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Reflective Wax Blooms on Black Namib Desert Beetles Enhance Day Activity

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Reversible colors brought about by wax blooms are not normally found in arthropods. However, many beetles in the Namib and other deserts are covered with reversible pastel wax blooms. These desert beetles are day-active, and moreover, substrate-dependent as they cannot fly. Do the wax blooms confer a means of off-loading radiant energy, due to increased reflectance, thus slowing down heat gain and water loss for the beetles? If so, this would allow access to surface conditions deleterious to their black counterparts. We assessed the color qualities and reflectance properties of these various wax blooms. This was carried out over the visible spectrum which covers some 50% of solar radiation. All the wax bloom colors found on beetles were of low purity and saturation, characteristics of mixed colors. These properties contributed to the flat reflectance curve obtained over a wide range of wavelengths comprising the visible spectrum. Up to one-half of the visible sunlight can be reflected by beetles having a wax bloom. This probably accounts for their ability to be active on the sand surface during times of the day denied beetles with a black cuticle surface.

Colors and reflective properties of desert arthropods have been the subject of much controversy. If highly reflective, the surface of desert arthropods is thought to be of little thermal value due to the amount of radiant energy in the environment. Also, the paradox of so many species living in deserts being black has led people to believe that black coloration must not add significantly to their heat load [1]. The small size and surface-to-volume ratios of arthropods would further prevent protection by surface color. However, evidence is accumulating which indicates that surface colors and their reflective properties are important in the thermal strategy of desert arthropods [2 – 5]. Reflectance measured in the field for a number of insect species indicates that increased reflectance of the surface correlates with habitats having increased irradiance levels [6]. Therefore, might the color and the reflective properties of wax blooms of Namib Desert beetles enhance their diurnal activity? In the Namib Desert, Namibia, many species of tenebrionid beetles have a black cuticle covered with a wax bloom. Wax blooms on these species are either localized or widespread over the surface of the beetle. The ventral surface of the insect is always white while the dorsal surface is colored. These wax blooms are yellow, white, red, or pink. The number of beetle species having a wax bloom increases from the cool coastal fog desert (few) to the hot dry inland desert (many) [7].

We collected tenebrionid beetles belonging to the tribes Adesmiini and Zophosini throughout the central Namib desert and transported them to CSIR in Pretoria, South Africa where reflective properties were measured in the visible region of the spectrum (380 to 750 nm). The apparatus used to measure reflectance of the surface colors was modified from equipment orginally designed to measure colorimetric properties of small diamonds [8]. The trichromatic components, X, Y, Z, derived from the spectral measurements, which define a color, were plotted on a C.I.E. (Comm. Int. de l'Eclairage) 2° Chromaticity diagram (Photo Research, Burbank, California). The purity and dominant wavelength for each colored wax bloom was obtained from this diagram. In addition, the total spectral power which could be reflected by the beetle's integument in sunlight was calculated for the visible wavelength region. The solar radiation of these wavelengths repre-

