Beetling the heat: the thermal cons

Onymacris plana, a Namib Desert beetle
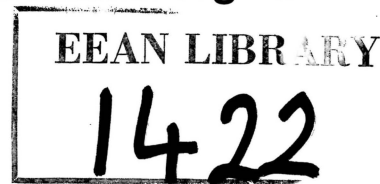
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Short title: Running cools a desert beetle

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Abstract. *Onymacris plana* (Coleoptera: Tenebrionidae) is a black beetle which runs, at a high speed for a pedestrian insect, in direct solar radiation in the Namib Desert, a behaviour expected to impose potentially lethal thermal stress. In the laboratory, we exposed male and female beetles to combinations of radiation, air temperature and wind comparable to desert conditions, and simulated the forced convection of running by a head wind. Peak radiation caused the temperature of stationary male beetles to rise at about $6°$ C min^{-1} and females at almost $4°$ C min^{-1}. However, at peak radiation, the simulated convection of running could drop the equilibrium body temperature of the beetles by more than $10°$ C. Using fine thermocouples attached to a fishing rod, we measured the body temperature of male beetles active in their natural habitat, with only slight disruption of their locomotion. We confirmed that, in the conditions of high radiation, low ambient temperature and low wind characteristic of the morning surface activity period, body temperature dropped, rather than rose, when the beetles ran. The effect depends partly on efficient locomotion, and consequently lower than expected metabolic heat production. We believe that ours is the first report of exercise-induced cooling in a pedestrian animal.

Introduction

The apterous beetle *Onymacris plana* (Coleoptera: Tenebrionidae) lives on the sparsely vegetated dunes of the central Namib Desert, an arid environment subject to intense solar radiation which creates extremely high sand surface temperatures. Any organism which is active diurnally on the dune surface must be able to maintain its body temperature below lethal limits by restricting heat gain or by augmenting heat loss, preferably by non-evaporative means if it is to avoid dehydration.

O.plana is distinctive amongst Namib tenebrionids both for the speed at which it runs as well as for its peculiar discoid-like shape. It is the swiftest runner of all the Namib beetles and, to our knowledge, the fastest pedestrian insect ever recorded, having an average running speed close to 1 m s^{-1} (Nicolson, Bartholomew & Seely, 1984), a speed equivalent to 50 body lengths per second. The beetles are commonly seen sprinting, sometimes covering distances of more than 100 m, from one vegetation clump to another in their search for food and mates, even at times when sand surface temperatures is above 50°C. Despite its small size *O.plana* runs at low mass-specific metabolic cost (Bartholomew, Lighton & Louw, 1985). The beetles are dorso-ventrally flattened, with fused elytra which are flared out laterally giving the animal a stream-lined appearance (Fig. 1a). Although this shape, purported to act as an airfoil and generate aerodynamic lift (Bartholomew, Lighton & Louw, 1985), is well developed only in the male beetles (Fig. 1b), the females, with their slightly rounder body forms (Fig. 1c), are able to run at speeds equal to that of the males. The large horizontal surface areas of the beetles expose them to high radiant heat loads, which are intensified by their black coloration (Henwood, 1975a; McClain, Kok & Monard, in press).

This paper addresses the possibility that *O.plana* may ameliorate its thermal status by running. Increased convectional cooling may exceed the rate of heat gain from metabolic processes during running, and the excess cooling may partially offset radiant heat gains. Initially we conducted a laboratory study, in which radiation, wind speed and ambient temperature were controlled, and demonstrated that substantial cooling could indeed be induced in a radiant field, by increased air movement across the body surface. Field studies corroborated these results and indicated that *O.plana* is active under conditions favourable for exercise-induced cooling, though its tolerance of thermal stress during surface activity depends not only on running but also on access to the shade of sparse vegetation.

Materials and methods

The work was carried out at the Desert Ecological Research Unit of Namibia situated at Gobabeb (23°34'S, 15°03'E; elevation 408 m), in the Namib Desert. The animals used in laboratory studies were collected from dunes near Gobabeb that are well-populated with the beetles. In captivity, the beetles were housed on dune sand at air temperature of 20–25° C with a photoperiod following that of the external environment, and maintained on an *ad libitum* diet of rolled oats, lettuce and apple. Dead beetles required in the experiments were killed over ethyl acetate immediately prior to use.

