

Body color and body temperature in white and black Namib desert beetles

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This paper concerns the thermal significance of body color in two tenebrionid beetles from the Namib desert of Namibia. One, *Onymacris unguicularis* is black, while the other, *Onymacris bicolor* is mostly white. We compared in the laboratory how body temperatures of these two species are affected by the various modes of heat exchange a beetle in nature might experience. Body color affects only one avenue of heat exchange—absorption of direct shortwave and visible radiation. It is irrelevant to all other avenues of heat exchange—convection heat loss, reflected short-wave and visible radiation and heat from the ground. Of all the factors that affect beetle temperature, the most important is convection heat loss. Of lesser importance, but still significant are: ground temperature, ground color and incident visible irradiance. Long-wave radiation from the ground is a negligible component of beetles' exchanges of heat. In semi-natural conditions, these factors interact to render color a negligible influence on the body temperatures of these beetles, despite their stark differences in body color.

Introduction

Does body color have any thermal significance? This question (a persistent one in animal energetics) is especially interesting when it concerns animals living in extreme environments, such as hot deserts or polar regions, where the colors of animals vary widely and, seemingly at times, paradoxically (Norris, 1967; Hamilton, 1973; Cloudsley-Thompson, 1976, 1978; Øritsland & Ronald, 1978; Walsberg, Campbell & King, 1978).

In the world's deserts, tenebrionid beetles are important members of the insect fauna. Many desert tenebrionids are large (100–100 mg), conspicuous beetles, and often they are found active in hot, sunny conditions. Desert tenebrionids are also often dark in color. This fact has prompted many to wonder why a beetle living in a hot desert would be a color that would apparently make its body even hotter. This problem has been termed the 'black desert beetle paradox' (Hamilton, 1973; Cloudsley-Thompson, 1976, 1978).

The tenebrionid fauna of the Namib desert of Namibia is one of the world's most diverse (Koch, 1961, 1962). While most of the Namib tenebrionids are dark, a few species have white elytra which render the body predominantly white in color. These white beetles sometimes co-exist with black congeners. A species of white beetle living sympatrically under very hot conditions with a species of black beetle would seem to make a useful 'natural experiment' on the problem of animal color and thermoregulation. Indeed, this situation has been exploited in the past by several other scientists (e.g. Bolwig, 1957; Hadley, 1970; Edney, 1971; Hamilton, 1973).

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As part of a larger examination of the problem of animal color and temperature regulation, we have undertaken a study on the thermal ecology of two Namib tenebrionid beetles: a white beetle, *Onymacris bicolor*, and a black beetle, *Onymacris unguicularis*. In this paper, we compare in the laboratory how white and black body color affect the various ways a beetle exchanges heat with its surroundings. We identify those avenues of heat flux that specifically are affected by body color. We then consider how the different avenues of heat flux interact, with the aim of evaluating how body color affects body temperature under conditions similar to those a beetle might experience in its natural environment.

Materials and methods

Beetles

The beetles used were *Onymacris bicolor*, a beetle with prominent white elytra, and *Onymacris unguicularis*, a black beetle. Body masses averaged about 600 mg (Table 1). We found the two species to be indistinguishable in total body mass, in the distribution of mass among the body parts, and in the content of water in the body (Table 1). The beetles differ in cross-sectional shape (Fig. 1). *O. unguicularis* is oval in cross section, while the ventral portion of *O. bicolor* is more polygonal (Fig. 1).

O. unguicularis was collected at Rooibank, near Walvis Bay, Namibia. *O. bicolor* was collected at the Skeleton Coast National Park in northern Namibia. The beetles were

Table 1. Characteristics of the beetles used in this study. Numbers reported are mean \pm standard deviation (sample size)

	<i>Onymacris bicolor</i>	<i>Onymacris unguicularis</i>
Wet mass (g)		
Body	0.656 \pm 0.101 (15)	0.596 \pm 0.136 (15)
Cephalothorax	0.144 \pm 0.039 (5)	0.147 \pm 0.027 (5)
Abdomen	0.475 \pm 0.107 (5)	0.460 \pm 0.158 (5)
Elytra	0.039 \pm 0.006 (5)	0.034 \pm 0.011 (5)
Dry mass (g)		
Body	0.278 \pm 0.058 (5)	0.312 \pm 0.058 (5)
Cephalothorax	0.067 \pm 0.018 (5)	0.077 \pm 0.013 (5)
Abdomen	0.180 \pm 0.036 (5)	0.204 \pm 0.041 (5)
Elytra	0.031 \pm 0.005 (5)	0.032 \pm 0.009 (5)



Figure 1. Approximate cross-sectional shapes of (a) *Onymacris unguicularis* and (b) *Onymacris bicolor*.

