 mm long, sintered filter tip at 100 mm below surface, a depth at which beetles are known to spend time (Seely 1979; Seely, Mitchell & Louw 1985). The humidity probe was located within one metre of the temperature probe and also allowed to equilibrate for a minimum of 10 h. The probe was calibrated over standard salt solutions.

Temperature and relative humidity above ground were measured with a standard sling psychrometer (Lambrecht). The psychrometric charts of Barenbrug (1974) were used to calculate vapour pressure.

Results and discussion

Very varied surface and subsurface temperature (Figures 2, 3) and humidity (Figure 2) conditions occurred during the period of measurements. The range of ambient conditions above ground was not unusual, however, for at this time of year extremes of ambient temperature are the norm (e.g. Lancaster, Lancaster & Seely 1984). At Site 1 where unusual rainfall conditions were encountered, the subsurface temperature profile was skewed toward lower temperatures near the surface, indicating cooler conditions during the day of measurement than had occurred in the recent past. At both sites, mean temperatures on the surface were lower (Site 1: 8,5°C, Site 2: 4,7°C) than mean temperatures at – 300 mm, as would be expected with decreasing radiation mid-way between summer and winter.

The surface sand (and sand at a depth of – 25 mm at Site 2) experienced a diel temperature range greater than that of the dry-bulb temperature above ground. Below these depths the range was less than that above ground and, moreover, the mean temperature was moderate (30,2°C and 31,0°C at – 300 mm).

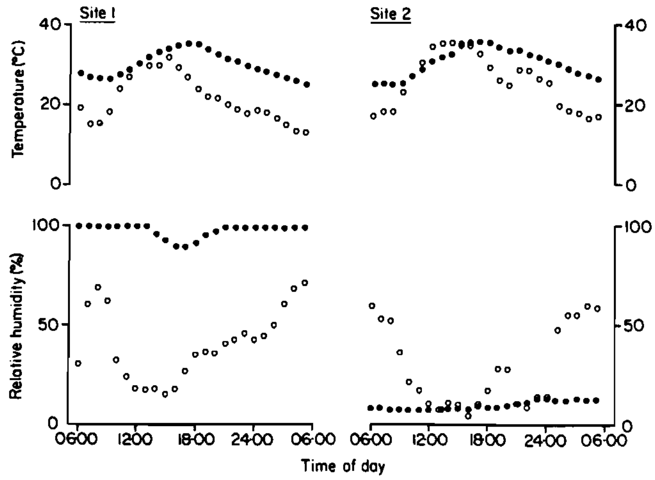

Figure 2 Temperature and relative humidity above ground (○) and at – 100 mm (●) at Site 1 and Site 2 during 24 h of measurements.

