

THE BODY TEMPERATURE OF TENEBRIONID BEETLES IN THE NAMIB DESERT OF SOUTHERN AFRICA

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(Received 20 January 1971)

INTRODUCTION

A good deal is now known about the climate of various desert habitats in which arthropods may live. Information about desert macroclimates is reviewed by Reitan & Green (1968), and desert microclimates are referred to by Cloudsley-Thompson (1962*a*), Cloudsley-Thompson & Chadwick (1964), Délye (1968), Edney (1967, 1971), Hadley (1970*a*), Kühnelt (1969), Pierre (1958) and in UNESCO symposia (1958, 1962). But accurate measurements of actual body temperatures in these desert habitats are still scarce. One or two recent studies, notably those of Stower & Griffiths (1966) on desert locusts and of Hadley (1970*a, b*) on a scorpion and two beetles, provide useful information of the kind required, and much further work on other animals in other environments is needed if we are to understand the complex relationships between the various factors which affect thermal balance in these situations.

The work now reported was undertaken to get information about body temperatures of desert beetles in their natural habitat, and in particular to assess the effects of surface colour, orientation and behaviour in this respect. The observations were made in the Namib desert, where there is a rich variety of tenebrionid beetles, some showing extreme desert adaptations (Koch, 1961, 1962). The macroclimate in the Namib is referred to by Logan (1960) and by Schultze (1969), and some microclimatic information is also contained in a number of publications, including those of Hamilton & Coetzee (1969) and Kühnelt (1969).

MATERIAL AND METHODS

With one exception, the species used all occur in the vicinity of the Namib Desert Research Station, and they were collected in the field immediately before being used in the experiments. The exception is *Onymacris brincki*, which occurs nearer the coast and was kept in the laboratory and fed on corn flakes and bran.

Much of the work was done during the summer (January and February) of 1968 near the Research Station at Gobabeb, situated at 23° 34' S latitude and 15° 03' E longitude, and at an elevation of 408 m above sea level. Laboratory work was done in the Zoology Department at the University of Cape Town, using material sent by air from the desert.

Body temperatures were measured by fine thermocouples made from 46 s.w.g. constantan and copper wires. Thermocouples were calibrated against mercury-in-glass thermometers and could be relied upon to ± 0.2 °C. An Atkins multi-channel

thermistor thermometer was used for some of the environmental temperature measurements, and this was found to be reliable to ± 0.25 °C. Only the tips (about 0.2 mm long) of the thermocouples were joined, the rest of the fine wires being insulated with varnish. About 5 mm back from the tips the original cotton covering of the wires was left intact and heavily varnished in order to reduce heat flow to or from the junction.

Body-temperature measurements were made in the thoracic muscles (referred to as 'thoracic temperatures', and on the surface of the abdomen under the elytra ('abdominal temperature')). In either case a fine hole, about 0.2 mm in diameter, was made in the cuticle, the thermocouple junction was inserted to a depth of about 4 mm (less in *Stenocara* spp., which are smaller beetles) and sealed in place with white glue. The glue hardened within a few minutes and the whole process appeared not to have any adverse effect upon the beetles. The beetles were not anaesthetized during insertion of the thermocouples but they were attached to the substrate by adhesive paper strips over the tarsi. Insects with inserted thermocouples could remain alive for months and they fed normally. Plate 1, fig. 1 shows a specimen of *Onymacris rugatipennis* with a thermocouple mounted in the thorax. Methods of mounting the beetles during temperature observations were varied according to the needs of the experiment and will be described below.

Radiation values, where stated, were measured in the desert by a Robitzsch-Fuess registering radiometer and at Cape Town by a Belfort Pyreheliograph. These instruments measure total solar radiation.

All temperatures are reported in degrees centigrade.

RESULTS

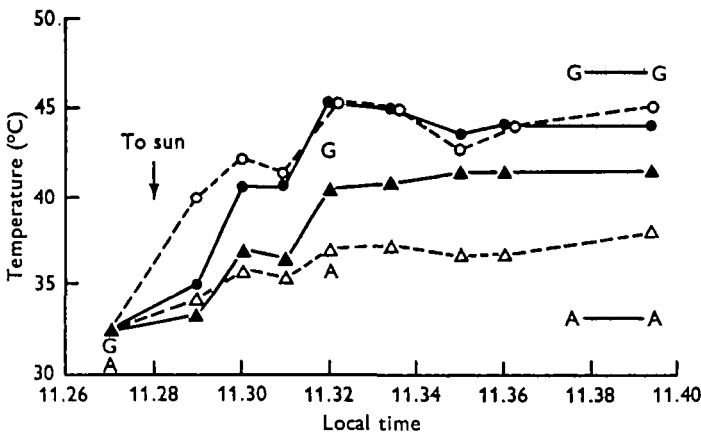
A. *The effect of surface colour on the body temperature of beetles in direct sunshine*

Several different views about the effect of surface colour on body temperature have been advanced (see below for further discussion). The presence in the Namib desert of two species of tenebrionid beetles with white elytra provided an opportunity to study this question.

In the first series of experiments, one *Onymacris rugatipennis* which is all black and one *O. brincki* which is all black except for the white elytra (Pl. 1, fig. 3) were mounted side by side on a wooden base, by holding tarsi down with fine slips of masking tape, and the wooden base was covered with local sand. The two beetles were similar in shape and size. Thermocouples were inserted into the thorax and sub-elytral cavity of each, and two other thermocouples measured the air temperature 2.0 cm above the ground and the ground temperature. During exposure each beetle was horizontal, with its long axis normal to the sun's rays.

The preparation was exposed in the natural habitat of *O. rugatipennis* – the dry river bed. Initial temperatures were taken with the preparation in the shade, after which it was exposed to sunshine and temperatures were read periodically. The results for one exposure, on 24 January 1969, are shown in Text-fig. 1. At this time the sun's altitude was 68° and radiation was from 1.1 to 1.2 cal cm⁻² min⁻¹ on a flat horizontal surface. Temperatures were somewhat unsteady at first owing to variable wind. However, during a calm period it became clear that the thorax and abdomen of *O. rugatipennis*

are similar in temperature (about 43 °C), while the ground was 47.5 °C and the air was 33 °C. At the same time the abdomen of *O. brincki* at 38 °C was about 3–4 °C cooler than its thorax. In fact the thorax of *brincki* was a little cooler than either the thorax or abdomen of *rugatipennis*.



