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Body temperatures of Namib Desert tenebrionid beetles: their relationship in laboratory and field

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ABSTRACT. The body temperatures of six apterous species of Namib Desert tenebrionid beetles were measured continuously with indwelling thermocouples under laboratory conditions and in the field. The range of body temperatures selected was within the upper half of their 'tolerated range', which we defined as the temperatures lying between measured critical thermal maximum and critical thermal minimum. In the field, individuals also maintained their body temperatures within the upper half of the 'tolerated range'. These beetles maintained higher body temperatures than those recorded for any other ectothermic insect. Three of the six species maintained lower body temperatures in the field than they selected in the laboratory. The other three species showed no significant difference between field and laboratory body temperatures. We conclude that these beetles are not forced by biotic or abiotic factors to adopt thermal niches which present them with physiological difficulties.

Key words. High body temperatures, desert beetles, Tenebrionidae.

Introduction

Many deserts are characterized by low rainfall, low productivity and highly variable temperatures. Despite these seemingly adverse conditions, they are inhabited by a diverse biota of small diurnal ectotherms, of which tenebrionid beetles (Tenebrionidae) form a conspicuous component (Seely et al., 1988; Parmenter et al., 1989). The environmental temperatures at which these beetles are active and their body temperatures during surface activity have received considerable attention (Slobodchikoff, 1983; Seely et al., 1988; Parmenter et al., 1989). By behavioural means they adjust to the continual temporal and spatial variation of their thermal environment (Hamilton, 1971; Seely, 1979). Physiological and morphological adaptations also affect their temperature relationships (Hamilton, 1973, 1975). What is less clear is whether they are attempting to regulate their temperature to some selected level or are simply avoiding extremes and accepting a range of body temperatures during surface activity related to acquisition of required resources. This is the primary question which we address in this paper.

We report here the results of continuous measurement with indwelling thermocouples of body temperatures of the adults of six species of Namib Desert tenebrionid beetles under laboratory conditions and in the field. All six are long-lived species, diurnal and active throughout the year. They occupy sandy habitats ranging from dune slipfaces to sandy, dry riverine water courses and dry flood plains. Earlier observations of the thermal environment and body temperatures of some of the same species have indicated that: they vary between unimodal and bimodal activity periods depending on environmental temperatures; different species occupy different habitats in a manner that appears to be at least partially related to the thermal characteristics of the habitats; a variety of morphological adaptations appear to be related to body temperature; the body temperatures of several species in the field appear to be among the highest measured for tenebrionid beetles and, indeed, for any ectotherm (Hamilton, 1973). This finding has led to the 'maxithermy hypothesis' (Hamilton, 1973) as an explanation for the apparent regulation of high temperatures.

Materials and methods

Study animals

Tolerated and selected temperatures of six species of apterous adesmine tenebrionid beetles (Table 1) from the Namib desert were measured. These species were: *Physadesmia globosa* (Haag), *Onymacris rugatipennis rugatipennis* (Haag), *O. plana* (Peringuey), *O. unguicularis* (Haag), *O. marginipennis* (Breme), and *O. bicolor* (Haag). These beetles were chosen to represent a wide variety of morphologies and habits among the larger adesmine tenebrionids in the Namib, and because they are found in habitats ranging from the coast to the eastern edge of the Namib (Fig. 1).

Twenty beetles of each species were used in the laboratory experiments. They were collected from the field, placed in terraria on sand, with a diet of rolled oats, fresh cabbage and apple. The beetles were maintained in environmental conditions close to those prevailing in the ambient environment. All temperature measurements were taken within 30 days of removal from the field; different individuals were used for each measurement.

Body temperature measurements

It has been common in studies of insect thermoregulation to use 'grab and stab' methods to measure body temperature (e.g. Hamilton, 1971; Kenagy & Stevenson, 1982; Nicolson et al., 1984). However, these methods can lead to considerable measurement errors (Stone & Willmer, 1989). We measured body temperature (T_b) continually using indwelling copper-constantan thermocouples (40 gauge) implanted 2-3 mm to the right of the midline in the pro-thorax of an individual beetle. The wire was inserted to a depth of 2-3 mm into the thoracic musculature and secured by a small drop of cyanoacrylate adhesive (Pattex® superglue) or acrylic dental cement (de Trey's Rapid Repair Material). The thermocouple wire was supported from above, leaving locomotion relatively unimpeded. Following measurement, the wire was removed and the beetle released. Thermocouples were connected to a Bailey Bat 4 temperature recorder in the laboratory and Bailey Bat 12 in the field. The thermocouples were calibrated against a standard mercury thermometer with an accuracy of ±0.1°C.

