

High body temperatures of Namib dune tenebrionids — why?

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The body temperatures assumed by six species of Namib Desert diurnal tenebrionid beetles active on sandy substrates throughout the year were measured in laboratory and field and found to range from 30 to 39°C. Two factors are thought to have led to these high body temperatures: the aseasonality of the Namib environment and the presence of a readily available thermal refuge.

Introduction

When animal adaptation to extreme arid environments is being considered, tenebrionid beetles are often mentioned as examples of well adapted organisms (Cloudsley-Thompson, 1975). If population size is taken as a measure of adaptation, tenebrionids certainly are successful: the adult forms are a conspicuous and numerous component of the desert epigaeic fauna (Crawford, 1981; Koch, 1962). Their thermal biology has been the subject of much speculation and some research; in particular, attention has been directed towards the black colouration of the adults of many desert species (Buxton, 1923; Cloudsley-Thompson, 1979; Hadley, 1979; Hamilton, 1973; Wharton, 1980) and the temperature and water relations of some species (Buxton, 1924; Cloudsley-Thompson, 1975; Edney, 1971*a,b*, 1977). Such attention is not misplaced, for the adults of some species of tenebrionid are relatively long lived (>1 year) (Crawford, 1981, p.123) and most must be active on the surface to forage and mate (Seely, 1983), so they could be exposed repeatedly to environmental extremes. The tenebrionids may choose to escape the extremes: some species are crepuscular or nocturnally active, some are inactive during the hottest and/or the coldest months, and some species shift their surface activity periods between day and night with the seasons (Ahearn, 1971; Cloudsley-Thompson, 1970). In this paper we discuss a group of six closely related adesmine tenebrionids (Penrith, 1975, 1979) that are strictly diurnal and active on the Namib desert surface throughout the year. Although these species adjust their surface activity with daily changes in weather (Hamilton, 1971; Holm & Edney, 1973; Louw & Hamilton, 1972), they are not nocturnal nor do they remain inactive for prolonged periods. We have confirmed the high body temperatures of some Namib tenebrionids previously measured by Edney (1971*a*) and Hamilton (1973) and suggest two interpretations of the high body temperatures of these tenebrionid beetles.

Methods

We have measured the preferred body temperatures (T_b) of Namib tenebrionids (four all-black species and two with 'white' elytra) under laboratory conditions and their mean

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temperatures during activity in the field (Seely *et al.*, in preparation). These species (Table 1) occupy a variety of sandy habitats from vegetationless dune slipfaces and lightly vegetated dunes to dry sandy water courses, their geographical distributions varying from cool coastal to warmer inland habitats.

Table 1. Mean minimum ($n = 19$ or 20), maximum ($n = 10$ or 20) and preferred ($n = 20$) body temperatures ($^{\circ}\text{C} \pm \text{SD}$) of six Namib *adesmine tenebrionids* measured in the laboratory and mean body temperatures ($^{\circ}\text{C} \pm \text{SD}$) ($n = 20$) assumed by free-ranging beetles in the field

Species	Minima	Maxima	Laboratory	Field
Ou	8.9 ± 2.5	48.9 ± 1.0	36.5 ± 2.4	32.2 ± 2.1
Ob	10.7 ± 2.5	48.4 ± 1.2	34.2 ± 3.3	34.4 ± 3.7
Om	9.6 ± 1.7	47.5 ± 1.2	36.9 ± 1.3	34.6 ± 2.4
Op	12.1 ± 3.5	50.6 ± 1.2	38.3 ± 1.5	38.8 ± 3.8
Or	10.2 ± 2.5	50.0 ± 1.6	36.7 ± 1.8	37.0 ± 3.7
Pg	13.6 ± 2.7	50.5 ± 1.5	35.8 ± 1.5	29.9 ± 4.2

Ou, *Onymacris unguicularis*; Ob, *O. bicolor*: occupy dune slipface habitats. Om, *O. marginipennis*; Op, *O. plana*: occupy lightly vegetated sand dunes. Or, *O. rugatipennis*; Pg, *Physadesmia globosa*: occupy dry, sandy vegetated riverbed habitats.

We used fine indwelling thermocouples and a thermocouple thermometer (Bailey Bat 12) to measure the body temperatures of individual beetles continuously in laboratory and field. In the laboratory individual body temperatures were measured for 6 hours in a circular thermal gradient (after Kramm & Kramm, 1972). To obtain the field measurements, an extension of the indwelling thermocouple wire was passed through the eyes of a fishing pole 2 m long. The beetle could thus move unhindered and undisturbed as temperatures were recorded at a distance from the free-ranging individual. The only body temperatures used for analysis were those recorded from individuals that remained voluntarily active on the sand surface for at least 10 min during periods when a large proportion of the local population of that species was also active.