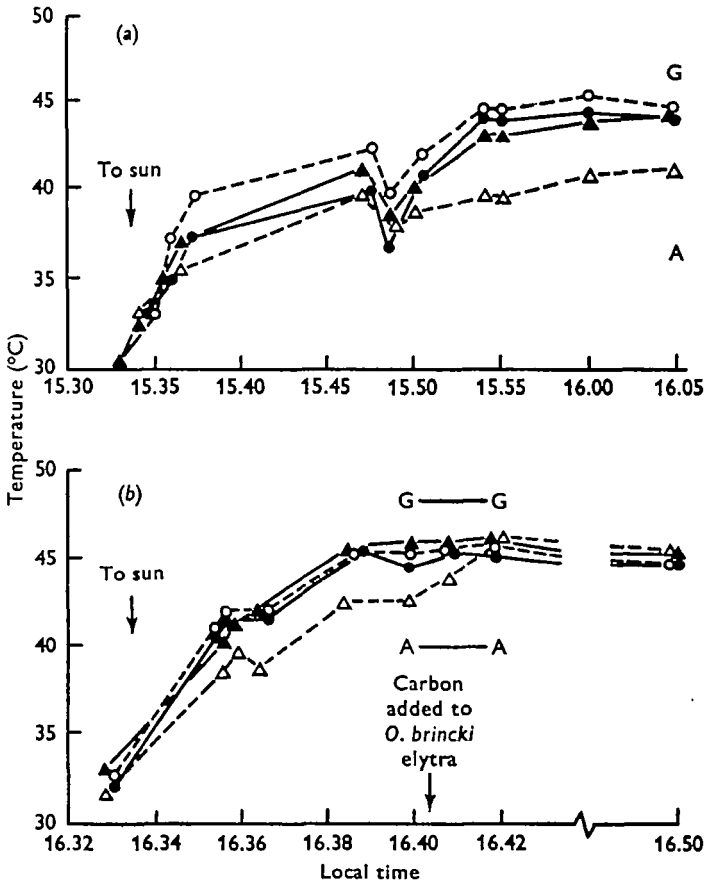
Text-fig. 1. Body temperatures of living *Onymacris brincki* (with white elytra) and *O. rugatipennis* (entirely black), when both insects were transferred from the shade to sunshine. The abdomen of *brincki* was cooler than its thorax, while the abdomen and thorax of *rugatipennis* had about the same temperature. G, Ground; A, air 2 cm above ground. ▲, *O. brincki* thorax; △, *O. brincki* abdomen; ●, *O. rugatipennis* thorax; ○, *O. rugatipennis* abdomen.

Two replicate exposures, using different insects, gave essentially similar results: after equilibration, during a calm period, the abdomen of *brincki* was 2.5 °C cooler than the thorax in one exposure. 3 °C cooler in the other, while the thorax and abdomen of *rugatipennis* were similar in temperature to each other and to the temperature of *brincki* thorax. We may conclude either that the white colour of *brincki* elytra reflected more solar radiation than the black thorax or that activity of the thoracic musculature produced a higher temperature there. The beetles did struggle when their temperature rose above about 42 °C, but *rugatipennis* did so as much as *brincki*, so that muscular heat production does not seem to be a likely explanation.

An experiment to make sure on this point was carried out by using recently killed beetles, the conditions otherwise being just the same. The results of one such exposure are shown in Text-fig. 2a. At this time the sun's elevation was about 56° and solar radiation was 1.1–1.05 cal cm⁻² min⁻¹. When the ground temperature was 47 °C and the air 37 °C, *brincki* abdomen was at 41.5 °C while its thoracic temperature was 44 °C, and the abdomen and thorax of *rugatipennis* were also about 44 °C. Since both insects were dead, the difference between thoracic and abdominal temperatures of *O. brincki* must have been due to the white elytra of that species.

If the above conclusion is true, then it should be possible to raise the abdominal temperature by changing the colour of the elytra. The same insects as those shown in Text-fig. 2(a) were again exposed to sunshine, and as soon as the temperatures had settled down, the whole elytral surface of *brincki* was painted with carbon black. At this time the sun's elevation was about 45° and solar radiation was 0.80 cal cm⁻² min⁻¹. The result, shown in Text-fig. 2(b), was that the abdominal temperature of *brincki*

rose. In the experiment shown, the 'black' abdomen of *brincki* was about $0.5-1.0$ above that of its thorax. In two further similar exposures with different insects the carbon-coated abdomen was the same temperature as the thorax in one, and 0.5 °C below it in another. These small differences may well result from experimental error. In a fourth exposure, however, the carbon-coated abdomen was 1.5 °C cooler than the thorax – a somewhat unexpected result, which could have been caused by faulty

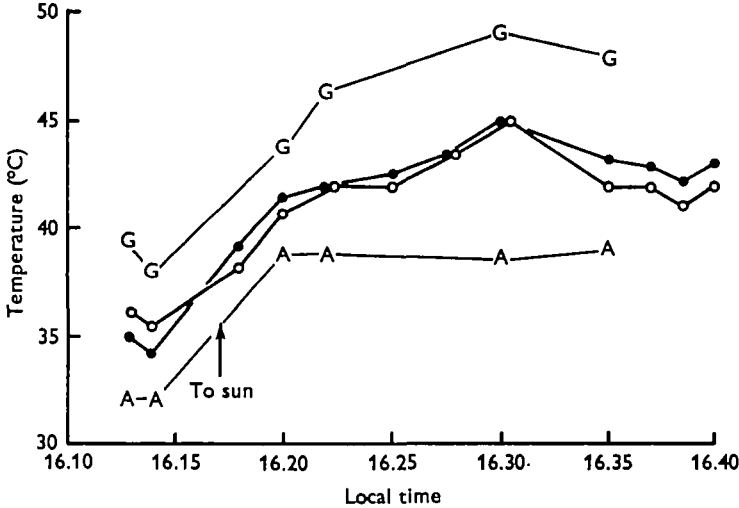


Text-fig. 2. Body temperatures of dead *Onymacris brincki* and *O. rugatipennis*. (a) In sunshine *brincki* abdomen was cooler than its own thorax or the abdomen and thorax of *rugatipennis*; (b) when the white elytra of *brincki* were covered with carbon black, the abdominal temperature rose to equal that of the black abdomen of *rugatipennis*. G, Ground; Δ, air 2 cm above ground. ▲, *O. brincki* thorax; △, *O. brincki* abdomen; ●, *O. rugatipennis* thorax; ○, *O. rugatipennis* abdomen.

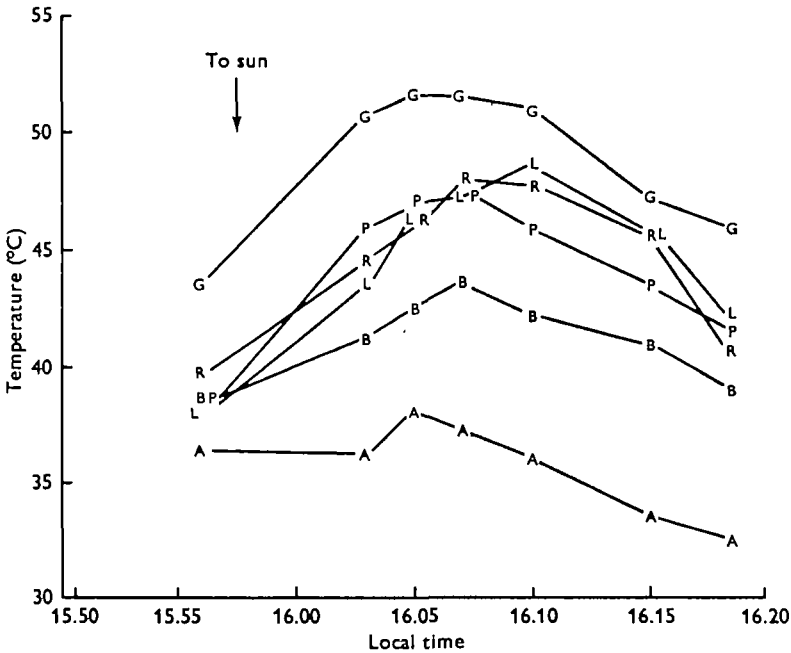
orientation to the sun. Further experiments reported below deal with this possibility. Apart from this aberrant result, the first three replicates provide additional evidence that the elytra of *brincki* reduce its abdominal temperature by some 3 or 4 °C compared with that of *rugatipennis*, under high solar radiation.