Tolerated temperature range

The Critical Thermal Minimum (CTmin) was defined as the lowest body temperature at which a beetle, placed on its back, could right itself. This was determined using a square glass container (with a 30 mm layer of sand) standing in a bath of ice. One beetle, into which a thermocouple had been fitted, together with 10 other beetles of the same species, sex and size, was placed in the container on the layer of sand. After equilibration, the T_b of the beetle with the thermocouple was assumed to be the same as that of the other beetles in the beaker. When T_b was reduced to less than 5°C, the beetles were turned on to their backs using forceps. After confirmation that the beetles were unable to right themselves at that temperature, the container was removed from the ice bath to room temperature (± 25°C). As each beetle righted itself (as container temperature increased), the T_b of the beetle with the thermocouple was recorded and taken as the CTmin of the righted individual. CTmin was determined for 10 males and 10 females of each species.

The Critical Thermal Maximum (CTmax) was defined as that temperature at which a beetle lost muscular coordination. To measure this temperature a 3-l Pyrex beaker was used as a heating chamber. On top of a 1 cm layer of sand a sheet of cardboard was fitted, to prevent burrowing of the beetle. The beaker was placed in a larger container of water to a level well above the sand layer. The beaker was covered with glass and the surrounding water temperature heated at ±0.6°C per min. CTmax was determined for 10 males and 10 females of each species. A single beetle was fitted with a thermocouple and placed into one of the chambers. The T_b of the beetle was allowed to equilibrate and then the container of water was slowly heated. Temperature and coordination of the beetle was recorded at 2 min intervals. When the beetle lost muscular coordination (unable to right itself when turned over), T_b was recorded and the beetle removed from the chamber.

Selected temperature

Temperature preferences were measured in the laboratory using a circular temperature gradient modified from that described by Kramm & Kramm (1972) in a 100 mm wide circular, metal trough with an outside diameter of 1 m. The temperature gradient, ranging from about 28-44°C, was established using a counter-current heat exchange system with hot and cold water running through adjacent copper tubes lining the floor of the trough. The tubes were covered with about 10 mm of sand. If at any time the beetle was found at either extreme of the gradient for more than 5 min, the range of temperatures was shifted until this behaviour was terminated. Sand-surface temperatures at the extremes of the gradient were measured at half-hourly intervals using 26 gauge copper-constantan thermocouples connected through a switchbox to a thermocouple thermometer (Bailey Bat-12). This gradient apparatus had several advantages: cornering by the beetle was prevented; the temperature gradient could be adjusted at any time; and the conductant heat source prevented confusion from phototaxic responses (evenly-dispersed lighting was provided by fluorescent tubes directly above the gradient).

Prior to measurement, the beetles were observed and an individual seen active and eating was selected for the day's trial. After the thermocouple had been implanted, the beetle was placed into the apparatus while the gradient was being established 30-60 min before measurements began. During the trial, beetle T_b was recorded at intervals of 2 s, and averaged over 5 min, using a Bailey Bat-4 and YSI model 80 recorder. Activity was monitored and the trial terminated if the beetle persisted in attempting to bury into the sand. Ten males and 10 females of each species were tested in the gradient, individually, for 6 h each. The 5 min average values were used to calculate a mean value for each individual. These individual mean values for 10 males and 10 females were then used to calculate a mean value for the species (known hereafter as selected T_b).