Concomitant environmental temperatures were recorded in the field on a data logger (Campbell CR-21) with attached thermistor probes. These values included hourly mean values of air temperature (T_a), soil surface temperature (T_s), and black bulb or globe temperature (T_{bb}).

Although there is good reason to measure T_{bb} routinely in field studies of thermal biology (see Results), it is seldom reported. To compare our observations with some made in other deserts, we used a regression technique to estimate T_{bb} from T_a . T_{bb} is a function of T_a , wind speed and radiation intensity (Yaglou, 1949); in desert conditions, theory predicts that T_{bb} should be a rough linear function of T_a . Data for 5 winter days and 5 summer days give $T_{bb} = 0.87 T_a + 9.1$ ($r = 0.969$) for the intervals when the subject species were active. We used this equation to estimate maximum T_{bb} temperature at Gobabeb ($23^{\circ} 34' \text{S}$, $15^{\circ} 03' \text{E}$) in the Namib Desert and Phoenix, Arizona (33°N , 112°W) in the Sonoran Desert (from Strahler, 1973, p. 181). Assuming that minimum T_a values were recorded at night, when $T_a \approx T_{bb}$ in the desert, we took minimum T_a values as an approximation of minimum values of T_{bb} .

Results

Mean body temperatures of the six closely-related species of tenebrionid measured directly with indwelling thermocouples ranged from 34.2 to 38.3°C in the laboratory and from 29.9 to 38.8°C in the field (Table 1). We calculated, for four species, the difference

between values of Tb measured in the field and the concomitantly measured values of Tbb. The values of Tb paralleled, and were slightly below those of Tbb: the difference between Tbb and Tb was $+0.55 \pm 0.32^{\circ}\text{C}$ (mean \pm SE, $n = 80$); i.e. microclimate variables influenced the beetles in much the same way that they influenced the standard globe thermometers and Tbb could be used as an estimate of Tb. Tbb has been used previously as an approximation for body temperatures (Clarke, 1967; Wellington, 1949). For a different model predicting Tb from environmental measures see Kenagy & Stevenson (1982).

Maximum and minimum Tbb for summer and winter were estimated for Gobabeb and Phoenix (Table 2). Maximum Tbb was calculated from maximum Ta using the regression equation above, and minimum Tbb was taken to be the same as minimum Ta. These values approximate the maximum and minimum temperatures the beetles could attain in the field. Beetles at both locations may experience a large circadian variation in temperature ($20\text{--}25^{\circ}\text{C}$) in both summer and winter if they remained on the surface (Table 2). Summer temperatures of black bulbs and beetles at Phoenix would be almost 10°C higher than those at Gobabeb, and winter body temperatures 10°C lower.

Table 2. *Estimated mean maximum and mean minimum black bulb (Tbb) temperatures ($^{\circ}\text{C}$) in summer and winter (January and July) at locations in the Sonoran and Namib Deserts*

	Summer	Winter	Difference
Phoenix			
maxima	44.5	25.5	19.0
minima	23.3	0.5	22.8
Gobabeb			
maxima	37.3	35.4	1.9
minima	15.6	11.4	4.2

Discussion

Although it is generally accepted that surface activity of desert tenebrionids is adjusted to either avoid extreme, and sometimes potentially lethal, conditions (Holm & Edney, 1973), or to actively regulate temperature (Hamilton, 1971, 1973), few measurements have been made of actual body temperatures of tenebrionid beetles in the field. Such measurements usually have been obtained from individuals fitted with indwelling thermocouples and tethered in locations selected by the investigator (Edney, 1971a), maintained in enclosures (Hadley, 1970), from dead beetles (Edney, 1971a), or are single measurements from free-ranging individuals obtained by 'grab and stab' methods (Hamilton, 1975; Henwood, 1975; Nicolson *et al.*, 1984). In the laboratory, maximum, minimum and preferred body temperatures of desert tenebrionids have been recorded (Cloudsley-Thompson, 1962; Edney, 1971a; El Rayah, 1970; Hamilton, 1973; Kramm & Kramm, 1972; Slobodchikoff, 1983), and in the field measurements have been made of the microclimatic conditions under which beetles are active (Ahearn, 1971; Hadley 1970; Hamilton, 1971; Henwood, 1975; Holm & Edney, 1973; Kramm & Kramm, 1972). The results of these various studies indicate that maximum tolerated temperatures range from $C. 43$ to 53°C for beetles from a variety of deserts.