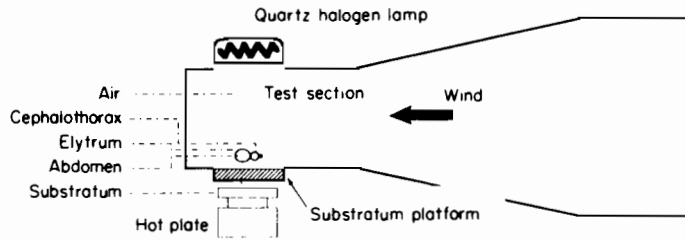


Figure 2. Schematic diagram of wind tunnel and experimental apparatus. -----, thermocouples.

brought to Cape Town and kept in terraria until used. They were fed a diet of lettuce, and were given heat from an incandescent lamp for part of each day.

For each series of measurements, only freshly killed beetles were used. Prior to the experiment, a beetle was removed from the terrarium and killed by freezing. The beetle was weighed, and attached at the posterior to a small wooden sting (1 mm diameter), to hold the beetle in position during the measurements. Beetles were positioned so the bottom of the abdomen was 2–3 mm above the floor of the test section. This approximated the posture of living beetles.

Beetle equilibrium temperatures

For each experiment, three 36 Ga thermocouples (Type T) were implanted into a beetle's body: one in the abdomen, one in the cephalothorax, and one in the subelytral space, positioned so the junction touched the inside surface of the elytron. The wounds were sealed and the thermocouples secured in place by small dabs of cyanoacrylate cement.

During an experiment, the three body temperatures, along with the air and substratum temperatures, were recorded by a microcomputer-based data acquisition system. For each condition tested, an equilibrium temperature (T_{∞}) and time constant (τ) were estimated from a temperature transient, using the method described by Bakken (1976). Where possible, the equilibrium temperature was also estimated directly.

Experimental procedures

All measurements were done in a small, open-flow wind tunnel (Fig. 2), that could generate wind speeds greater than 3 m s^{-1} through a test section of $17 \text{ cm} \times 17 \text{ cm}$. A 300 W quartz halogen lamp (Sylvania L2270) was mounted in an overhead port of the test section to provide direct visible radiation. A quartz halogen lamp has a color temperature of about 3300 K, with a peak spectral emittance at a wavelength of about 900 nm. Therefore, the light used in this study is 'redder' than natural sunlight, which has a color temperature of roughly 6000 K. The direct irradiation at the floor of the test section was roughly 1 kW m^{-2} . A circular hole, 15 cm in diameter, was cut from the floor of the test section, which enabled us to place different substrates (described later) beneath the beetles. The container for the substrate, a 15-cm diameter petri dish, had a thermocouple mounted to place the junction just at the surface of the substratum being used. A thermocouple to measure air temperature was mounted about halfway up the side wall of the test section, and was shielded from radiation by an aluminum foil shield.

We examined heat exchange under four conditions: (1) convection heat loss only; (2) direct and reflected visible radiation, in combination with convection; (3) conduction through the air which emitted long-wave radiation from heated ground, in combination with convection; (4) over natural sands, with heat inputs from all the sources listed above.

Convection alone. Five *O. bicolor* and four *O. unguicularis* were used for this experiment. The beetles were prepared as described above.

The wind speed was adjusted to 0, 1, 2, or 3 m s^{-1} , and the beetles were warmed by the

lamp. When the abdominal temperature had equilibrated, or had warmed to 40–45°C, the lamp was switched off and the beetle allowed to cool. While the beetle was cooling, its abdominal temperature was recorded for 5 min, and the time constant and equilibrium temperature calculated, as described above.

Direct and reflected visible radiation. Five *O. bicolor* and four *O. unguicularis* were used for this experiment. The beetles were prepared as described above.

To measure the effect of direct illumination alone, the floor of the test section beneath the beetle was removed and replaced with a 2-mm nylon mesh (Fig. 3). This provided little surface to reflect radiation back onto the beetle, and hence a very small reflected component of the radiative heat load. Preliminary tests showed that removal of the floor did not affect the convection environment around the beetle.

To estimate the maximum contribution reflected visible light could make, the floor of the test section was replaced with a highly reflective substratum, polished aluminum foil (Fig. 3) which was stretched over a 15-cm petri dish filled with agar gel. The foil was in contact with the agar gel over the entire surface of the dish. The agar gel acted as a high-capacitance thermal buffer to keep the foil substratum cool and relatively constant during the short heating periods.