Field body temperature

The T_bs of surface-active beetles in the field were measured using implanted thermocouples. The beetle, with indwelling thermocouple, was placed on the sandy substratum at the same time and in the same place that a population of beetles of the same species was active. The beetle was allowed a short acclimation period before measurements were initiated. To avoid interference from the experimenters on the beetle's behaviour, the fine thermocouple wire inserted into the beetle (40 gauge, about 1 m long) was connected to more robust thermocouple wire (26 gauge) which was then threaded through the eyes of a 2 m fishing pole. T_b and behaviour were recorded at 30 s intervals. The duration of the trials varied; the longest period of activity was 40 min. Only measurements from individuals continuously active on the surface for more than 5 min were included in the analyses. Body temperatures of 10 males and 10 females of each species were measured. The temperature values measured at 30 s intervals were used to calculate a mean temperature for each individual from which values for the species were determined. Measurements on each species covered the entire range of the beetles' activity periods (08h00 - 19h00).

Environmental temperature was measured hourly with a black-bulb, or globe, thermometer (hereafter known as T_{bb}). T_{bb} is a function of ambient temperature, wind speed and radiation intensity (Yaglou 1949). The large volume of this thermometer (diameter = 15 cm) causes a large time constant and, thus, temperature is integrated over a long period of time. As a result, hourly instantaneous temperature measurements provide a realistic environmental temperature (Seely et al., 1988).

Statistics for comparisons of selected and field body temperatures

Kruskal-Wallis non-parametric analyses of variance were run for mean selected T_b values for all six species. Non-parametric techniques were used here because of the skewed distribution of these data (towards higher T_bs). Square-root and logarithmic transformations of the data (to use in parametric tests) proved inadequate. Mean values for each individual were used in order to avoid the 'pooling fallacy' (Machlis et al. 1985), i.e. where a single individual contributes more than one observation to the data set. In addition, the proportion of time that T_b fell within 1°C classes from 20-40°C was compared among sexes and species for laboratory and field T_b measurements using Kolmogorov-Smirnov two-sample tests. This test has greater power-efficiency than comparable Wilcoxon, Chi-square and median tests (Siegel & Castellan, 1989). The Kolmogorov-Smirnov test is effective for comparing data such as these, allowing comparison over the range of body temperatures selected. Comparisons of mean field T_bs were made using analyses of covariance (ANCOVA), using black bulb temperature as the covariate. ANCOVA's were used to account for differences in environmental temperatures among sampling periods. Comparisons of CTmin and CTmax were made with conventional ANOVA techniques because these data were normally distributed.

Results

Critical thermal temperatures

The tolerated range of body temperatures (CTmax-CTmin) was 37.3-40.0°C (Fig. 2). Although the differences among the tolerated ranges for the six species were not large, they were significant in some instances (Table 2). The values of CTmax and CTmin for Onymacris plana and Physadesmia globosa were higher than those of the other four species, significantly so in 11 of 16 instances. There was no clear pattern for the order of values for the remaining species.

For individuals active in the field, the highest measurement of body temperature voluntarily attained by an individual was 50°C (Onymacris plana) and the lowest was 23°C (Physadesmia globosa). In the laboratory, the highest temperature voluntarily attained was 46°C (O. unguicularis) and the lowest was 22°C (O. bicolor). Even the lowest body temperatures measured in the laboratory or during activity in the field did not extend far into the lower half of their tolerated range (Fig. 2).

Selected and field body temperatures

A 3-way ANOVA indicated that there was no significant difference ($P > 0.05$) between sexes in mean selected or field T_b, thus values for both sexes were combined in all further analyses.

The mean selected body temperatures of the six species, determined in the circular temperature gradient, varied from 34.2-38.3°C (Fig. 2). The only significant interspecific differences in selected T_b were between O. plana and O. bicolor (Kruskal-Wallis tests, $P < 0.05$). Comparisons among species of the proportion of time that selected T_b fell within 1°C classes (Kolmogorov-Smirnov tests) showed that O. plana had higher T_bs than the other species (Table 3a). By this test, no other interspecific comparisons were significant ($P > 0.05$) for selected T_b.

For field T_b, only O. bicolor and O. marginipennis did not differ significantly from one another (Kruskal-Wallis tests, Fig. 3). All other interspecific comparisons were significant (Kruskal-Wallis tests, $P < 0.05$). O. plana had the highest field T_b and P. globosa the lowest. However, comparisons among species of the proportion of time that selected T_b fell within 1°C classes (Kolmogorov-Smirnov tests) showed that only O. plana and P. globosa were significantly different from one another (Table 3b).

Four of the six species showed significant differences between field and laboratory T_b (Table 3c, Fig. 4a-f).