The specimens of *O. rugatipennis* and *O. brincki* used weighed about 0.7–0.8 g. A much smaller pair of species, *Stenocara eburnea* (with white elytra) and *S. depressa* (all

back), were also available (Pl. 1, fig. 4). They weighed between 0.2 and 0.25 g, and in view of their small size it seemed unlikely that surface colour would have a measureable effect on their body temperature, or that this would differ markedly from the ambient air temperature. The experiment was carried out, however, on 25 January 1969, and



Text-fig. 3. Abdominal temperatures of two species of *Stenocara* in sunshine. These beetles weigh about 0.2 g and temperature differences were small, but when they were present the white abdomen of *S. eburnea* was always the cooler of the two. G, Ground; A, air 2 cm above ground. O, *S. eburnea* (white); ●, *S. depressa* (black).



Text-fig. 4. Abdominal temperatures of several tenebrionid species. *Onymacris brincki* was always cooler than all other species. A, Air 2 cm above ground; G, ground. Abdomen of: R, *O. rugatipennis*; L, *O. laevis*; P, *P. cribripes*; B, *O. brincki*.

the results are shown in Text-fig. 3. At this time the sun's elevation was 45° and solar radiation was $0.9-0.8 \text{ cal cm}^{-2} \text{ min}^{-1}$. After settling down there was little difference between the abdominal temperatures of the two species, but when any differences did exist, *eburnea* was always cooler. Towards the end of the exposure, *eburnea* was fairly consistently 1°C or less cooler than *depressa*. The fact that the temperature of both beetles was well above that of the air suggests that radiation from the hot ground may have been important. Only one such exposure was made, and the result suggests that, even in small species such as these, surface colour may affect body temperature, but only to the extent of about 1°C .

Finally in this series of experiments, four different species of beetles were exposed side by side: *O. rugatipennis*, *O. laeviceps* and *O. brincki* (which are all about the same size), and *Physosterna cribripes* which is a little smaller. All save *brincki* are entirely black, and *O. laeviceps* appears to have a rather more shiny surface than the rest. The results of an exposure on 5 February 1969 are shown in Text-fig. 4. At this time the sun's elevation was 50° , and solar radiation was about $1.1 \text{ cal cm}^{-2} \text{ min}^{-1}$. The only consistent feature of these results is that *O. brincki* is cooler than the rest. Neither the apparently shiny surface of *laeviceps* nor the smaller size of *cribripes* resulted in any maintained temperature difference. The exposure was repeated once with different insects, and the results were essentially the same.

Table 1. *Temperatures ($^\circ\text{C}$) of the inner surfaces of triangles of cuticle when suspended with the outer surfaces exposed to direct sunshine*

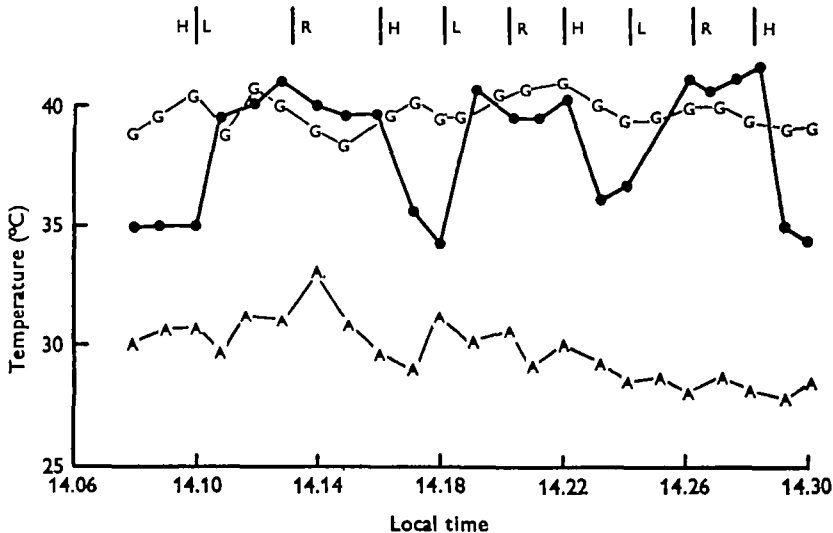
	Experiment no.			
	1	2	3	4
<i>O. rugatipennis</i>	42.0	44.0	42.0	43.5
<i>O. brincki</i>	40.0	42.5	40.0	42.0
Difference between <i>rugatipennis</i> and <i>brincki</i> *	2.0	1.5	2.0	1.5
Ground temperature	45.0	46.0	49.5	49.0
Air temperature	37.5	38.5	40.0	39.0

* Mean 1.75 .

If, as the above experiments suggest, reduction of abdominal temperature in *O. brincki* is due to elytral surface reflectivity, and not to shape or to any other factor, it should be possible to demonstrate the effect by means of a model, and an experiment on these lines was carried out on 6 February 1969, when the sun's elevation was about 45° and solar radiation was $1.1 \text{ cal cm}^{-2} \text{ min}^{-1}$. A model consisted of a triangular piece of elytron measuring 13 mm high by 3 mm across the base. A thermocouple was attached by a small spot of glue to the inner surface of the elytral fragment, which was then suspended by the fine wires over a sand base in direct sunshine. Models made from elytra of *rugatipennis* and *brincki* were suspended side by side, and the temperatures of their inner surfaces were read periodically. The results have not been graphed because they are similar to those for living or dead intact animals. Instead, the results from four replicates are shown in Table 1. They indicate clearly that the *brincki* model reflected more solar radiation than the *rugatipennis* model, since the temperature of the former was on average 1.75°C cooler.

B. *The effect of orientation to the sun and of movement between sunshine and shade on the body temperature of living beetles*

During the experiments reported above, wild beetles (*O. rugatipennis*) often wandered across the experimental area. However, they did not stay long in direct sunshine but moved between this and the shade offered by bushes of the grass *Eragrostis spinosa* (Pl. 2, fig. 1). Observation suggested that the beetles might thermo-regulate by moving between sunshine and shade, and in order to find the effect of such movements the following experiments were carried out, using *O. rugatipennis*.



Text-fig. 5. The effect of orientation to the sun's rays on the thoracic temperature of *Onymacris rugatipennis*. When the beetle was head-on to the sun its thoracic temperature was about 4 °C cooler than when its long axis was normal to the sun's rays. ●—●, *O. rugatipennis* thorax; △, air 2 cm above ground; G, ground; H, head; L, left side; R, right side to the sun.