The beetles were positioned so they were directly under the lamp. The wind speed was adjusted to 0, 1, 2 or 3 m s⁻¹. The lamp was switched on, and the temperatures were recorded for a period of up to 5 min. To preclude heating damage to the beetle, its temperature was never allowed to go higher than 45°C. Equilibrium temperatures were estimated as described above.

Emitted long-wave radiation and conduction from the substratum. Five individuals of each species were used for these experiments. The beetles were prepared as described above. The wind speeds tested were 0, 1, 2, and 3 m s⁻¹.

The petri dish that comprised the floor of the test section was filled with sand. Aluminum foil was stretched tightly over the dish so that it was in contact with the sand and both sand and foil were warmed to 45–55°C by a hot plate placed underneath the petri dish (Fig. 4).

Two types of aluminum foil covering were used. In one set of measurements, it was left shiny. The emissivity of polished aluminum foil is roughly 0.08 (Thomas, 1980). Therefore, very little radiation was emitted from the hot, shiny foil, and any heating of the beetle would be mostly by conduction through the air and convection from the warmed substratum. In a second series of measurements, the foil was coated with carbon black,

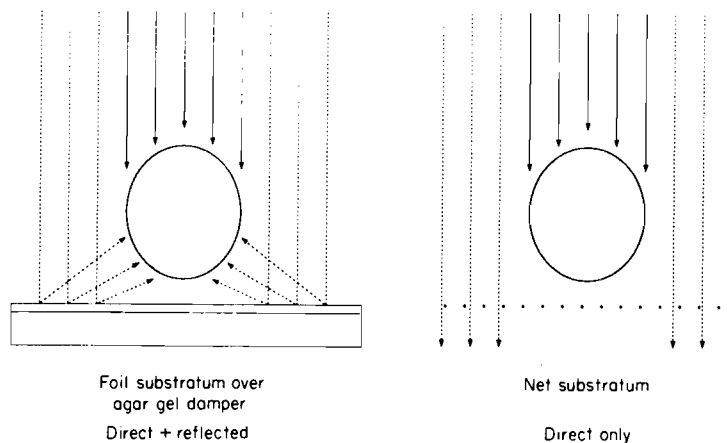


Figure 3. Schematic outline of experiments to test the effects of absorption of direct and reflected visible light.

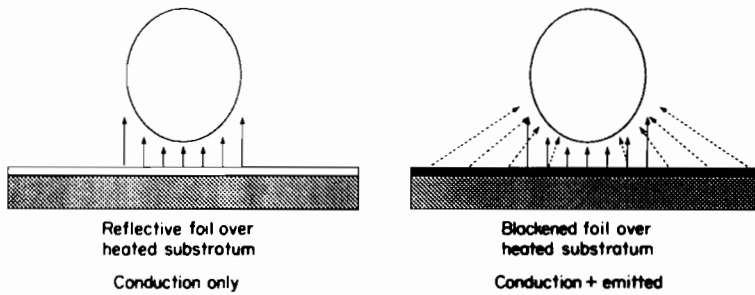


Figure 4. Schematic outline of experiments to test the effects of heat absorbed from the substratum, by either conduction through the air, or by emission of long-wave radiation.

Table 2. Analysis of variance for abdominal time constants during cooling

Factor	<i>F</i>	<i>p</i> > <i>F</i>	<i>r</i> ²
Main effects			
Species	0.42	0.524	0.001
Wind speed	89.62	<0.001	0.895
Interactions			
Species × wind speed	1.00	0.409	0.010

which has an emissivity close to unity (Thomas, 1980). The blackened foil would therefore emit long-wave radiation, and the beetle could be warmed both by conduction through the air and by absorbed long-wave radiation. Any difference in the beetles' temperatures between the shiny foil and the blackened foil would be due to absorption of long-wave radiation from the ground.

The data were analysed by analysis of covariance, with substratum temperature being the covariate.

Semi-natural conditions. Four individuals of each species were used for these experiments. Beetles were prepared as described above. The wind speeds tested were 0, 1, 2, and 3 m s⁻¹.

Two types of sands were used: (1) a white sand from a beach along the False Bay coast, south of Cape Town. This sand is somewhat whiter than sand from the white dunes along the Skeleton Coast; (2) a dark reddish sand, brought to Cape Town from the dunes near Rooibank.

The sand in the petri dish was trowelled so that its surface was flat and coplanar with the floor of the wind tunnel. The overhead lamp was used to illuminate the substratum. The sand was not heated from below by the hot plate, but the overhead lamp was sufficient to warm the sand surface to roughly 50°C. Prior to an experiment, the beetle was positioned downwind from the illuminated area of the test section. The experiment was begun by moving the beetle forward into the illuminated area and over the warmed substratum. The beetle's rate of temperature change and equilibrium temperature was measured as described above.