Preferred temperatures selected in the laboratory by nine North American tenebrionid species inhabiting arid and subarid habitats ranged from 21 to 28°C (Slobodchikoff, 1983), and those of tenebrionids found in the coastal dunes of California ranged from 15 to 20°C

(Doyen & Slobodchikoff, 1984). Two species of *Eleodes* inhabiting a desert environment in California preferred body temperatures of 15.5°C and 17.6°C and were active in the field at environmental temperatures between 12 and 28°C (Kramm & Kramm, 1972); six species of tenebrionid beetle inhabiting the arid shrub steppe of eastern Washington preferred body temperatures between 7.0 and 32.7°C (mean 20.4°C of 225 'grab and stab' measurements) and were active in the field at a slightly broader range of environmental temperatures (Kenagy & Stevenson, 1982). In contrast are the temperature preferences of tenebrionid beetles from unspecified habitats in the deserts of northern Africa. *Pimela grandis*, a nocturnal beetle, has a preferred temperature of 28–34°C, slightly lower than that of *Adesmia antiqua*, a diurnal beetle, whose preferred temperature is 34–38°C (El Rayah, 1970). In the Namib Desert, body temperatures of free-ranging tenebrionids, varying between 21.5 and 43.8°C, have been recorded using 'grab and stab' techniques (Hamilton, 1973; Henwood, 1975; Nicolson *et al.*, 1984). Thus, in literature there is considerable variation in temperatures measured in the laboratory and in the field, and preferred temperatures do not approach the high lethal temperatures of the beetles.

The body temperatures we obtained from field measurements (Table 1) were as high as most recorded for desert tenebrionids, although somewhat lower than those recorded for some of the same species by Hamilton (1973) using 'grab and stab' methods in the field. To explain the unusually high temperatures of Namib tenebrionids, Hamilton (1973) invoked his 'maxi-thermy' hypothesis, which suggests that high temperatures are sustained because they lead to increased rates of many biological processes, and are therefore advantageous. We shall present an alternative explanation, based upon consideration of the nature of the desert environment.

Desert environments in general are characterized by high levels of solar radiation. As a result, small diurnal animals, with a relatively low thermal inertia, easily attain a body temperature (T_b) above that of the surrounding air (T_a) (Heath, 1964). In contrast, options for lowering T_b below T_a are limited. Heinrich (1974) has suggested that many invertebrate species regulate their body temperature at a high level simply because the heat transfer situation is conducive to maintaining a relatively stable high body temperature but not a stable low body temperature. Such an argument would apply equally well to non-regulators in deserts, where body temperature is determined by passive heat transfer.

For desert tenebrionids, the preferred range of body temperature may be less than 10°C, whereas the tolerated range (maximum – minimum) often is greater than 30°C (El Rayah, 1970; our Table 1). Moreover, preferred temperatures for most of the species examined are in the upper half of the tolerated range. Why this should be the case, in view of the great daily range of temperatures available in deserts (Strahler, 1973), has not been explained fully and only Hamilton (1973) has put forward a potential explanation. Heinrich (1977), in the context of endothermy has proposed that enzyme specialization, coupled with inability rapidly to dissipate heat produced as a by-product of high activity rates, accounts for the relatively high, stable temperatures at which endothermic animals thermoregulate. This proposition may apply equally well to diurnal ectotherms with high preferred body temperatures.

These arguments do not predict why the preferred body temperatures of Namib Desert tenebrionids are so much higher than those measured for beetles inhabiting other deserts. This question is even more intriguing when one considers that the preferred temperatures of at least some species in another group of desert organisms with relatively low thermal inertia, namely lizards, are equally high in all deserts in which they have been measured (Mayhew, 1968). We propose that, for some Namib dune tenebrionids, preferred temperatures are high because such temperatures lie within the range of temperatures easily attainable by small, diurnal ectotherms for the longest period of time during the course of a year and that they are sustainable because a thermal refugium is always readily available.