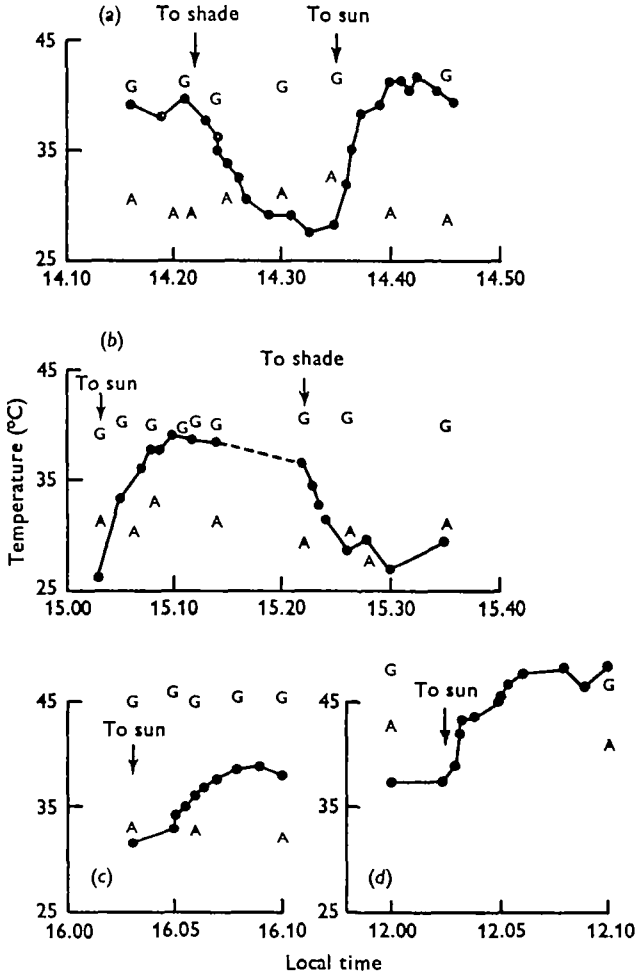
The effect of orientation to the sun's rays

A beetle was mounted on a small slip of wood, 77 × 25 mm, as described above. A thermocouple junction was inserted into the thoracic musculature, the fine leads were joined to coarser thermocouple wires and the latter were attached firmly to the wooden base, so that the whole preparation could readily be moved from place to place. The base was covered with local sand, and the beetle was mounted so that it was free to stilt but not to walk independently, or substantially to alter its orientation to the sun (except for stilting). (See Pl. 1, figs. 1, 2.) The preparation was exposed to direct sunshine on 17 July 1969, when the sun's elevation was about 43° and radiation was 0.95 cal cm⁻² min⁻¹. Exposures were made in one of three positions alternately: head, left side or right side facing the sun. Left and right presentations were made to check that the thermocouple was not displaced badly to one side.

The results are shown in Text-fig. 5. In conditions where the ground temperature varied between 38 and 41 °C, and air temperature between 28 and 33 °C, when the head was presented to the sun the temperature of the thorax was about 35 °C, i.e.

some 4 °C cooler than when either side was towards the sun. There was a slight tendency for the thermocouple in the thorax to read a little lower when the insect's right side was presented, but the difference was not entirely consistent. Two other similar exposures provided confirmatory results: in both, the lateral exposure gave thoracic temperatures between 3 and 4.5 °C cooler than head-on exposures.

In the following experiments beetles were suddenly shifted from shade to sunshine, and vice versa, and left in the new position long enough for their temperature to



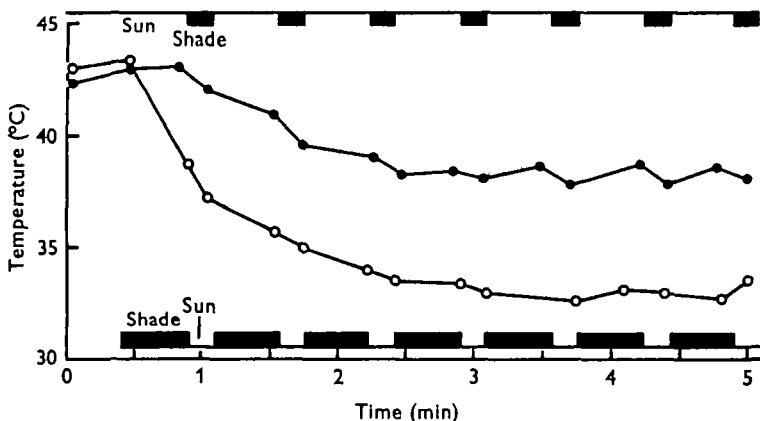
Text-fig. 6. The extent and rate of change of body temperature when *Onymacris rugatipennis* was moved from sun to shade and vice versa. Full equilibration took some 4–5 min, but the greater part was accomplished in 2 min or less. In (c) and (d) the time scale is expanded. ●—●, *O. rugatipennis* thorax; A, air 2 cm above ground; G, ground.

equilibrate (about 10 min). The results of experiments on 9 July and 24 July 1969 are shown in Text-fig. 6. In Text-fig. 6(a) the thoracic temperature fell from about 39 to 29 °C in 8 min when the beetle was transferred from sunshine to shade. Upon return to direct sunshine the beetle's temperature rose from 28 to 42 °C in 5 min, most of the

Equilibration occurring during the first 2 min. This beetle was taken through another complete cycle (not shown in the figure) and gave essentially the same results.

Text-fig. 6(b) shows the response of another beetle starting this time with a change from shade to sunshine. Its temperature again rose by about 12 °C in 5 min, followed by a fall of some 10 °C in 8 min, most of the change occurring during the first 4 min.

Text-figs. 6(c, d) show two more examples. (Note that the time scale is expanded in these two text-figures.) In 6(c) the beetle's temperature rose rather more slowly and to a lesser extent (8 °C in about 6 min), but in 6(d), another beetle at another time, the temperature rose rapidly, by 10 °C in 4 min.



Text-fig. 7. The effect of rapid alternation between sunshine and shade on the body temperature of *Onymacris rugatipennis*. One beetle (●—●), exposed to 30 sec sunshine alternating with 10 sec shade, reached a temperature of about 38 °C, while another, (○—○) in the reverse conditions, reached a temperature some 4–5 °C lower. In both cases temperature fluctuations were reduced to 1 °C or less in consequence of the heat capacity of the body. Ground in sun, 41.5–43.5 °C; ground in shade, 22.5 °C; air in shade, 2 cm above ground, 28.7–32.5 °C.

The effects on body temperature of rapid alternation between sunshine and shade

Observation of actively moving wild beetles showed that they seldom spent as long as 10 min in either sunshine or shade. Consequently it was of interest to find the effect on body temperature of rapid alternations, particularly when the proportions of time spent in each condition were unequal.

For this purpose beetles were restrained only by fine thermocouple wires (they were not attached to base boards) and were free to walk. However, they could be restrained in either sunshine or shade, and transferred rapidly from one to the other, by thermocouple wires attached to the end of a long stick. Two systems of exposure were used: 10 sec in sunshine alternating with 30 sec in the shade, or 10 sec in the shade alternating with 30 sec in sunshine. One such series of exposures was made on 20 July 1969, when the sun's elevation was 45–40°, and the results (Text-fig. 7) show that the beetles' temperature reached a steady level about 5 °C higher when the exposure was to 30 sec sunshine 10 sec shade than in the reverse condition.