Results

Convection alone

From 0 to 2 m s⁻¹, wind speed significantly affected the time constant for cooling (Fig. 5; Table 2). There was no significant difference between the time constant for cooling at 2 and 3 m s⁻¹ (Fig. 5). The color of the beetle had no significant effect: time constants did not differ significantly between the two species, either as a main effect or as an interactive factor with wind speed (Fig. 5; Table 2).

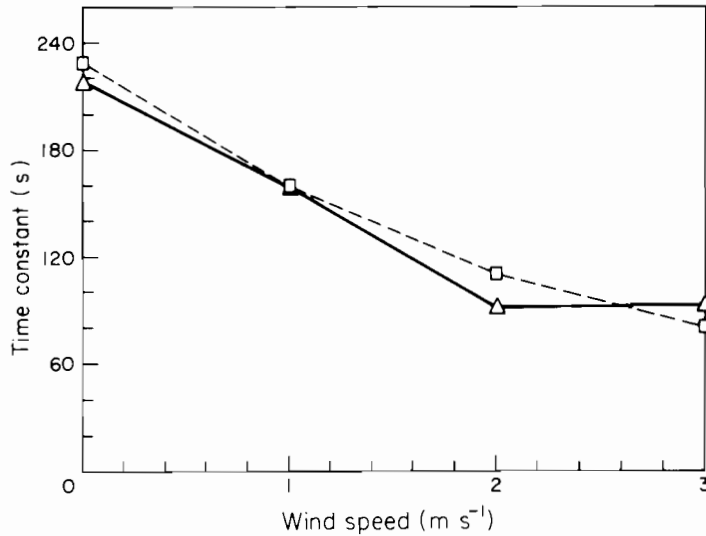


Figure 5. Time constants (s) for cooling of abdominal temperature of two Namib tenebrionids as a function of wind speed. Points represent means. —, *O. unguicularis*; ----, *O. bicolor*.

Direct and reflected visible radiation

The results of this experiment are plotted in Fig. 6, and the results of the analyses of variance are reported in Table 3. At all wind speeds tested, illuminating the beetles with a quartz halogen lamp warmed them above air temperature, signifying that both species absorb significant amounts of visible radiation. Except in still air, the elytron was on average warmed the most, and the cephalothorax was on average warmed the least (Table 3). The beetles were warmed the most in still air, and here, the abdomen of *O. unguicularis* was warmed more than its elytron. As wind speed was increased, the elevation of temperature experienced by the beetles was lessened (Fig. 6; Table 3). The black beetle, *O. unguicularis* was warmed, on average, about twice as much as the white beetle, *O. bicolor* (Fig. 6; Table 3). Beetles exposed to both direct and reflected visible light were significantly warmer than beetles exposed to direct radiation alone (Table 3). The cephalothorax was warmed the most by reflected radiation—the proportional increase of temperature when a reflected component is added was higher for the cephalothorax (roughly 90%) than for either the abdomen (roughly 34%) or the elytron (roughly 48%). *O. unguicularis* appears to be warmed more by reflected radiation than *O. bicolor* is (Fig. 6).

Emitted long-wave radiation and conduction from the substratum

Beetles were warmed when they were placed over a warm surface, but only if the wind speed was very low (Fig. 7; Table 4). At wind speeds of 1 m s⁻¹ or greater, beetle temperature was statistically indistinguishable from air temperature (Table 4). Temperatures of a beetle over an emitting substratum were slightly, but significantly higher than over a non-emitting substratum (Table 4). From Fig. 5, it appears that this difference was entirely attributable to *O. unguicularis*; the temperature of *O. unguicularis* was raised by the addition of surface long-wave radiation, while the temperature of *O. bicolor* was not.

In contrast, when there was little long-wave radiation emitted from the substratum, *O. bicolor* was warmed significantly more than *O. unguicularis* (Fig. 7; Table 4). Ground temperature was a significant covariate factor in determining the temperature elevation of