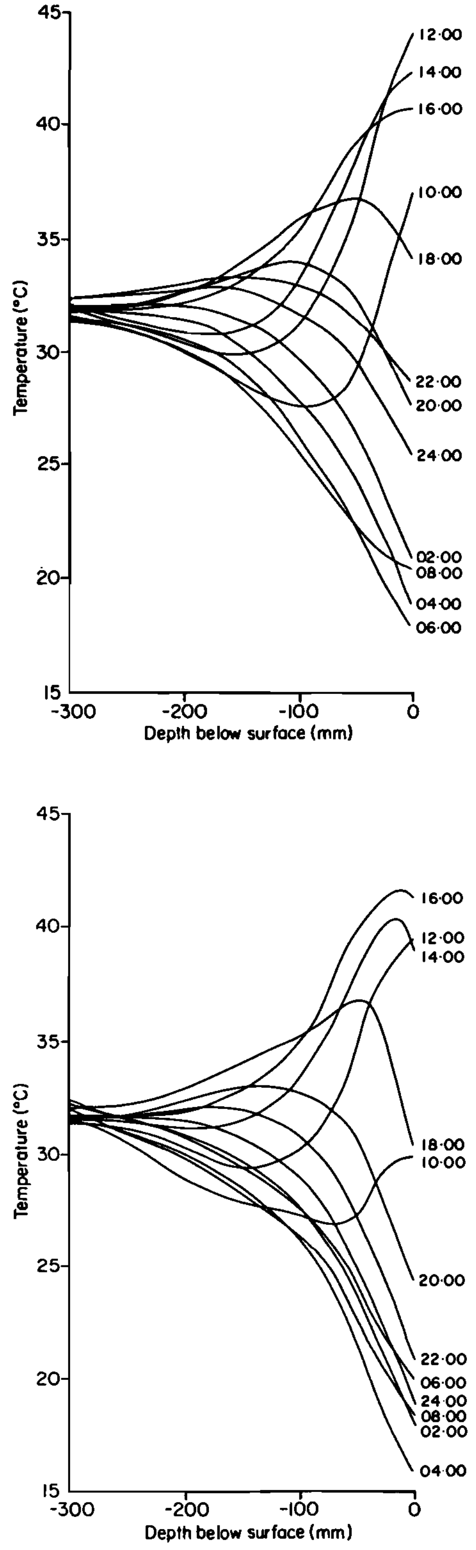

Figure 3 Temperature of the sand at depths between the surface and – 300 mm for periods of 24 h at Site 1 (top) and 2 (bottom).

Without providing quantitative data, some authors have stated that considerable amounts of moisture are to be found not far below the surfaces of dunes, even in very arid conditions (e.g. Bagnold 1941; Norris & Kavanau 1966). Bagnold (1941) considers that such moisture results from rare showers of rain rather than capillary action, which is not effective over a depth greater than – 400 mm. In the Namib many animals, particularly tenebrionid beetles, Thysanura, and lizards, live in the slipface and upper parts of the dunes. The sand there may shift several metres back and forth under the influence of alternating seasonal winds and our measurement of relative humidity at − 100 mm at Site 2, therefore, was likely to be representative of conditions within this relatively dry, highly mobile sand. Thus, while the availability of trapped rain water below sand surfaces in other deserts may represent an essential or significant water reserve for insects, it is not likely to be relevant to Namib animals living in the upper reaches of the sand dunes.

At both sites relative humidities varied less at − 100 mm beneath the sand surface than above the surface. The values obtained at Site 2, where rainfall had not recently occurred, were lower than those previously measured by Robinson & Seely (1980) on a slipface at the same site, nine and fifteen months after a regional rainfall of greater than 100 mm. Our measurements, although showing the temporary effects of a recent, unusual shower at Site 1, were taken four years after the last regional rain. At Site 2, for example, only 5,3 mm had fallen in the year preceding our measurements. As annual rainfalls greater than 100 mm are thought to occur at intervals of perhaps forty years in the Namib (Seely & Louw 1980), values reported here for humidity at Site 2 probably are more representative of the area than the somewhat higher values of Robinson & Seely (1980).

We calculated the theoretical vapour pressure differences between the surroundings and a hypothetical beetle (considered to be saturated with water vapour) for conditions prevailing on the surface and − 100 mm below the surface (Figure 4). We assumed the beetle to be at the prevailing temperature of the surroundings, which approximates closely to the real state for beetles below the surface, and for those above the surface but protected from radiation. We found that conditions at − 100 mm were less desiccating overall, than those on the surface, only at the site where the unusual shower had occurred. At the more typical Site 2, the vapour pressure gradient beneath the surface was less desiccating for a beetle than that above surface for only 3 h of the day, around midday. For Site 2, we also calculated the vapour pressure gradient at − 100 mm using a value of 35% for relative humidity, a value appropriate for this site after the 1976 rain (Robinson & Seely 1980). At this higher relative humidity the time at which the vapour pressure gradient was more favourable beneath the surface increased, but only to 9 h.

We also calculated vapour pressure gradients for the case of a beetle above ground and in the sun; we assumed a body temperature of 40°C, a value proposed by Hamilton (1975) as within their preferred temperature range. Such beetles always would be under greater desiccation stress than if they were beneath the surface.