In summary, the preceding experiments show that the body temperature of *O. rugatipennis* (and presumably of other insects of similar shape and size) is some 12 °C higher in sunshine than in shade, that equilibration after movement from one to the

other takes about 5 min with the greater part of the change occurring in the first two or 3 min, and that body temperature is strongly affected by orientation to the sun. Most important, perhaps, is the observation that the beetle is of such a size that its heat capacity may effectively reduce temperature fluctuations, the body temperature remaining constant within 1° or so as the insect moves among sunny and shaded areas in its environment. So far as can be judged from this sort of experiment, conducted in the field without close control of environmental factors, the beetles behave as physical bodies, where the rate of change of temperature declines as the equilibrium temperature is approached. There is no suggestion of physiological temperature regulation, but more refined laboratory experiments would be necessary to make sure on this point.

C. Laboratory analysis of the effects of orientation and surface colour

During the exposures in section A above (the effects of surface colour), air movement, orientation and the position of the thermocouples in the insect's body could not be rigorously controlled. Consequently, as mentioned on page 256, some of the results were not entirely trustworthy. In any case it seemed desirable to re-examine the effects of orientation and of colour in a more controlled situation, and this was done in the laboratory at the University of Cape Town.

Earlier work had shown the importance of orientation. An experiment was designed to estimate and thus to allow for this effect, so that the significance of surface colour could be clarified.

Living specimens of *O. brincki* and *O. rugatipennis* were used as well as recently killed ones. Each had a thermocouple in its thorax and another below the elytra on the abdomen. In order to avoid conduction and reflexion from the substrate, each beetle was suspended in the centre of a metal ring by means of four cotton threads attached to the front and hind tarsi (Pl. 2, fig. 2). The metal ring was held in a clamp. By moving the ring the long axis of the beetle could be held at any angle to the horizontal, and by means of a simple goniometer the angle of the sun's rays to the beetle's long axis could be measured.

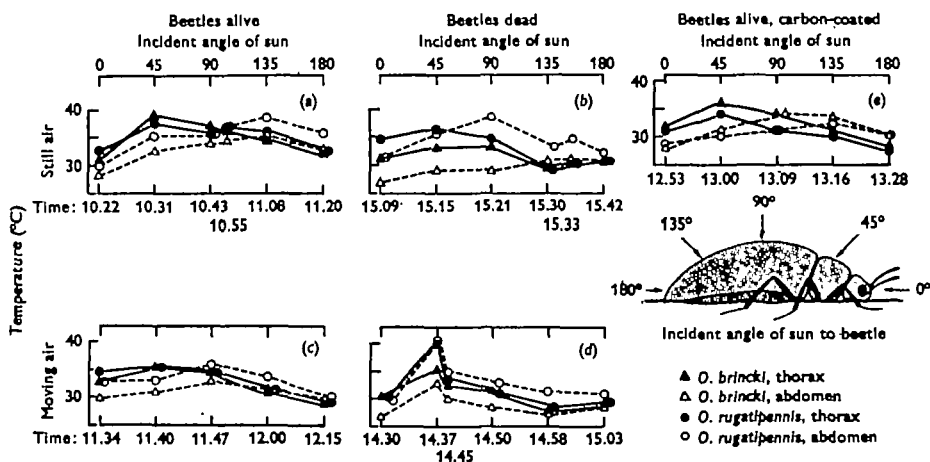
The beetle was oriented so that the sun was always in its median sagittal plane, but the angle of incidence was varied from 0°, when the head was directly towards the sun, to 180°, when the head was directly away from the sun (Text-fig. 8).

One specimen of *O. brincki* (white elytra) and one of *O. rugatipennis* (black) were exposed at the same time, each mounted on its own ring, but having identical orientations to the sun. They were exposed near a window which was either closed for the 'still air' exposures or open for the 'moving air' exposures. Exposures were made using either live or recently killed beetles.

The results of four such exposures, on 1 March 1969, are shown in Text-fig. 8. During the exposures shown in Text-fig. 8 (*a*, *b*, *c* and *d*) the sun's elevation (at Cape Town) was 43°, 47°, 55° and 52° respectively, and the solar radiation on a horizontal surface varied from about 0.7 cal cm⁻² min⁻¹ at 10.30 h to 0.9 cal cm⁻² min⁻¹ at 13.45 h, and fell again to 0.8 cal cm⁻² min⁻¹ at 15.00 h. Radiation as measured by a Belfort Pyreheliometer was reduced by about 15% when window glass was interposed between the sun and the instrument.

In Text-fig. 8 the temperatures shown are those to which the insect equilibrated in each set of conditions. Distances along the abscissa do not therefore represent equal time intervals, rather they represent equal intervals of incident angle.

When the beetles were alive and in 'still air' (Text-fig. 8a), *brincki* thorax was warmer than its abdomen by several degrees until the incident angle of the sun's rays was 135° (i.e. the sun was at 45° elevation and directly behind the insect), and then the abdominal temperature was about 1 °C higher than the thorax. In *rugatipennis* (black elytra), however, the cross-over point (where the abdomen becomes warmer than the thorax) occurred at 90°, and at higher incident angles the abdomen was substantially (about 3 °C) warmer than the thorax. A dead beetle showed very similar results (Text-fig. 8b), although here the cross-over point for *rugatipennis* occurred between 45° and 90°, while for *brincki* it occurred only at 135°, and even at 180° the abdomen was hardly warmer than the thorax.



Text-fig. 8. Thoracic and abdominal temperatures of *O. brincki* and *Onymacris rugatipennis* when subjected to solar radiation from different directions. When the incident angle was varied from 0° (head-on) to 180° (sun directly behind, the abdomen of *brincki* remained cooler than its thorax until the incident angle was 135–180°, and even then was scarcely warmer. In *rugatipennis*, however, as the incident angle varied, the abdomen became warmer than the thorax at 45–90°, and at 135° and 180° was considerably warmer. The effects are clearest in (b) (beetles dead in still air). In (e), carbon painted on the white elytra of *brincki* eliminated most of the difference between its temperature and that of *rugatipennis*.

In two further replicates of this experiment using different beetles the cross-over points for *brincki* were both nearer to 135° than to 90°, while for *rugatipennis* they were at 90°. At 180° incident angle, in the two replicates, the abdomen of *rugatipennis* was warmer than the thorax by 2.5 to 3.0 °C, while in *brincki* the differences, with the same sign, were 0 and 1 °C respectively. In dead beetles two replicates showed cross-over points with the same sign very close to those in Text-fig. 8(b), and differences at 180° between abdomen and thorax were 0.0 and 0.5 °C for *brincki* and 2.0 and 2.5 °C for *rugatipennis*.

In moving air essentially similar results were obtained, although, as shown in Text-fig. 8(d) (dead insects), air movement caused greater variability and less stability. No replicates were carried out in moving air.

Finally, in Text-fig. 8(e), the effect of painting a *brincki* abdomen with carbon black is shown. The cross-over point for both species was at 90° incident angle, and at 180° both abdominal temperatures were higher than the respective thoracic temperatures by about 3 °C. This last experiment was carried out on 4 March 1969, when the sun's elevation was about 58° and there were no replicates.