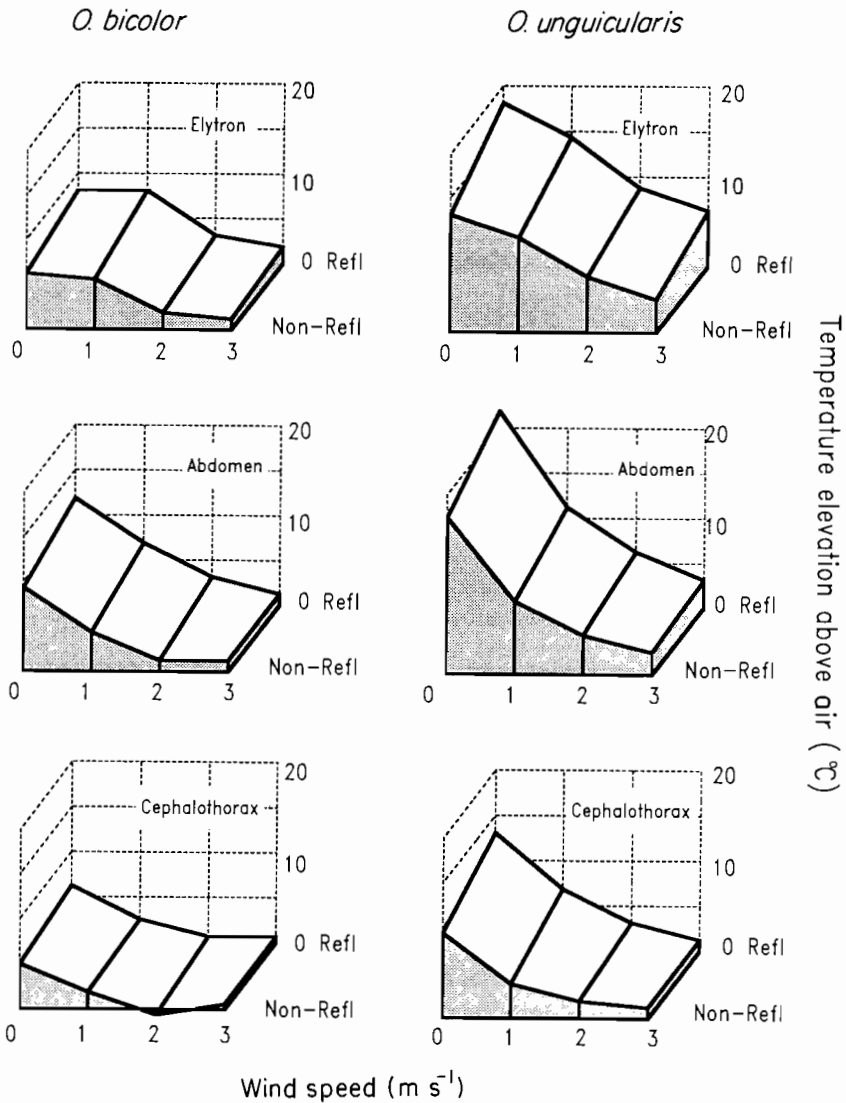


Figure 6. Equilibrium temperatures of two Namib tenebrionids exposed to direct and reflected radiation from a quartz halogen lamp. Temperature elevation is the difference between the body temperature and the air temperature. Four wind speeds (0, 1, 2 and 3 m s⁻¹) and two substrata (reflecting and non-reflecting) are the independent variables. Main effects means are tabulated in Table 3.

the abdomen ($p = 0.032$) and the cephalothorax ($p = 0.023$), but not of the elytron ($p = 0.088$).

Semi-natural conditions

The elytron of *O. unguicularis* was warmed significantly more than the elytron of *O. bicolor* (Table 5; Fig. 8). However, the abdomen was warmed by the same amount for both beetle species (Table 5). The temperature of the cephalothorax differed only slightly between the species, *O. bicolor*'s being the warmer (Table 5).

Table 3. Main effects means for elevation of body temperature above air temperature of *Namib tenebrionids* during illumination by direct and reflected visible radiation

Main effects means	Elytron		Abdomen		Cephalothorax	
	Mean	L.S.D.	Mean	L.S.D.	Mean	L.S.D.
Species						
<i>O. bicolor</i>	4.53	1.23	4.98	1.33	1.92	0.95
<i>O. unguicularis</i>	10.03	—	9.38	—	4.90	—
Wind speed						
0	10.83	1.73	14.61	1.86	7.76	1.33
1	9.42	—	7.46	—	3.30	—
2	4.53	—	3.36	—	1.14	—
3	3.11	—	2.31	—	0.80	—
Substratum						
Reflecting	8.21	1.23	7.95	1.32	3.80	0.95
Non-reflecting	5.73	—	5.92	—	2.01	—

As in all previous experiments, wind speed was a significant factor, with higher winds forcing beetle temperatures close to air temperature (Table 5; Fig. 8). At the highest wind speeds, beetle temperatures were not more than a few degrees above air temperature (Table 5). At slow wind speeds and still air, beetle temperature was tens of degrees above air temperature (Table 5; Fig. 8).

Sand temperature was a significant component of variation in beetle temperature ($p < 0.001$ for all body segments). In the case of cephalothorax temperature, ground temperature explained as much of the variance as wind speed did ($r^2 = 0.405$ and 0.431 , respectively). The dark sand was on average about 2°C warmer than the light sand. Despite this, beetles over light sands were warmer than beetles over dark sands (Table 5), indicating that reflection from the sand contributed significantly to the beetles' energy budgets. Indeed, sand color explained more of the variation of beetle temperature ($r^2 = 0.129$ for the abdomen) than did beetle color itself ($r^2 = 0.001$ for the abdomen).