Our hypothesis rests on two characteristics of the thermal environment of the Namib dunes: its relative constancy and the availability of thermal refugia. The Namib climate shows remarkably little seasonality. The difference between the monthly mean air

temperature of the three warmest months (summer) and that of the three coolest months (winter) ranges from 4.2°C on the coast to 6.2°C 100 km inland (Lancaster *et al.*, 1984). This difference contrasts, for example, with the Sonoran and Mojave deserts, where the difference between summer and winter mean temperature at six sites ranges from 8.6°C (Vizcaino — a coastal desert) to 20.2°C (Mojave) (Turner & Brown, 1982). The consequences for beetle temperature of the relative constancy of the Namib thermal environment are evident in the striking difference between potential body temperatures attainable in the Namib at Gobabeb and in the Sonoran at Phoenix (Table 2). In the Namib, estimated mean monthly Tbb is always within the range of preferred Tb and varies by only 2°C , whereas in the Sonoran, mean summer Tbb is above the range of preferred Tb of beetles in any desert, and mean winter Tbb values are 19°C lower (Table 2). The second characteristic of the Namib dune environment, the thermal refugium, derives from its sandy substrate. The fine fluid sand, through which many species of Namib animal 'swim' without the benefit of constructed burrows (Coineau *et al.*, 1982), contrasts with other desert substrates, in which refuge from the surface extremes may require the animal first to locate a stone upon which to stilt (Henwood, 1975), or a plant or crevice or hole in the ground into which to retreat (Casey, 1981; Willmer, 1982). Within a sandy habitat,

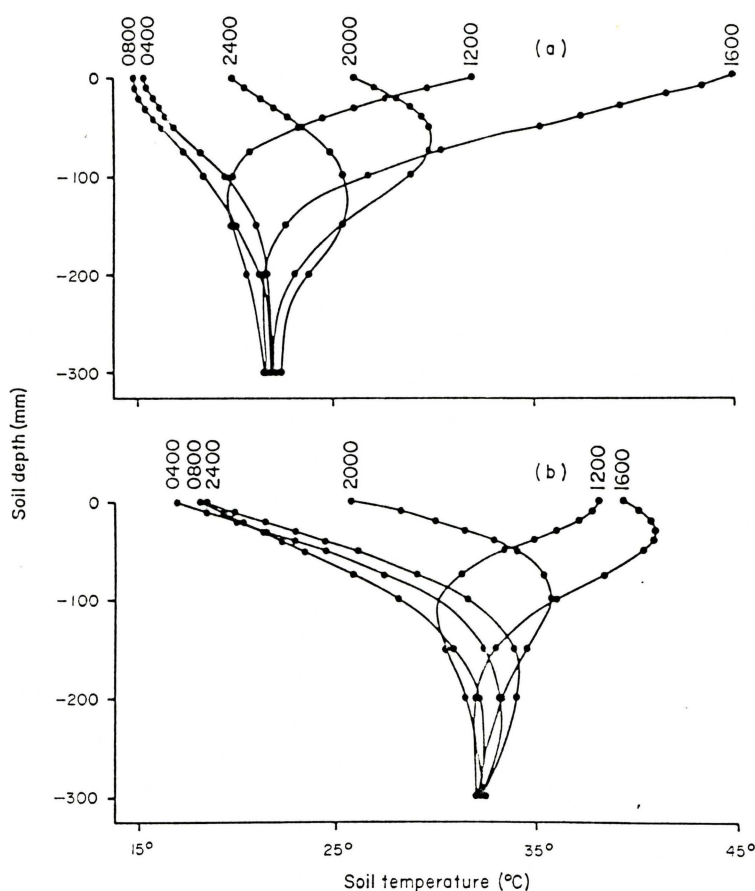


Figure 1. Temperature of subsurface sand (0 to -300 mm) in winter (a) and summer (b) at four-hourly intervals on a slipface in the Namib Desert. Temperature at -300 mm varied between 22 and 32°C .

nevertheless, there is a difference in the degree of compaction of sand at different locations, which may have thermal consequences (e.g. Louw & Seely, 1982, p. 64). Whereas escape is virtually instantaneous on the mobile slipfaces, the compaction of sand on the dune base increases the transit time of the beetle through sand which could induce lethal to near-lethal temperatures. Once below the sand surface, however, a range of moderate temperatures is available at all times of the day and year (Fig. 1). Annual temperature variations below the sand surface in the Namib (c. 10°C at -300 mm) are less extreme than those in other deserts (e.g. c. 35°C at -300 mm in the Colorado Desert; Edney, 1974).

Thus Namib beetles on a sand surface can allow their temperatures to approach near-lethal levels, because refuge and recovery are available instantaneously: behaviour which is a viable proposition in the dune environment may not be acceptable in other habitats. Advantages which might be conferred by familiarity in a more heterogeneous environment play no role, as a thermal refuge is available almost anywhere on a sand dune (e.g. Chelazzi & Calzolari, 1986). The subsurface refugium has one great disadvantage, however, in that activity is severely restricted beneath the sand surface. In contrast, a plant offers degrees of protection from solar radiation ranging from dappled to dense shade, from which animals can select or between which they can 'shuttle' back and forth (Casey, 1981); in either circumstance, they remain alert and continue at least some activity.