Relationships between field T_b and environmental variables

The relationship between T_{bb} and T_b was examined for all six species (Table 4). T_b of three of the species, O. plana, O. bicolor, and O. unguicularis, showed significant positive correlations with black bulb temperature (T_{bb}). O. bicolor had a significantly steeper slope than O. plana ($t=2.16$, $p<0.05$) and O. unguicularis ($t=2.53$, $p<0.05$). There was no significant difference between the slopes of the regressions for O. plana and O. unguicularis ($t=0.72$, $p>0.05$). The latter two species had lower slopes than O. bicolor. All three species had slopes of regression lines less than 1.

For the three other species, O. marginipennis, O. rugatipennis and P. globosa, there was no significant correlation between T_b and T_{bb} ($P>0.05$). This lack of correlation with environmental temperature is not an indication of endothermy, however, but rather a result of moving in and out of the shade of vegetation (all environmental measurements were made in direct sunlight).

Discussion

Range of body temperatures

Our measurements of high body temperatures, in laboratory and field, confirm similar results for the same and related species of adesmine tenebrionids by previous authors (Hamilton 1975, Seely et al. 1988). For all species, mean body temperatures measured were in the upper half of their tolerated range in laboratory and field.

It is interesting that, while two species showed no difference between selected and field T_b, the other four species had lower T_bs in the field than selected in the laboratory. Thus, there is no evidence that these beetles are being forced by some environmental factor (biotic or abiotic) to select higher field T_bs than they select in the laboratory.

The wide range of tolerated temperatures which we measured may possibly be explained, at least in part, by the fog-water uptake behaviour of two of these species (O. bicolor, O. unguicularis). Precipitating advective fogs in the Namib desert occur most commonly in the pre-dawn hours at temperatures ranging from about 0-20°C (Seely, 1979). In order to take advantage of fog-water as a moisture source, tenebrionids must be active at these times and temperatures, under conditions which are quite different from those experienced during foraging and other surface activities. Minimum activity necessary to obtain fog-water consists of emerging from beneath the sand surface, slowly moving across the sand surface to orient on a dune, and returning beneath the surface when the fog lifts (Seely, 1979). Although O. bicolor and O. unguicularis may be active during fogs at temperatures below their CTmin determined under laboratory conditions (Seely, 1979), only occasionally have we observed uncoordinated beetles unable to right themselves after being blown over by a fog wind.

Why selected T_b and T_b of surface activity were found to be in the upper part of their tolerated ranges is perhaps less easy to explain. One possibility, as suggested by Heinrich (1977) for endothermic flying insects and by Seely et al. (1988) for the species in the present study, is that, while it is relatively easy for small diurnal invertebrates to maintain temperatures higher than ambient, it is very difficult for them to attain temperatures lower than ambient.

Body temperatures and microhabitats

The study species are found in three major habitats of the sandy part of the desert: the vegetationless dune slipfaces, sparsely-vegetated dune plinths and the dry, sandy riparian woodland of the Kuiseb River (see Table 1). Three of the species are restricted to the cooler, coastal half of the desert, whereas the other three also occur further inland (see Fig. 1). The mean body temperature of O. plana, which occurs throughout the sand sea wherever some vegetation is found, was higher than that of all other species in both the laboratory and the field. We argue that, despite the sparse vegetation which occurs in its habitat, O. plana is exposed to some of the most extreme temperatures in the dune habitat (Seely et al., 1988). Certainly, of all the species investigated, it is the only one which develops a waxy bloom, thought to be an adaptation for prevention of water loss under conditions of high ambient temperature and low humidity (McClain et al., 1985). In the field, O. rugatipennis attained significantly higher T_bs than all species except O. plana (Kruskal-Wallis test). O. rugatipennis occupies the sparsely-vegetated, sandy courses of the usually dry riverine habitat; it is never far from a thermal refuge and its high body temperatures were not expected. The area between the thermal refuges, however, has been shown to be one of the more extreme in the Namib for thermophilic ants because of its sheltered position protected from the cooling winds (Marsh, 1985). Thus, O. rugatipennis may attain high T_bs when travelling or feeding in these open areas.