Table 4. Main effects means for elevation of body temperature above air temperature of *Namib tenebrionids* during heating by long-wave emission and conduction from a heated substratum. Means are least squares means corrected for substratum temperature by analysis of covariance

Main effects means	Elytron		Abdomen		Cephalothorax	
	Mean	S.E.M.	Mean	S.E.M.	Mean	S.E.M.
Species						
<i>O. bicolor</i>	2.66	0.27	4.04	0.38	3.32	0.30
<i>O. unguicularis</i>	1.88	—	3.00	—	2.55	—
Wind speed						
0	10.66	0.38	12.23	0.54	11.40	0.42
1	0.22	—	1.81	—	0.88	—
2	-0.91	—	0.01	—	-0.36	—
3	-0.88	—	0.05	—	-0.17	—
Substratum						
Emitting	2.67	0.27	4.09	0.38	3.48	0.30
Non-emitting	1.87	—	2.96	—	2.39	—

Discussion

A beetle's body temperature is determined by its thermal energy balance, which comprises several avenues of heat flux. For the black *O. unguicularis* and the white *O. bicolor*, our results show that body color affects only one of the components of the heat balance, absorption of visible light. Direct absorption of visible light warms the black beetle significantly more than it does the white beetle (Fig. 6). The black beetle is also warmed more by reflected visible radiation than the white beetle. The additional warming from an added reflected component was of the order of 50 to 80% more heat than from direct radiation alone (Table 3). It is important to remember that the reflected component of

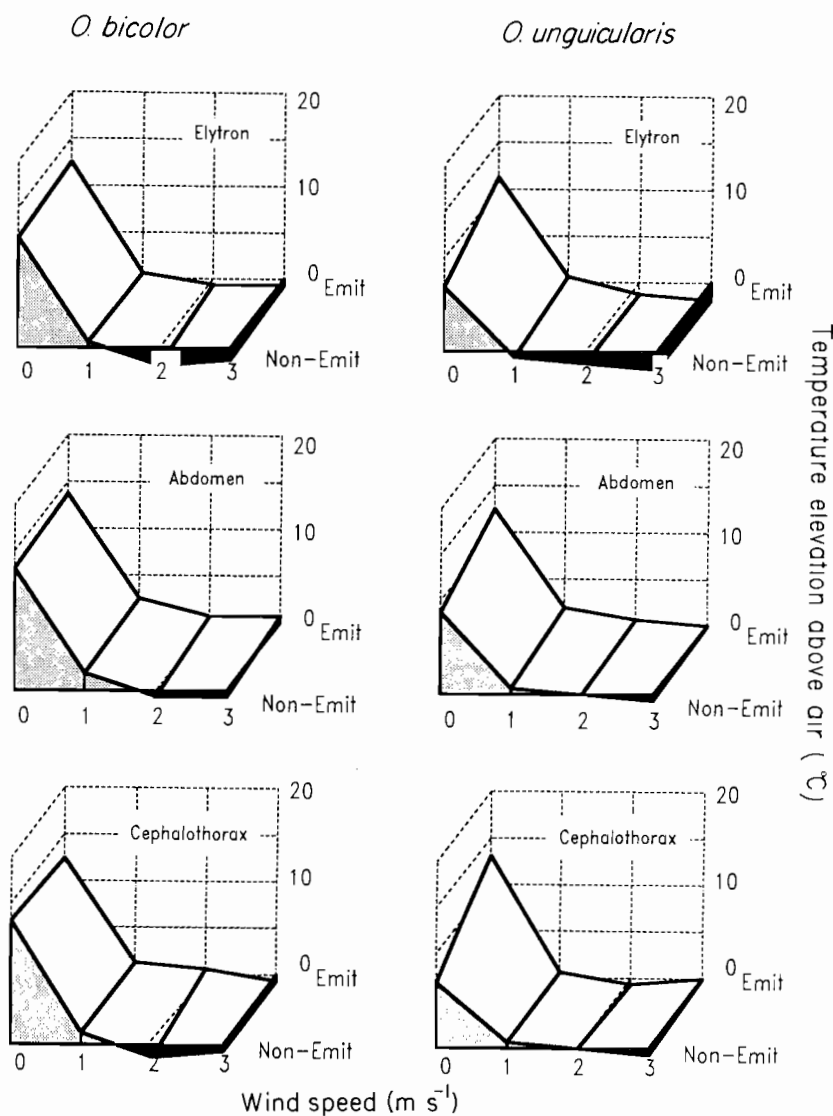


Figure 7. Equilibrium temperatures of two Namib tenebrionids exposed to a heated substratum. Temperature elevation is as defined in Fig. 6. Points are the least squares means, corrected for variation of ground temperature by the analysis of covariance. Four wind speeds (0, 1, 2 and 3 m s⁻¹) and two substrata (emitting and non-emitting) are the independent variables. Main effects means are tabulated in Table 4.