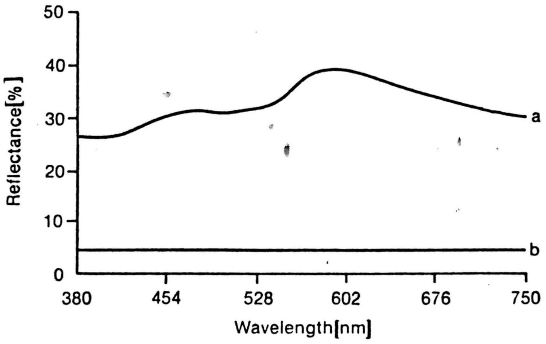

Fig. 1. Reflectance of the dorsal surface of *Zophosis mniszechi* with the pink wax bloom (a) and without (b). The spectrophotometric measurements were made between 380 and 750 nm in steps of 10 nm. Sixty readings were taken at each wavelength and averaged. A quartz halogen projector lamp with a compact filament was used as a light source. It was placed inside a cylindrical housing in order to reduce unwanted stray light. One condenser lens focused the image of the lamp filament on a small aperture of an iris diaphragm of which the size could be varied. The second condenser lens focused the image of the diaphragm aperture through a 25-mm diameter aperture at the front towards an 8-mm aperture at the back of the 100-mm integrating sphere, whose inside was painted with high-reflecting barium sulfate paint. The dorsal surface, covered with the wax bloom, of the beetle was mounted onto the back of the hole in the integrating sphere and affixed with matt black tape. Integrated light from the sphere passed through a third aperture into a 100-mm focal length double monochromator which had a photomultiplier tube as detector, powered by a stabilized high-voltage supply. The signal from the photomultiplier was amplified by an operational amplifier, measured by a digital voltmeter and recorded by a desk-top computer (HP 86B). The computer also controlled the step motor which selected the appropriate wavelength on the exit of the monochromator. Since glass lenses were used it was not possible to extend measurements to shorter wavelengths as the lenses absorbed most of the ultraviolet radiation. Care was taken in handling the beetles as the wax bloom was easily abraded off the surface

sents about 50% of the total solar radiation which reaches the earth. For these calculations the spectral irradiance values of total daylight as measured in Pretoria, South Africa were used [9].

The wax bloom colors were all unsaturated, as indicated by the low purity values (Table 1). This should be advantageous for these substrate-dependent diurnal beetles; since saturation reduces light reflection over a wide spectral region [10]. The light reflection over a wide spectral range is also advantageous in reducing rapid heat gain from sunlight for these beetles. Indeed, if the wax bloom is removed from *Zophosis testudinaria* (pink) and the cuticle temperature is monitored under desert conditions, the black surface soon reaches a lethal level of 44 °C (unpublished data) [11]. Therefore, wax blooms enhance the effect of behavioral thermoregulation as the cuticle surface slowly accumulates solar energy when beetles are out on the surface shuttling between small grass clumps across open patches of sand. In contrast, cuticle colors of much higher saturation (narrow reflectance), as in the metallic colors of tiger beetles, are ineffective in reducing heat gain from solar radiation [12].

In all species of diurnal tenebrionid beetles examined the wax bloom increased the reflectance of the cuticle surface. Furthermore, a fairly flat re-

Table 1. Color characteristics of wax blooms of selected Namib Desert beetles. The field-collected beetles were killed in ethyl acetate and mounted onto the back of the integrating sphere, exposing a 2-mm surface area, covered with max bloom, centered in the light beam. Care was taken not to abrade off the wax bloom by handling the insects with forceps. From the spectral reflectance measurements the trichromate components X, Y, and Z which define a color were plotted on a C.I.E 2° Chromaticity diagram in order to obtain the purity and dominant wavelength of each colored wax bloom

Name	Field-perceived color	Trichromatic components		Dominant wavelength [nm]	Purity	Color from C.I.E. 2° diagram
		X	Y			
Onymacris plana	Bluish-white	0.312	0.328	489	0.08	Blue-green
O. rugatipennis albotessallata	White	0.352	0.358	573	0.12	Green-yellow
Epiphysa arenicola	Blue	0.324	0.345	506	0.03	Black
Zophosis orbicularis	Blue	0.317	0.335	494	0.05	Black
Z. mniszechi	Pink	0.372	0.373	578	0.22	Yellow-orange
Z. testudinaria	Pink	0.397	0.372	585	0.30	Yellow-orange
Z. omnigena	Red	0.402	0.369	587	0.31	Yellow-orange
Z. fairmairei	Yellow	0.395	0.413	573	0.42	Yellow

Table 2. Total amount of solar energy (mW/cm^2) reflected by Namib Desert beetles with and without the surface wax, calculated from total daylight radiation of Pretoria, South Africa between 380 and 750 nm. This was found to be 40 mW/cm^2 and is about 50% of the total radiation