Activity patterns of the beetles were studied in a well vegetated interdune valley, 10 km WNW of Gobabeb. Perennial plants, *Trianthema hereroensis*, *Stipagrostis sabulicola* and *Cladoraphis spinosa*, occur between large hummocks of sand covered with the desert-adapted

cucurbit *Acanthosicyos horrida*. The valley supports a rich fauna of *O.plana* which bury beneath the plants when inactive and forage on wind-blown detritus in the open at the base of the hummocks. The beetles are most commonly found running between clumps of the perennial plants on the dune base, but are also found in areas of the dune field devoid of vegetation. *Onymacris plana* is an active animal; its mean sprint length is 40 m ($n=63$) and may be over 100 m. Beetles may travel 10 km in a day (Roer, 1975).

Body temperature measurements. The body temperature (T_b) of both dead and live beetles was measured using indwelling thermocouples. A fine thermocouple (copper-constantan, TW40) was implanted dorsally into the thoracic musculature at a depression on the pronotum occurring to the right of the midline, thereby avoiding any damage to the dorsal vessel. The thermocouple was inserted to a depth of three millimetres through a small hole made in the cuticle with an insect pin (size two) and secured in place with a drop of cyanoacrylate adhesive. The fine thermocouple wire was stepped up to a more robust wire (TW26) and terminated in a digital thermocouple thermometer (Sensortek Inc., New Jersey). On completion of the measurements the thermocouple was removed from the beetle. Neither the implantation nor removal of the thermocouple had any apparent effect on the beetles' behaviour; animals released after removal of the thermocouple were found active in their habitat on subsequent days.

For the measurement of T_b of beetles active in the field, a three metres long thermocouple was threaded through the eyes of a fishing rod and the junction inserted in the beetle. In this way the beetle did not carry the weight of the thermocouple and the observer was able to follow behind the beetle at a distance and thus avoid affecting its temperature by shadowing the beetle, or influencing its behaviour by too close proximity. Measurements

could be taken frequently without direct contact with the free-ranging animal.

Morphological data. The mass of 58 beetles (29 females, 29 males) was determined (Mettler, AE100). The length and width of their elytra and the dorso-ventral depth of their abdomens, were measured to 0.1 mm with dial calipers. The dorsal surface area, excluding the legs, of 20 dead beetles (10 males, 10 females) was measured from photographs of their dorsal surface, using a polar planimeter (System Amsler, Germany).

Heat transfer in the laboratory. The effect of forced convection on body temperature was tested in the laboratory where radiation, wind speed and ambient temperature (T_a) could be controlled. The body temperature of 18 beetles (6 dead males, 6 live males, and 6 dead females) was examined at an ambient temperature of about 25° C, and a further 6 beetles (dead males) were studied at about 36° C. The ventral surface of the thorax of the beetle was glued to a glass capillary tube and the beetle oriented to face head-on to an air stream of speed 1 m s^{-1} produced by a fan. The fan mimicked the convection produced by a beetle running at its natural speed. A second fan at right angles to the first was used to mimic ambient wind, of different wind speeds: 0.00 m s^{-1}, 0.35 m s^{-1}, 1.00 m s^{-1} and 1.60 m s^{-1} The orthogonal geometry was chosen to separate the effects of simulated running from those of ambient wind: in the field the beetles did not appear to run at any preferred orientation to the prevailing wind (contrary to Nicolson, Bartholomew and Seely, 1984). Wind speed was measured with a hot wire anemometer (Alnor). The coefficient of variance of the wind speed values was used as a measure of air turbulence; a quasi laminar flow of air over the beetle was ensured by attaching louvres to the front of each fan.

A quartz halogen lamp overhead was used as the radiant heat source. By varying the distance between the lamp and the beetle, three radiant fluxes equivalent to those found at

different times of a typical day in the Namib Desert were generated, namely 200 W m^{-2}, 500 W m^{-2} and 900 W m^{-2}. Radiation was measured using a pyranometer (Middleton Instruments, Australia).

Temperature measurements were made at each of the 12 combinations of three radiations and four transverse wind speeds. At each combination the equilibrium thoracic body temperature (T_{be}) of the beetle, under conditions of simulated "running" (front fan on) and "rest" (front fan off), was determined; body temperature was considered to have reached equilibrium when the rate of change in thoracic temperature (T_{th}) was less than 0.2° C min^{-1}. Abdominal temperature (T_{ab}) was measured simultaneously with another indwelling thermocouple. Air temperature (T_a), measured concurrently with T_{be}, using a shaded, white-tipped (Christian & Tracy, 1985) thermocouple (copper-constantan, TW26) was subtracted from T_{be} to give the temperature excess (T_e) of the beetle. The difference between the temperature excess during simulated "running" and that at "rest" was used as an index of the amount of cooling induced by simulated running at each combination of radiation and wind speed.