D. Upper lethal temperatures

In section A above, when measurements were made during the high temperatures of summer in the Namib desert, body temperatures of beetles recorded in natural conditions were as high as 45 °C. It was therefore of interest to determine the upper lethal temperatures of these and of other species of beetles from the desert habitat, and to see how they compared with those for other more mesic beetles. This work was done in the laboratory at Cape Town with beetles sent by air mail from the desert and from Grahamstown.

The first experiments in the series were carried out in temperatures rising at about 1.5 °C min⁻¹, the aim being to determine the temperature at which heat coma occurred in each species. The results were very erratic because it was difficult to determine the onset of coma. Another method was therefore used in which beetles were exposed for a constant time (30 min) to constant temperatures. If, after an exposure, the beetles were able to walk away from a 50 W tungsten lamp in a metal shade suspended directly over them at a height of 6 in. they were considered to have survived.

Table 2. Number of insects alive (A) or dead (D) after 30 min exposure to saturated air at the temperatures shown

Temperature (°C)	<i>Ctenolepisma terebrens</i>		<i>Onymacris plana</i>		<i>Onymacris rugati- pennis</i>		<i>Onymacris laeviceps</i>		<i>Trigonopus capicola</i>		<i>Trigonopus</i> sp.	
	A	D	A	D	A	D	A	D	A	D	A	D
42.5	4	0	4	0	—	—	4	0	4	0	4	0
45.0	4	0	4	0	—	—	4	0	0	4	0	4
46.0	4	0	4	0	4	0	4	0	0	4	0	4
47.0	4	0	4	0	4	0	4	0	0	4	0	4
48.0	7	3	4	0	4	0	7	1	—	—	—	—
49.0	0	4	4	0	8	2	0	8	—	—	—	—
50.0	0	4	8	0	5	5	0	4	—	—	—	—
51.0	0	4	0	10	0	4	0	4	—	—	—	—

Beetles were exposed in a glass jar, four at a time, in air saturated with water vapour, thus avoiding the complication of evaporative cooling. The jar was almost completely immersed in a large container of stirred water whose temperature was controlled to within 0.2 °C. After the temperature of the air in the jar had equilibrated (i.e. reached the temperature of the outside water) the beetles were rapidly inserted, and their own temperatures and that of the air in the jar were monitored by thermocouples. Brief opening of the jar caused only a brief (20 sec) drop in air temperature, but the largest beetles (*Onymacris plana*) did not reach air temperature for 7 min. For smaller beetles the lag was much less.

Three species of desert tenebrionid beetles and two species from a mesic habitat were used. The desert species were *O. plana*, *O. rugatipennis* and *O. laevis*; the mesic

Species, which occur in lightly wooded hillsides in the Grahamstown area, were *Trigonopus capicola* and *Trigonopus* sp. The desert thysanuran *Ctenolepisma terebrans* was also included. The upper lethal temperature was considered to be that at which half of the beetles survived. Four beetles were used at most temperatures, but the number was increased in the neighbourhood of the lethal temperature.

The results are shown in Table 2, and Table 3 shows the relation between habitat and upper thermal limit. In general the relationship conforms to expectation (although many more species and individuals would have to be tested for confirmation). Insects that are most exposed to high temperatures during their active period are those with the highest temperature tolerance, and all the desert tenebrionids have higher lethal temperatures than those of the mesic species tested.

In the field some desert beetles have body temperatures which would be lethal to some mesic forms: *O. rugatipennis* for example, voluntarily accepts a body temperature of 45 °C in the field while *Trigonopus* would die at this temperature.

Table 3. *Habitats, activity habits and upper lethal temperatures in desert and other tenebrionids and a desert thysanuran*

Species	Upper lethal temperature (°C)	Habitat	Activity habit
<i>Onymacris plana</i>	50-51	Desert sand dunes and valleys	Diurnal, summer
<i>O. rugatipennis</i>	50	Desert river bed	Diurnal, summer (and winter)
<i>O. laeviceps</i>	48-49	Desert sand dunes and valleys	Twilight, summer (and winter)
<i>Trigonopus capicola</i>	42.5-45	Mesic, light woodland	?
<i>Trigonopus</i> sp.	42.5-45	Mesic, light woodland	?
<i>Ctenolepisma terebrans</i> (thysanuran)	48	Desert dunes and plains	Nocturnal

DISCUSSION

There has been a good deal of discussion about the significance of surface colour in determining the body temperature of insects. Some of the earlier work, notably that of Buxton (1924), suggested that colour is indeed important. He measured temperature differences up to 4.5 °C between dark and light forms of the grasshopper *Calyptamus* when these insects were exposed to sunshine. Pepper & Hastings (1952), however, did not find such an effect in *Melanoplus*. Digby (1955) found that surface colour had a slight effect on body temperature, but for various reasons he concluded that 'temperature differences due to colour will be of minor importance'. Stower & Griffiths (1966) also found no significant difference in dark and light forms of the desert locust *Schistocerca*. Bolwig (1957) found, in rather artificial laboratory conditions, that the temperature of *Onymacris bicolor marshalli*, which has white elytra, was about 1-2 °C lower than that of *O. multistriata*, which is entirely black, when both were irradiated by an electric heater. Above 38 °C, however, *multistriata* became cooler than *marshalli*, and Bolwig ascribed this to a ventilatory mechanism in the sub-elytral cavity.

Hadley (1970*a*) painted the black elytra of *Eleodes armata* white, and obtained somewhat inconsistent results, the sub-elytral cavity of the 'white' beetle usually being less than 1 °C cooler than that of the black. For the normal black beetles, assuming a surface reflectivity of 63%, Hadley arrived at a heat balance showing net radiation of +0.141 cal cm⁻² min⁻¹, and convection of 0.134 cal cm⁻² min⁻¹, when the temperature excess of the beetle was 10 °C.

In the present experiments total solar radiation was usually in the region of 1.0 cal cm⁻² min⁻¹, and this being so, both metabolism and evaporation in all probability contributed little to the heat balance. Metabolism may be ruled out on general grounds for insects in direct sunshine (Parry, 1951). Evaporation was measured and amounted to about 30 mg day⁻¹ for a 500 mg insect at 27 °C, involving a loss of about 0.0012 cal min⁻¹, which is clearly negligible. Conduction was probably low, since the only contact with the ground in the case of living insects was through the six feet – or there was no contact at all, as in the laboratory exposures with suspended beetles. Body temperature in these circumstances must be determined by net radiation load and convection according to the expression

$$R_n = h_c \Delta T,$$

where R_n is net radiation load, h_c the convection coefficient, and ΔT the temperature excess of the beetle over the ambient air.