Name	No bloom	Daylight reflected [%]	With bloom	Daylight reflected [%]
Onymacris plana	1.5	3.0	5.7	11.4
Zophosis fairmairei	4.1	8.2	10.0	20.0
Z. testudinaria	1.8	3.6	10.4	20.8
Z. mniszechi	1.8	3.6	13.2	26.4
Onymacris rugatipennis albotessallata	2.0	4.0	5.9	11.4

flectance curve throughout the visible spectrum was obtained. For example, *Zophosis mniszechi* with and without the pink wax bloom is seen in Fig. 1. The spectral daylight reflected power of the wax bloom of the same beetle is seen in Fig. 2. The total amount of daylight reflected by the surface wax of *Z. mniszechi* represents over one-half of the radiation in the visible spectrum (26.4 %; Table 2). Species with a bluish or whitish wax bloom appeared to reflect only about half this amount (*Onymacris plana,* 11.4 % and *O. rugatipennis albotessallata,* 11.4 %; Table 1, 2); apparently due in part to the fragile nature of the waxy material which easily abrades. If field measurements could be made on these beetles without handling them, the total amount of solar energy reflected would be greater. The waxy material found on these beetles has a very rapid rate of renewal [13]. Under field conditions of the Namib, wax blooms can be renewed in 8 to 24 h [13]. This is much more rapid than the 7 to 10 days required for renewal of the wax bloom for a Sonoran desert beetle, *Cryptoglossa verrucosa* [14]. Certainly, this rapid rate of renewal could be a useful adaptation for life in the Namib, where humidity is low and sand surface temperatures are often above 70 °C. *Onymacris plana,* a Namib beetle extending across the entire climatic gradient is an indicator of this aridity. Along the coast in the cool fog desert it has little or no wax bloom but it is completely covered with it in the hot inland portion of the desert [15]. Another Namib species, *Cauricara phalangium,* is a seasonal beetle which emerges with a white bloom. Water loss rates measured from field-collected beetles after emergence were significantly less than those measured at the end of the season when the glands responsible for the wax bloom secretion were inoperative [16]. Field reflectivity measurements of this beetle confirmed increased reflectance of the surface white wax bloom [17].

For all these Namib beetles the wax blooms play a role in water balance by lowering the transpiration rate and in their thermal balance by retarding the rate at which radiant energy is accumulated. For example, two species, *Zophosis mniszechi* (pink) and *Z. moralesi* (black), which are found in the same Namib Desert habitat, were observed for several days in order to determine their surface activity. It was found that the beetles which produced the wax bloom over the black cuticle were surface-active for longer periods of time than the black species which produces no bloom (unpublished data) [18]. The waxed bloomed species, *Z. mniszechi,* stayed out longer in the heat of the day (0.5 h) and reemerged earlier (2.5 h) in the afternoon when air temperatures still exceeded 40 °C and sand surface temperatures were 68 °C [18]. The advantage, therefore, which the wax blooms confer, enables beetles to stay on the surface for longer periods of time for foraging and mating while being protected against high radiant energy.

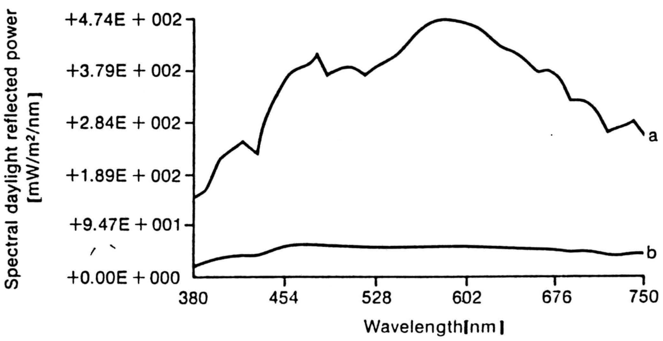

Fig. 2. The spectral daylight reflected powers (mW/m²/nm) for *Zophosis mniszechi* with its pink bloom (a) and without (b). For these calculations the spectral irradiance values of the total daylight as measured in Pretoria, South Africa were used [9]

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