Parmenter et al. (1989) have shown that tenebrionid beetles of the genus Eleodes in the deserts of the southwestern United States have a high correlation between mean field T_b and mean annual environmental temperature. This was not the case in our study: O. marginipennis occupies the coolest, coastal habitat, yet O. unguicularis has a lower mean T_b; O. plana and O. rugatipennis occupy similarly hot habitats, yet O. plana has a significantly higher T_b than O. rugatipennis; and O. rugatipennis and P. globosa are syntopic in the riverine habitat, yet P. globosa has the lowest T_b of all species measured here and O. rugatipennis one of the highest.

However, the differences between species recorded in the above three points may be due, in part, to the statistical comparison we used. Unlike the Kruskal-Wallis tests, Kolmogorov-Smirnov tests revealed that O. plana had significantly higher selected T_bs than all other species. We suggest that the Kolmogorov-Smirnov tests provide a more realistic comparison of T_b because the frequencies of temperatures over the entire range are compared. Given this proviso, we find that the only significant interspecific differences in field T_bs are between P. globosa and O. plana, which occupy the most shaded and most exposed habitats, respectively. Nonetheless, there is little evidence to suggest that body temperatures of these beetles are related to environmental temperatures in their habitats at large.

The relationship of T_b with T_{bb} varied among species. The three species for which there was no significant correlation move out into the sun to feed in the morning peak of activity but then spend the rest of the day in the shade (personal observations, Ferguson, 1989). As a result, the measured environmental temperatures are not always those experienced by the beetles.

The regression slopes for T_b versus T_{bb} for all three species for which they could be derived were <1 (range = 0.32-0.93). This should, however, not be regarded as an indication of endothermy (Stone & Willmer, 1989). This is probably due to behavioural adjustment of T_b, for example by keeping contact with warm sand when air temperatures are low in order to raise T_b. The reasons for behavioural adjustment of T_b and the significant differences among some species in the slope of the regression of T_b and T_{bb}, are not known and bear further investigation.

<u>Phylogenetic constraints</u>

Kenagy & Stevenson (1982) have summarized the available data on beetle body temperatures, and show that only endothermic, flying beetles have higher T_bs than the flightless, ectothermic African tenebrionids. Even the North American desert tenebrionids (genus <u>Eleodes</u>) studied by Slobodchikoff (1983) and Parmenter <u>et al.</u> (1989) had far lower selected temperatures than the Namib species (range of mean selected T_b = 21-28°C). The lower T_bs recorded in all non-Namib species are probably even more marked if one considers that all the other T_bs were obtained with 'grab and stab' methods, which are known to give spuriously high T_b values for endothermic insects which warm up during the interval between grabbing and stabbing (Stone & Willmer 1989). The extent of this error may be lessened for ectothermic insects such as tenebrionid beetles, although erroneously high T_b values are often recorded (Seely et al., 1988). The only similar T_bs to those of the Namib tenebrionids we studied are those of North African tenebrionids (28-38°C; Cloudsley-Thompson, 1962; El-Rayah, 1970), also measured with 'grab and stab' methods.

Why do the African species have such high body temperatures ? The mean maximum temperatures obtained in the Namib desert are lower than those in the North American Sonoran desert for example, and the annnual range in temperature is less (Seely et al., 1988). However, the Panamanian beetles (non-tenebrionids) studied by Bartholomew & Casey (1977) experience less variation in annual temperatures than Namib tenebrionids, yet they have lower T_bs. This suggests that there may be some phylogenetic constraint on body temperature that allows the African beetles to function at high ambient temperatures.

In the absence of support for Hamilton's (1973) adaptive 'maxithermy hypothesis' (i.e. that high body temperatures have evolved to maximize metabolic rate and, thus, energetic efficiency) (Heinrich, 1977; Seely et al., 1988; Ward, in press), and in view of the relatively small differences in T_b among species in spite of large differences in environmental characteristics, phylogenetic inertia may be a useful alternative hypothesis. The most recent phylogenetic treatment of the genus Onymacris (Atmore, 1985), suggests that O. plana and O. rugatipennis share a more recent common ancestor than with any other species measured here. These two species are more similar to one another in T_b than to any other species. Similarly, P. globosa differs considerably from all the other species in T_b and is only distantly related to Onymacris. Also, O. marginipennis and O. bicolor are more similar to one another in T_b than either is to O. unguicularis. The two former species share a more recent common ancestor than either does with O. unguicularis. Thus, the phylogenetic argument that closely-related species will be similar in T_b is supported by these data. However, in the only study that has thus far considered the phylogenetic constraint option, Slobodchikoff (1983) found that congeneric tenebrionid species in the Sonoran desert were, in all but one case, more different in their ecophysiological characters from one another than non-congeners. Comparison among a greater range of Namib tenebrionid species is therefore needed in order to test this hypothesis, albeit inductively.