Consider the situation depicted in Text-fig. 1 at 11.40 h when temperatures were (approximately): air 33 °C, ground 47.5 °C, *brincki* abdomen (white) 38 °C, *rugatipennis* abdomen (black) 45 °C. Net radiation, R_n , on each was equal to R_i (incident radiation) less R_{refl} (reflected radiation, mostly short wave) less R_{rad} (re-radiation in the long-wave region). Using the subscript b for the black beetle and w for the white one, we can write

$$R_{n_w} = R_{i_w} - R_{\text{refl}_w} - R_{\text{rad}_w} \quad (1)$$

and

$$R_{n_b} = R_{i_b} - R_{\text{refl}_b} - R_{\text{rad}_b}. \quad (2)$$

But R_{i_w} and R_{i_b} are assumed to be the same, since the beetles were about the same size and shape, and were exposed together. Then by rearrangement and by substitution of $h_c \Delta T$ for R_n we obtain

$$R_{\text{refl}_w} - R_{\text{refl}_b} = (h_c \Delta T_b - h_c \Delta T_w) + R_{\text{rad}_b} - R_{\text{rad}_w}. \quad (3)$$

Following Gates (1962) and Porter & Gates (1969), we can estimate $h_c \Delta T$ for convective loss from a cylinder as $h_c = 6.17 \times 10^{-3} \times (V^{1/3}/D^{1/3})$. Assuming each beetle to be a cylinder 0.5 cm in diameter, and assuming air movement to be 10 cm s⁻¹ (it was very calm), the values are $h_c \Delta T_b = 0.253$ and $h_c \Delta T_w = 0.106$ cal cm⁻² min⁻¹.

R_{rad_b} is 0.83 cal cm⁻² min⁻¹ and R_{rad_w} is 0.75 cal cm⁻² min⁻¹, from the radiation laws for black bodies. Substituting in (3) we now have

$$R_{\text{refl}_w} - R_{\text{refl}_b} = 0.253 - 0.106 + 0.83 - 0.75 = 0.227 \text{ cal cm}^{-2} \text{ min}^{-1}. \quad (4)$$

This value for the difference in rates of heat reflexion is reasonably secure since it involves only one assumption in each case – the value for the convective heat loss. It says nothing about actual values for reflectivity, but if we are prepared to make a few further assumptions such values can be arrived at by solving the equation (from 1 above)

$$R_{\text{refl}_w} = R_{i_w} - R_{n_w} - R_{\text{rad}_w}. \quad (5)$$

We have values for R_{n_w} and R_{rad_w} , and R_{t_w} may be estimated from the relation

$$R_{t_w} = R_{t_{solar}} + R_{t_{sky}} + R_{t_{ground}}$$

$R_{t_{solar}}$ was measured in the situation being considered and found to be about $1.1 \text{ cal cm}^{-2} \text{ min}^{-1}$ on a flat horizontal surface; $R_{t_{sky}}$ may be obtained from the air temperature according to Swinbank (1963), and works out at $0.62 \text{ cal cm}^{-2} \text{ min}^{-1}$ in the present case. $R_{t_{ground}}$, from black-body radiation laws, was $0.86 \text{ cal cm}^{-2} \text{ min}^{-1}$ at the same time.

Since solar and sky radiation fall on the upper half of each beetle while ground radiation falls on the lower half, we have (for the whole beetle)

$$R_t = \frac{1.1}{2} + \frac{0.62}{2} + \frac{0.86}{2} = 1.29 \text{ cal cm}^{-2} \text{ min}^{-1}$$

as the mean rate of incoming radiation.

Substituting in (5) above, we have

$$R_{refl_w} = 1.29 - 0.106 - 0.75 = 0.434 \text{ cal cm}^{-2} \text{ min}^{-1},$$

and either by substitution in (4) or by doing the calculation for the black beetle we arrive at $R_{refl_b} = 0.207 \text{ cal cm}^{-2} \text{ min}^{-2}$.

Since reflexion of solar radiation took place from the dorsal half of the insect (and we have assumed that this represents half of its surface), the rate for that surface will be $0.207 \times 2 = 0.414 \text{ cal cm}^{-2} \text{ min}^{-1}$ for the black beetle and $0.434 \times 2 = 0.868 \text{ cal cm}^{-2} \text{ min}^{-1}$ for the white one. Incoming solar radiation on the dorsal surface was about $1.1 \text{ cal cm}^{-2} \text{ min}^{-1}$, so that the reflectivities would be $0.414/1.1$ or 38% for *O. rugatipennis* and $0.868/1.1$ or 79% for *O. brincki*.

Rücker (1933) measured surface reflectivity in the visible region for several beetles and obtained values ranging from 74% for the white *Comptos niveus* to 4.7% for *Silpha obscura*. More recently Porter (1967) measured a reflectivity of 8.6% (for the solar spectrum) in a black carabid beetle.

However, the absolute values arrived at after calculations such as those above should not be given a great deal of weight because too many assumptions are involved. For example, we do not know the temperature of the ground below the beetle, only that of the ground a few centimetres away in sunshine, yet it was mostly the ground below the beetle (at least partly in shade) that radiated to the beetle. The estimate for sky radiation is also insecure, and probably too high, since it is based on air temperature near the ground, while Swinbank's data refer to screen temperatures. Again, the estimate for wind speed may have been low, and this would give too high a value for reflectivity.

However, provided such exercises are recognized as tentative they can be helpful. At least they direct attention to the need for particular kinds of data which are so often missing.

In the present context the calculation at least indicates the strong probability that a white and a black beetle in sunshine will have different body temperatures as a result of different surface reflectivities.

This is not to say that the white elytra of *brincki* are white as a result of selection for a temperature effect. Indeed the very large temperature effects brought about by different orientation to the sun's rays, and the effects of the insects' movement between sunshine and shade, suggest that insects control their temperature effectively in these ways. The value of either a black surface for rapid warming in the morning, as

Hamilton (unpublished work) suggests, or a white surface for cooling in the heat of the day, has not been demonstrated. A black surface leading to rapid warm-up and activity would also lead to earlier retirement from activity as environmental temperatures rise, and vice versa for a white surface.

Cloudsley-Thompson (1964) concludes that the common black colour in desert beetles is probably a case of Mullerian mimicry, whereby a common distastefulness is advertised by a common colour, so that potential predators learn about it quickly. Certainly the black tenebrionids are rather conspicuous, and so too are the stark black and white colours of *O. brincki* or *Stenocara eburnea*. Perhaps the black and white pattern is also a warning one. However, not all desert tenebrionids are black, and many non-desert species are black. *Calosis amabilis*, which lives in the stony Namib desert, is a mottled brown and white, and this to human eyes at least renders these beetles very hard to see among the brown and white rocks and pebbles in their habitat.

A related question concerns the effect of the sub-elytral cavity on body temperature (apart from the colour of the outer surface of the elytra). Cloudsley-Thompson (1964) did not find any difference in temperature or humidity between the air inside and outside the sub-elytral cavity of the desert tenebrionid *Pimelia grandis*, even in sunshine. He did find, however, that transpiration increased if the elytra were removed, as did Deezer (1955) and Ahearn & Hadley (1969). Cloudsley-Thompson concludes that the size and shape of the sub-elytral cavity is not adaptive as regards heat and water balance. Certainly there is no indication that diurnal species have larger cavities than nocturnal ones; both flat and curved elytra are found in both groups, and in any case the size of the air space changes markedly with the degree of hydration and nourishment of the individual.

Nevertheless, on theoretical grounds it seems that a cover, such as is provided by the elytra, separated from the abdominal surface by a poor heat conductor, air, would lead to a reduction in abdominal temperature; and Hadley's (1970a) results tend to support such an expectation. The present work was not designed to answer this question, but further investigation would be worth while.