Radiant heat gain in the field. The ambient radiation at the field work site was measured with a pyronometer at hourly intervals over three days in summer and three days in winter. A mean hourly value for each three-day period was calculated. The radiant energy absorbed across the beetle's dorsal surface was calculated from surface area and radiant flux, assuming that *O.plana* absorbs 95% of the impinging radiation (Henwood, 1975b; McClain, Kok & Monard, in press; Willmer and Unwin, 1981).

Activity patterns. The activity patterns of *O.plana* were determined by walk-through censuses at the field site under a variety of weather conditions. Two paths, each 400 m long,

were walked at 20 min intervals, and the beetles seen within 12.5 m on either side of the path were counted; the black beetles are conspicuous within that distance. The two paths radiated, north and south, from a portable meteorological station where climatic and microclimatic variables were monitored at 20 min intervals concurrently with the walks. The censuses were carried out over six days (three in December, *i.e.* southern hemisphere summer, and three in April/May).

A portable, field data logger (CR21 Micrologger, Campbell Scientific Inc.) was used to record radiation, wind speed, and temperature (ambient, sand surface, 15 mm above the sand surface, and black bulb). The temperature of two dead beetles (one male, one female) was also measured every 20 minutes with indwelling thermocouples. The wind speed at "beetle height" (15 mm above the sand surface) was measured using a hand-held anemometer; the mean of six readings was measured over a minute. The temperature excess (T_e) of the beetle was calculated as the difference between body temperature of the dead beetles (T_{bdead}) and the air temperature at 15 mm above the sand surface (T_{15}), and regressed against the meteorological variables.

Body temperature of field active beetles. Thermocouples were implanted into live male beetles (el: 14.6 mm ± 0.3; mean ± SE, *n*=5) and into a recently killed male beetle (el: 15.5 mm ± 0.4; mean ± SE, *n*=5). Each dead beetle was placed on the sand surface in a "standing" position and each live beetle placed on the sand surface and then followed. Body temperature of the dead and live beetles were measured simultaneously at ten second intervals. Activity of the live beetles was noted, and wind speed at "beetle height" measured at ten second intervals.

Body temperature measured during seven periods (86 s ± 6; mean ± SE) of activity of

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five beetles and during four periods (50–460 s in length) of beetles sitting in the shade.

Results

Morphological data.

The morphological parameters defining the different body shapes of male and female beetles are listed in Table 1. The males were significantly broader, shorter, and more dorso-ventrally flattened (two-sample T-test; $P<0.05$) than the females.

Although the females were heavier (two-sample T-test; $P<0.05$), their mean surface area was no greater than that of the males. Regression analysis showed a linear relationship between mass and surface area of both males and females, with the line for male beetles having a significantly steeper slope (non-parametric ANCOVA multiple comparisons among slopes; $P<0.05$), indicating a higher surface area to mass ratio in males.

Heat transfer in the laboratory.

We found, under the controlled laboratory conditions, that, at any given time, radiation, wind speed, and simulated running interacted to determine the beetle's body temperature (non-parametric 3-way ANOVA; $P<0.05$).

The amount of cooling induced by simulated running is plotted against wind speed for four groups of beetles in Fig. 2. Cooling of male beetles by simulated running reduced the temperature excess by as much as 13° C at high radiation and low wind speed. Simulated running had a significant cooling effect at ambient wind speeds of 0 and 0.3 m s^{-1} for all three radiations (Kruskal-Wallis non-parametric ANOVA; P<0.05). At the two higher radiations, his cooling effect was significant even at ambient wind speeds of 1 m s^{-1} (Kruskal-Wallis non-parametric ANOVA; P<0.05). At wind speeds higher than 1 m s^{-1}, simulated running did not contribute additional cooling to the already substantial cooling induced by the ambient wind.

Female beetles (Fig. 2) showed less reduction in body temperature during simulated running than did male beetles. However, radiation had less effect on the temperatures of female beetles than on the males, when at rest (Kruskal-Wallis non-parametric ANOVA; P<0.05). The effect of radiation on male and female beetles did not differ under conditions of simulated running.