For beetles above the surface, desiccation stress depends not only on the vapour pressure difference but also upon prevailing wind speed. For an animal the size and shape of the beetles, convection, and consequently potential evaporation, is approximately proportional to the square root of wind speed (Mitchell 1972, 1974). Figure 5 shows the desiccation stress for beetles, above the ground at Site 2, when wind speed is taken into account. These calculations show a shift of the curve during the warm part of the day: during the morning activity period, conditions were relatively less desiccating than one would expect from the vapour pressure difference alone.

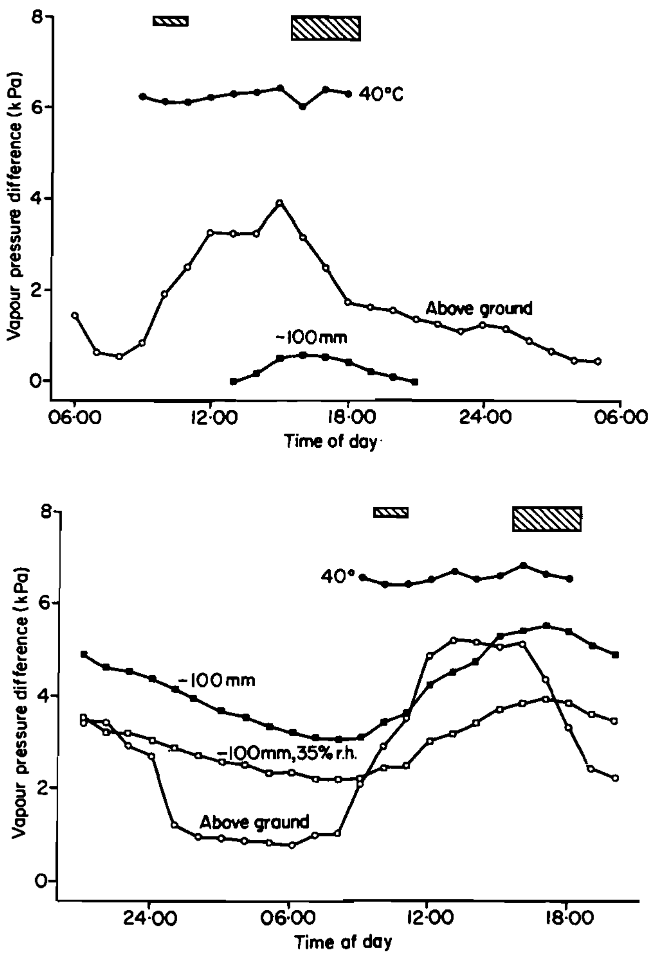

Figure 4 Vapour pressure differences, at Sites 1 (top) and 2 (bottom), between a hypothetical beetle at 100% relative humidity and its surroundings. ○ Above ground, beetle at air temperature; ● above ground, beetle at 40°C; ■ − 100 mm, beetle at sand temperature, prevailing relative humidity; □ − 100 mm, beetle at sand temperature, relative humidity 35%. Minor and major activity periods for dune tenebrionids (from Seely 1983) are shown as bars.

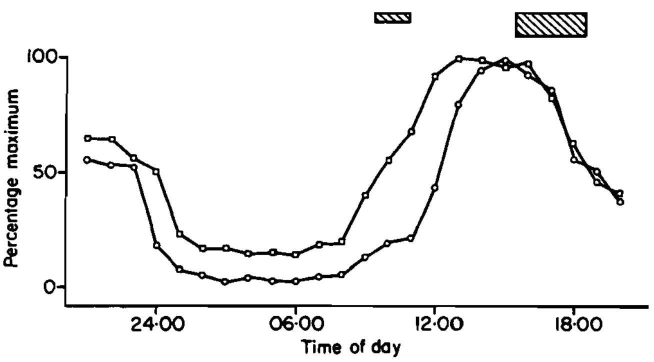

Figure 5 Effect of wind on desiccation stress at Site 2. □ Vapour pressure differences above ground, assuming beetle at air temperature, as % maximum; ○ vapour pressure difference × $V^{0.5}$ as % maximum. Minor and major activity periods for dune tenebrionids (from Seely 1983) are shown as bars.