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TABLE 1. Integument colour and microhabitat occupied by the study species.

SPECIES	COLOUR	MICROHABITAT
Onymacris unguicularis	black	vegetationless dune slipfaces
O. bicolor	black with white elytra	vegetationless dune slipfaces
O. marginipennis	black with brown elytra	near vegetation on sandy, coastal hummocks
O. plana	black	open sand and vegetation of lower dune slopes
O. rugatipennis	black	open sand and vegetation of dry water courses
Physadesmia globosa	black	vegetation of dry water courses and gravel plains

TABLE 2. Significant differences (ANOVA) between beetle species in: (a) Critical thermal minima, and (b) Critical thermal maxima. The species with the higher value is placed on the left in each case.

(a) Critical thermal minima

Species comparisons	_P_
O. plana vs. _O. unguicularis_	<0.01
O. plana vs. _O. marginipennis_	<0.05
P. globosa vs. _O. unguicularis_	<0.01
P. globosa vs. _O. marginipennis_	<0.01
P. globosa vs. _O. rugatipennis_	<0.01
P. globosa vs. _O. bicolor_	<0.05

(b) Critical thermal maxima

O. plana vs. _O. marginipennis_	<0.01
O. plana vs. _O. bicolor_	<0.01
P. globosa vs. _O. unguicularis_	<0.05
P. globosa vs. _O. marginipennis_	<0.01
P. globosa vs. _O. bicolor_	<0.01
O. rugatipennis vs. _O. bicolor_	<0.01
O. rugatipennis vs. _O. marginipennis_	<0.01

TABLE 3. Significant differences between species (Kolmogorov-Smirnov tests) in frequency of T_b recorded in: (a) selected T_b (b) field T_b and (c) significant differences between selected and field T_b within species.

(a) Body temperature in the laboratory

Species comparisons	*P*
O. plana vs. *O. unguicularis*	0.01
O. plana vs. *O. bicolor*	0.03
O. plana vs. *O. marginipennis*	0.007
O. plana vs. *O. rugatipennis*	0.04
O. plana vs. *P. globosa*	0.06

(b) Field body temperature

O. plana vs. *P. globosa*	0.005

(c) Laboratory *versus* field body temperature

O. rugatipennis	0.03
O. marginipennis	0.008
P. globosa	0.05
O. plana	0.004

Table 4. Regression equations for body temperature vs. black-bulb temperature in O. plana, O. unguicularis and O. bicolor.

SPECIES	REGRESSION	F-VALUE	P
O. plana	y = 0.59x+14.59	37.61	0.0001
O. unguicularis	y = 0.45x+17.01	8.56	0.009
O. bicolor	y = 0.93x+2.624	63.62	0.0001

FIGURE CAPTIONS

FIG. 1. Distribution of the six study species in Namibia and southern Angola. Closed circles = O. unguicularis, open circles = O. bicolor, triangles = O. marginipennis, diamonds = O. plana, squares = P. globosa and O. rugatipennis. Dotted line indicates the periphery of the Namib desert. Note that P. globosa also occurs sporadically in dry river beds between the two rivers indicated, while O. rugatipennis occurs only along the two river beds indicated in the figure.

FIG. 2. Mean CTmax and CTmin values and box-and-whiskers plots of selected T_b of the six study species.

FIG. 3. Box-and-whisker plots of field T_b of the six study species.

FIG. 4. Frequency of T_b measurements in 1°C increments. Hatched = field T_b, unhatched = selected T_b in the laboratory. (a) Onymacris plana, (b) O. rugatipennis, (c) O. unguicularis, (d) O. marginipennis, (e) O. bicolor, and (f) Physadesmia globosa.