At a higher air temperature (Fig. 2), where radiation had less effect on body temperature, the cooling effect of simulated running also was reduced (Kruskal-Wallis non-parametric ANOVA; P<0.05).

The abdominal temperature (T_{ab}) equalled that of the thorax (T_{th}) when the beetles were at rest; however, T_{th} fell significantly below T_{ab} during simulated running, the difference reaching 3° C under conditions of high radiation. The difference between T_{ab} and T_{th} temperature increased linearly with increasing radiation flux (paired T-test; P<0.05) but was not affected by wind speed.

Radiant heat gain in the field.

Figure 3 shows the mean ambient radiation over the summer and winter days, measured during the field activity censuses. The rate at which a beetle's body temperature would rise, as a result of exposure to such radiation, can be predicted from the flux, and the absorption, mass and specific heat of the beetle (left panel, Fig. 4). The predicted rate of rise at peak radiation in the summer was almost 6° C min^{-1} for male beetles and almost 4° C min^{-1} for female beetles. Consequently in the absence of cooling, beetles active in peak radiation would have survival times of no more than a few minutes, before reaching their lethal body temperature (51° C; Edney, 1971).

Activity patterns and micrometeorology.

As an example of beetle activity during warm and cool weather, activity and microclimatic variables are plotted against time in Fig. 5. The histogram illustrates how *O.plana* shifted its activity from a bimodal pattern on a warm day to a unimodal pattern on a cool day. Beetles were active at times when they were exposed to the potentially lethal combination of high radiant flux (above 600 W m^{-2}) and low wind speed (below 1 m s^{-1}).

The radiation-induced elevation of body temperature above air temperature (T_e) of dead male beetles, measured during the field censuses, did not differ from that of the dead female beetles. The data for the two sexes were, therefore pooled and summer ($n=6$) and winter

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($n=6$) values calculated through the day (Fig. 6). As a result of decreased radiation, the temperature excess of the beetles was lower in winter than in summer (Wilcoxon; $P<0.05$), except at 16:00 and 17:00 where the high summer-afternoon winds decreased the temperature excess dramatically. The peak of the summer temperature excess occurred earlier in the day than that of winter, and before the radiation high (13:00). This anomaly was the result of the cool on-shore, SW winds picking up in the late morning (see Fig. 5); a characteristic of seasonal weather changes in the central Namib (Robinson & Seely, 1980).

Body temperature of field active beetles.

Figure 7 compares the body temperature of running beetles and dead beetles in the sun. Body temperatures of running beetles were less than those of the dead beetle, and the deficit increased with duration of run, reaching significance when duration exceeded 60 s (Wilcoxon test; $P<0.10$). Run duration often exceeded the 80 s over which temperature was measured, and the deficit presumably continued to increase. The cooling induced by running was not as efficient as could have been achieved by standing in the shade. Confinement of dead beetles to the shade for periods of ten seconds and longer brought about a significant decrease in beetle Tb (Wilcoxon test; $P<0.05$). However, living beetles do not have the option of remaining permanently in the shade.

Discussion

We have shown that the greatest heat load on *O.plana* is that imposed by direct solar radiation. Not only is the beetle's habitat characterised by a high incident radiation (Fig. 3), but the black cuticle ensures high absorption of this radiation (Henwood, 1975b; McClain, Kok & Monard, in press). Contrary to situation with exercising animals, generally, ambient radiant heat load elevates body temperature more than metabolic heat load, even at maximum exercise (see Fig. 4). The amount of heat gained by male beetles from radiation was five times that gained from energy expended whilst running at high speed. It is therefore of no surprise that, at ambient wind speeds of 6 m s^{-1}, the body temperatures of resting beetles were found equal to those of beetles having completed a sprint across the dune base (Nicolson, Bartholomew & Seely, 1984). We have now shown that, particularly at lower ambient wind speeds, the heat loss by forced convection induced by running exceeds the metabolic heat produced, so exercise in *O.plana* actually can result in a drop in body temperature.

Exercise-induced cooling is not unknown in thermal biology. The rate of convective heat transfer is so great in water (Mitchell, 1974) that most aquatic animals have difficulty in maintaining body temperature significantly higher than the surrounding water temperature, even during exercise. Large aquatic endotherms, such as marine mammals, do maintain a higher temperature. In man, an occasional aquatic animal, the increased metabolic heat production during swimming does not compensate for the high convective heat loss rates (see Mitchell, 1977), and swimming leads to a drop in core temperature in cold water (Hayward, Eckerson & Collis, 1975; Sloan & Keatinge, 1973).