Several hypotheses, not necessarily mutually exclusive, may account for when Namib Desert beetles (and other animals) are on the surface and when they are below it. (i) Beetles need to minimize desiccation by minimizing the vapour pressure gradient between the animal and its surroundings. We reject this hypothesis. If it were true, then beetles in a typical desert area where there has been no recent rain, would elect to be on the surface throughout the night. Although there are nocturnal species, many Namib tenebrionids are diurnal. Furthermore, if avoidance of desiccation were a factor of major importance, one would expect the morning activity period to be more popular than the afternoon one, because the afternoon wind exacerbates desiccation, and this is not the case (Figure 5). So the behaviour of the beetles is not consistent with the suggestion that avoidance of desiccation is the principle determinant for burying and surfacing. Indeed, the underground environment is not a haven from desiccation, especially at night.

Desiccation, nevertheless, is a problem to the beetles, as to other desert animals. Some adaptation must occur to allow survival, and that adaptation is the presence of a highly impermeable integument (Edney 1968). If an animal has a relatively impermeable integument, the environmental vapour pressure has little effect on body function, and therefore little importance in habitat selection.

(ii) Another hypothesis is that the over-riding factor determining surfacing and burying is the need or advantage of maintaining a body temperature above some critical minimum level. Certain functions, for example egg production, are enhanced at warmer body temperatures (Seely 1983). By digging to an appropriate depth, the beetles could maintain a body temperature in excess of 30°C at all times (Figure 3). Even the preferred body temperature for diurnal Namib beetles of 36°C to 40°C (Hamilton 1975) may be attained by remaining underground, for example from 11h00 to 17h00 at Site 2 (Figure 3b) and from 12h00 to 17h00 at Site 1 (Figure 3a). Yet the beetles did not remain buried at these times. So the equitable temperature always available in the underground environment also is not the most important factor determining whether or not the beetles elect to be there.

We conclude that factors other than temperature and vapour pressure gradients control emergence and burying. Given that such a wide range of temperatures is available underground, and that desiccation underground is not a problem to animals with an impermeable integument, from the standpoint of coping strictly with the physical environment the beetles could spend their entire existence below the surface.

Surface activity is based upon resource acquisition and mating needs (Seely 1983), regardless of temperature or water vapour conditions. These needs may be met over a range of ambient conditions which do not necessarily include only preferred body temperatures. Failure to pursue resources at ambient conditions which result in body temperatures exceeding 40°C implies an inability to function without damage to some system (Hamilton 1973), perhaps because the integument becomes more permeable (Edney 1968; Toolson, White & Glaunsinger 1979; Ahearn 1970) and respiratory water loss becomes appreciable (Edney 1968). It appears that for these insects surface activity is not constrained by ambient conditions if body temperatures can be maintained below 40°C.

Addressing the question of activity and water balance and temperature preferences in a somewhat different way, Slobodchikoff (1983) postulated that activity patterns in tenebrionid beetles may be determined by physiological constraints. He bases this conclusion on the correlation between preferred temperature and water loss rates for nine tenebrionid species measured in the laboratory. Activity at temperatures much above the preferred ones may result in excess water loss, whereas activity much below preferred ones may not be metabolically or behaviourally efficient.

Although the predictions of Slobodchikoff (1983) may also be applicable to Namib tenebrionids, we have, nevertheless, found that activities necessarily confined to the surface take place over the entire and very wide range of ambient temperatures consistent with survival. Vapour pressure differences do not appear to be an important consideration directly influencing the activity of the chthonic tenebrionid beetles of the Namib Desert.

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