Actual body temperatures preferred by animals in differing habitats may also be influenced by the qualitative differences of potential thermal refugia (Fig. 2). Let us assume that, whatever the absolute preferred T_b values are, they extend over a similar temperature span. In a situation where a thermal refuge is available instantaneously, but which leads to total inactivity, the beetles may benefit from selecting high body temperatures. This pattern would allow them to forage most effectively when on the surface. In contrast, where a thermal refuge permits some activity, such as in the variable shade of a plant, a lower preferred temperature would allow a longer activity period. Total foraging time would be that spent in the full sun plus that time spent alert, but in the shade of a partial thermal refuge (Fig. 2). The model assumes that in each habitat the organism in question has a similar range (10°C) of temperature over which it can be fully active, and the potential for a similar total of effective foraging (function of temperature and activity). On the sand dune (Fig. 2.1) the organism has the choice of either being active above the surface or inactive beneath the sand. For example, anywhere between 28°C and 38°C the animal may

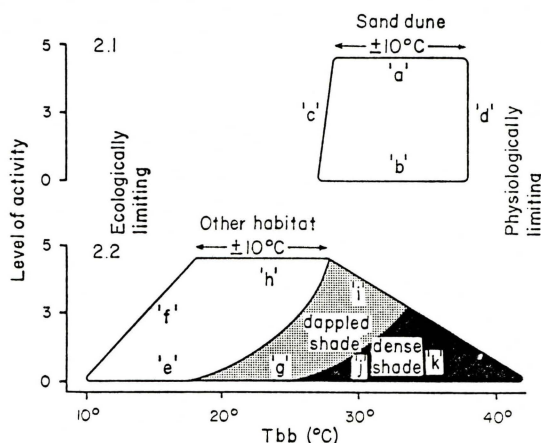


Figure 2. Conceptual model of an 'activity space' representing potential levels of activity that could be sustained at various temperatures on a sand dune slipface (2.1), where thermal refuge is at hand, and in a non-dune habitat (2.2) where topographic heterogeneity ensures a source of shade.

be on the surface at any level of activity between fully active (*a*) and inactive (*b*). Below this range (*c*), slower reaction times would leave the fully exposed animal subject to potential predation. Above this range temperatures are potentially lethal (*d*). This animal could remain active until it escaped below the sand surface. In the presence of shade (Fig. 2.2) the organism has the choice of being fully active in the sun, partially active in dappled shade or even less active in deep shade. Thus, at 15°C the animal may be inactive (*e*) to partially active (*f*) as it is warming up, perhaps at the mouth of its burrow. At 25°C it may be partially active in dappled shade (*g*), which provides some predator protection, or more active to fully active in the sun (*h*). At 30°C it requires the protection, from radiation afforded by dappled shade (*i*), where it has potential for some activity, or dense shade (*j*), where its activity is more restricted. Above 35°C it can maintain only minimal activity in dense shade (*k*). Although resource use may be more rapid at higher temperatures, this animal can extend its total time of activity over that available to the animal in the dune habitat, by foraging at lower temperatures in the full sun and then continuing to forage, at a somewhat reduced rate, as temperatures increase. Should this animal have the same range of temperature for full activity as the one living in the dune habitat, it would, of necessity, waste time at the upper end of this range searching for a thermal refuge and run the risk of not reaching one as its critical thermal maximum was approached.

According to this argument, qualitative aspects of the refugium offered by a sand dune could have led to the high preferred body temperatures of Namib dune tenebrionids.

In general, the ability to withstand high body temperatures is thought to be characteristic of desert animals (Cloudsley-Thompson, 1970; Edney, 1971*a*). Although the thermal characteristics of the environment are perhaps the proximate influence on the temperatures preferred and the behaviour patterns observed, other environmental factors, such as rainfall, productivity (e.g. Kenagy & Stevenson, 1982), and wind, undoubtedly play a role. Moreover, throughout this paper we have discussed body temperatures of adult tenebrionids whereas the tolerated or preferred temperatures of the egg or larval stage may have a great influence on the overall thermal biology of a species. The high preferred body temperatures of the Namib dune tenebrionids may therefore be influenced by both these additional considerations as they too are related to the aseasonality of the environment as it affects the surface and subsurface dune environment.

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