Table 5. Main effects means for elevation of body temperature above air temperature of Namib tenebrionids during semi-natural conditions, with wind, direct and reflected illumination and heated substratum. Substrata are light colored sand or dark colored sand. Means are least squares means corrected for substratum temperature by analysis of covariance

Main effects means	Elytron		Abdomen		Cephalothorax	
	Mean	L.S.D.	Mean	L.S.D.	Mean	L.S.D.
Species						
<i>O. bicolor</i>	8.02	2.22	11.17	2.14	8.45	0.91
<i>O. unguicularis</i>	12.21	—	10.49	—	7.38	—
Wind speed						
0	17.12	3.14	23.88	3.02	18.49	1.28
1	12.83	—	10.95	—	6.95	—
2	6.44	—	5.10	—	3.55	—
3	4.06	—	3.40	—	2.66	—
Substratum						
Dark sand	9.72	2.22	8.60	2.14	6.62	0.91
Light sand	10.50	—	13.06	—	9.21	—

visible light in the experiments was close to the maximum possible, and so these figures for additional heat absorption are higher than they normally would be in nature.

Turning to the other avenues of heat flux, we see that convection heat loss does not differ between the two species at all (Fig. 5). Additionally, we see that wind speed has a significant effect on rate of cooling, indicating these beetles are not trapped in a still boundary layer, as many small terrestrial animals are often thought to be. Consequently, these beetles should be significantly affected by the convective environment they live in.

At any wind speed faster than still air, ground temperature has a negligible influence on beetle body temperature (Fig. 7). In still air, beetles are warmed significantly by a heated substratum, and most of this is undoubtedly due to the warming of the air around the beetle. Curiously, it appears that *O. bicolor* is warmed more in this way than is *O. unguicularis* (Fig. 7). Long-wave radiation from the ground has only a slight effect: adding a substratum heat source from long-wave radiation increases temperature only slightly (Fig. 7), and then only in still air, and apparently only for *O. unguicularis* (Fig. 7). These results are in keeping with similar results of Digby (1955) and Parry (1951), who also showed that long-wave radiation from a substratum has a negligible influence on temperatures of other small insects.

To evaluate what effect body color might have on body temperature, one must consider the thermal environment a beetle is most likely to be found in. A beetle in nature experiences all these avenues of heat flux simultaneously and to different degrees. Under conditions where all avenues of heat flux are combined, it was found that the abdominal and cephalothoracic temperatures, i.e. the body temperatures of *O. unguicularis* and *O. bicolor* did not differ appreciably. One might conclude from this that body color is irrelevant to body temperature for these beetles, but we believe this would be only partly correct. The body temperatures of white and black beetles are not equivalent because color has no effect on body temperature, but apparently because the two species balance their thermal energy budgets differently, arriving nevertheless at the same 'bottom line', i.e. the same body temperature. *O. unguicularis* clearly absorbs more direct visible radiation because its elytra are warmer. *O. bicolor*, by some unknown mechanism, appears to absorb more heat from the substratum. The consequence is very similar body temperatures, despite the profound differences in body color. So, while color does matter to a beetle's thermal energy fluxes, its effect can be modified, obviated and negated in many ways. Indeed, it is striking how insignificant body color is relative to the other factors that govern