As regards the actual body temperatures observed, it is interesting to find that a beetle of the size of *O. rugatipennis* can, and probably does, regulate its body temperature by periodic excursions from sunshine to shade. The rate at which the beetles equilibrated when transferred from sunshine to shade (about 4–5 min) and their temperature excess in sunshine (up to about 15 °C according to conditions) were both comparable with the values found by Stower & Griffiths (1966) for *Schistocerca*. Large hoppers, they found, had a larger temperature excess (8 °C) than smaller ones (2.5 °C) and equilibrated more slowly (15 min as compared with 1 min).

However, the extent of temperature regulation is of course limited by the state of the environment. During the winter months ambient temperatures of the air and of the ground in sunshine and shade are such that *O. rugatipennis* can maintain satisfactory temperatures during the warmest part of the day, and its daily cycle of activity is unimodal. During the summer, however, environmental temperatures are so high that the beetles are obliged to retreat below the sand or to other cooler areas, and daily activity is bimodal. (Data supporting the above brief statement will be published elsewhere by Holm & Edney.)

It remains to comment briefly on the upper lethal temperatures measured. Tolerance of a body temperature of 50 °C by *O. plana* and *O. rugatipennis* is remarkable, and as Table 3 shows, the upper lethal limits of different species seem to correspond rather well with their habitat – those species which are most exposed (being active by day on open sand dunes), such as *O. plana*, have the highest lethal temperatures. Much lower lethal limits are shown by non-desert tenebrionids.

The presently established figure for *O. plana* (50 °C) must be one of the highest known. *Thermobia* dies at 51.3 °C after exposure for about 1 h (Edwards & Nutting, 1950) and Cloudsley-Thompson (1962*b*) found that *Galeodes*, a solpugid, can withstand 50 °C for 24 hr at 10% relative humidity, but that two desert beetles, *Pimelia grandis* and *Ocnera hispida* tolerated only 43 °C and 45 °C respectively, for the same period. Cloudsley-Thompson (1970) gives further information in a recent review. There are in fact many statements about the upper lethal limits of numerous arthropods, but they have been obtained in such a variety of ways and conditions that comparisons, let alone wide generalizations, are of doubtful value. More direct measurements of body temperatures in natural desert surroundings would be useful for the light they throw on the insect–environment relationship. Temperature is clearly a very important component of the environment, not only so far as the upper and lower limits for different species are concerned, but also, within the natural physiological range, as it affects all physiological and ultimately ecological processes. Study of the multiplicity of factors that determine body temperature of small poikilotherms in real life has only just begun; it is a difficult field, but its further exploration will be fruitful.

SUMMARY

1. In direct sunshine the abdomen of living *Onymacris brincki*, which is covered by white elytra, was 3–4 °C cooler than its thorax, while in the same conditions the abdomen and thorax of *O. rugatipennis*, which is an entirely black beetle, had the same temperature. Since similar effects were observed in dead beetles, the warmer thorax was not due to muscular activity. When the white elytra of *brincki* were covered with carbon black, its abdominal temperature rose to equal that of *rugatipennis*. Models, made of pieces of black and white elytra, showed similar effects.

2. The smaller species *Stenocara eburnea* (with white elytra) showed a smaller and less consistent temperature depression when compared with the similar-sized species *S. depressa* (which is black). Abdomens of *O. rugatipennis*, *O. laeviceps* and *Physosterna cribripes* (all large black beetles) were from 3–5 °C warmer than *O. brincki*, but showed no consistent difference among themselves.

3. When *O. rugatipennis* was oriented head-on to the sun in its natural environment its thorax was about 4 °C cooler than when its long axis was normal to the sun's rays. Beetles exposed to sunshine were 12–15 °C warmer than they were in the shade. When transferred from one to the other, the greater part of temperature equilibration occurred in about 2 min and equilibration was complete in about 4 min.

4. Observation suggested that beetles thermoregulate by moving between sunshine and shade. Measurements showed that a beetle exposed to alternating periods of 10 sec in sunshine and 30 sec in shade reached a steady temperature of about 33 °C, while the reverse conditions (10 sec in the shade and 30 sec in sunshine) led to a temperature

of about 38 °C. In continuous alternations thoracic temperatures remained constant within about 1 °C.

5. Laboratory experiments in which the angle of incidence of the sun's rays was varied through 180° confirmed the field results and showed that white elytra lower the abdominal temperature of living and dead beetles.

6. Upper lethal temperatures for 30 min in saturated air varied from 50 °C for the desert tenebrionid *Onymacris plana* to 42.5 °C for the mesic species *Trigonopus capicola*. In general, upper lethal temperatures correlated well with habitat and habit.

7. Making certain assumptions, analysis of the heat balance of beetles during one exposure in sunshine suggests that the difference between the white elytra of *brincki* and the black ones of *rugatipennis* as regards the amount of short-wave radiation reflected is 0.227 cal cm⁻² min⁻¹, and further, that the reflectivities of the two surfaces are 79% and 38% respectively.

8. The selective advantage of white elytra probably has little to do with heat balance; the vivid contrast between white and black suggests that the pattern may be aposematic.

I am grateful to the late Dr C. Koch for facilities at the Namib Desert Research Laboratory at Gobabeb and to Mr Eric Holm and other members of the staff there for much useful information and assistance. Mr Holm kindly collected beetles and sent them to me at Cape Town, and Mrs Gay Youthed did the same from Grahamstown. Dr. Mary Jensen kindly supplied living *Onymacris brincki*, which do not occur in the immediate vicinity of Gobabeb. Dr W. J. Hamilton and Mr Erick Holm have both allowed me to refer to their unpublished work. Dr Hyrum Johnson has given valuable advice on matters of heat balance. Grateful acknowledgments are due to the Guggenheim Foundation for a Fellowship, and to the National Science Foundation for financial support (grants GB 7931 and 8700).

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EXPLANATION OF THE PLATES

PLATE I

Fig. 1. *Onymacris rugatipennis*, the commonest tenebrionid beetle in the dry Kuiseb River bed, mounted on a wooden base with thermocouple inserted. This species is more plentiful in the summer (when it has a bimodal daily activity distribution) than in the winter (when its activity is unimodal). Weight about 600 mg.

Fig. 2. The same as Fig. 1, but the wooden base covered with local sand to provide a natural background.

Fig. 3. *Onymacris brincki*, a tenebrionid beetle with white elytra, the rest of the body black. This species occurs in the coastal area of the Namib desert. Mean weight about 500 mg.

Fig. 4. *Stenocara depressa* (black) and *S. eburnea* (white elytra). The former occurs in the river bed, the latter in the stony desert. Weight about 200 mg.

PLATE 2

Fig. 1. The habitat of *Onymacris rugatipennis* in the Kuiseb River bed. Clumps of tough, spiny *Eragrostis* grass and large trees (*Acacia albida*, *A. giraffae*), and *Tamarix* afford protection from the sun and from predators.

Fig. 2. Equipment for measuring and controlling the incident angle of the sun's rays during exposure of beetles. Thermocouples measured thoracic and abdominal temperatures. The beetle shown is *Onymacris laeviceps*, but the data reported refer to *Onymacris rugatipennis* and *O. brincki*, which are about the same size.