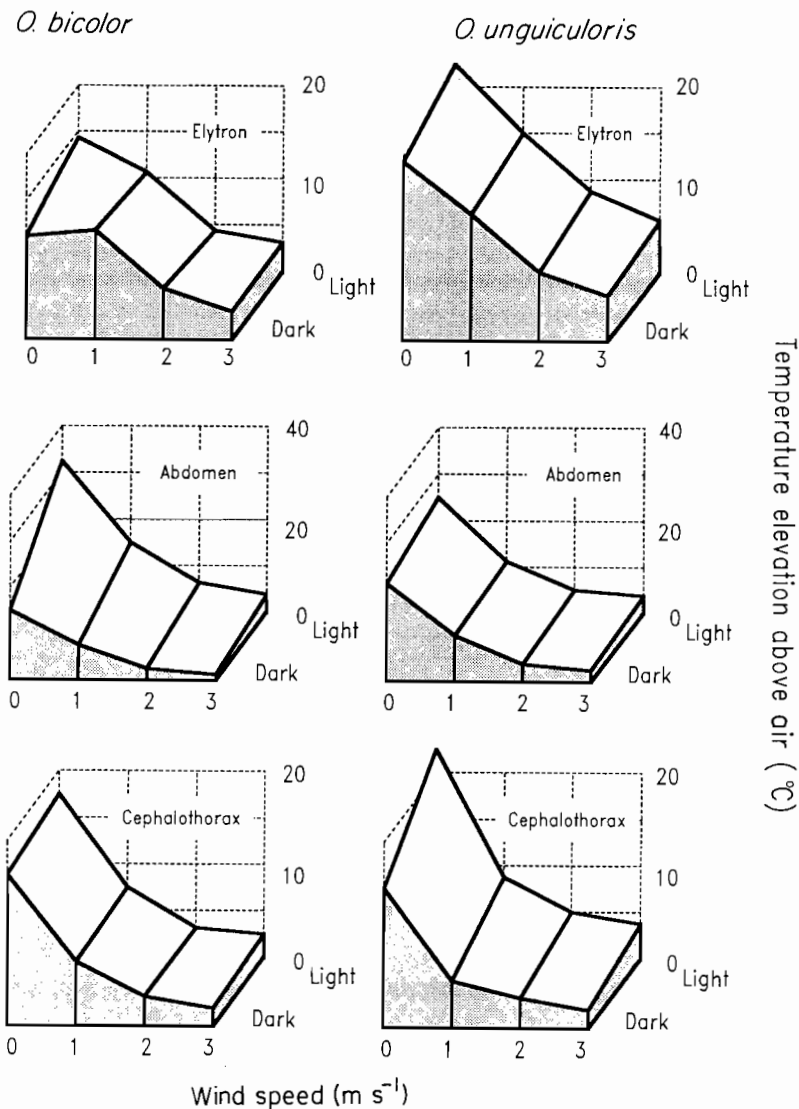


Figure 8. Equilibrium temperatures of two Namib tenebrionids exposed to ‘semi-natural’ conditions of short-wave radiation, heated sand and wind. Temperature elevation is as defined in Fig. 6. Note the scale change for abdominal temperatures. Points are the least squares means, corrected for variation of ground temperature by the analysis of covariance. Four wind speeds (0, 1, 2 and 3 m s⁻¹) and two substrata (light sand and dark sand) are the independent variables.

a beetle’s body temperature. Wind speed was by far the most important factor. Even sand color has a more significant impact on body temperature than body color does.

The stark color difference between *O. bicolor* and *O. unguicularis* presents an interesting case study in the evolution of animal coloration, and the role that thermoregulation might have played in it. Indeed, these beetles have been the objects of several studies with just this aim in mind (Bolwig, 1957; Edney, 1971; Hamilton, 1973; Cloudsley-Thompson, 1978). Some (Bolwig, 1957; Edney, 1971; Hamilton, 1973) have concluded that the white coloration of some Namib beetles has a definite thermoregulatory consequence. Some (Cloudsley-Thompson, 1978) have come to the conclusion that it does not, and that the color variations of these beetles are cryptic or aposematic rather than thermoregulatory.

In considering these contradictory claims, it is noteworthy that studies which favor a thermally important role for body color have tended to minimize the effects of wind. As an example, Edney (1971) made many careful measurements of temperatures of white and black beetles under field conditions, and he took pains to ensure the beetles were exposed to conditions he thought were as natural as possible. However, he concentrated on the beetle's radiative exchanges of heat, and he strove to minimize the effects of wind, doing his measurements only during calm periods, because even slight wind caused the beetle's temperatures to vary considerably. Hamilton (1973) did likewise for his experiments, noting that variations of wind speed made his measurements unrepeatable. We found in our laboratory measurements, however, that wind is the single most important influence on the energy balances of these beetles. Furthermore, observations of the activities of these beetles in the field indicate they are usually active during periods of brisk wind (Lombard *et al.*, in prep.). Thus, it seems a mistake to try to minimize or eliminate its importance, as Edney (1971) and Hamilton (1973) strove to do. Indeed, two independent studies of field temperatures of actively foraging *O. unguicularis* and *O. bicolor* (Seely *et al.*, 1988; Lombard *et al.*, in prep.) have been unable to show any differences between the species.

Our results imply that, when it is considered in its proper energetic context, the colors of the Namib tenebrionid beetles should have little relevance to their body temperatures in nature. Presumably, this would also indicate that the evolutionary impetus for body colors in these beetles has no, or only a slight thermal component, and that explanations of these unusual color patterns must be sought elsewhere.

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