Even in air, with much lower convective heat transfer coefficients, exercise-induced

cooling can occur provided air speed is high enough. Flying-induced convective cooling has been shown to be advantageous to heat-stressed animals. The tiger beetle *Cicindela tranquebarica* flies when temperatures on the ground become too high; its low wing load and low wing beat frequency generate little metabolic heat and the increased convective cooling during flight causes a decrease in body temperature (Morgan, 1985). Male blue-black grassquits (*Volatina jacarina*) of Central America are able to engage in an energetic aerial courtship display at times of the day when temperatures are stressful because the display dissipates as much heat convectively as it produces metabolically (Weathers, 1986).

As far as we are aware, however, ours is the first observation of exercised-induced cooling in a terrestrial animal. *O.plana* readily dissipates heat to the environment by convection: it has a high convective heat transfer coefficient and a high surface area to volume ratio. Furthermore, because it absorbs large amounts of radiant heat there is a substantial temperature gradient between the beetle and its surrounding air, even though the beetle is substrate dependent and confined within the surface boundary layer. *O.plana* runs at such great speeds that, under certain environmental conditions, it is able to augment heat loss above metabolic heat gain, thereby lowering body temperature during exercise.

Cooling by running is effective when conditions ensure a large temperature excess of the beetle above ambient temperature (*ie*. high radiation, low ambient temperatures, low ambient wind speed) and the run is of substantial length and in a direction other than that of the ambient wind so as to increase the relative wind speed. Our observations of activity show that *O.plana* indeed is active at times when radiation is high; wind speed can be low and temperature excess is at a maximum (see Fig. 5). It is at these times that it would not only be advantageous, but also physically possible, for the beetle to lower its body temperature by

running. From the field temperatures of beetles, we found, although the sample size was small, that running-induced cooling indeed takes place during longer runs ($\geq$50 s). Cooling may occur more readily under natural conditions than in our experiments, because the beetles were hampered somewhat by the indwelling thermocouples and may have run at slower speeds and experienced more air turbulence. The sprint time of *O.plana* without a thermocouple attachment was shorter; only 35% of the runs were longer than 50 s and the mean sprint time was 47 s (*n*=59).

Although no-one previously has reported exercise-induced cooling in pedestrian locomotion, in one species of dung beetle, *Heliocopris dillani*, body temperature did not rise during walking (Bartholomew & Heinrich, 1978). In other dung beetle species, and in the cockroach *Blaberus discoidalis* temperature did rise (Full & Tullis, 1990). These measurements were made in still air in the laboratory.

The ability of *O.plana* to cool by running depends not only on their high convective heat loss but also on their low metabolic heat production during exercise, that is their efficient locomotion. Bartholomew, Lighton & Louw (1985) measured the rate of oxygen consumption of male *O.plana* during exercise and at rest. Figure 8 shows the cost of locomotion of *O.plana* and some other insects in relation to the minimum cost of locomotion calculated for pedestrian species. The cost of locomotion of *O.plana* lies below the regression curve, though it is not as superior to other insects as suggested elsewhere (Bartholomew, Lighton & Louw, 1985). Locomotion in *O.plana*, however, does generate less metabolic heat than one would predict from the beetle's mass.

The difference measured between abdominal and thoracic temperatures of *O.plana* was greatest during the forced convection caused by running, especially at high radiations when

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body temperature was high. The forced convection has its greatest effect on the anterior, more exposed parts of the body, thereby cooling the thorax, and presumably the head, to a greater degree than the abdomen. The difference in temperature would not have resulted from the shunting of warm blood to the abdomen to off load heat as found in flying endothermic insects (Heinrich, 1976), because in our laboratory simulations, the beetles were not actually exercising.

Female *O.plana* beetles, due to their lower surface area to mass ratio, partly as a result of their rounder shape, have a greater thermal inertia than the males. The radiant heat gain was less for the females, and forced convection had less of a cooling effect. Examining the temperature excess of male and female beetles under field conditions masks their differences; male beetles heat up and cool down at a greater rate than females and would thus have a greater temperature excess in high radiation, still conditions and a smaller temperature excess in windy conditions. One cannot predict whether female beetles can dissipate enough heat by running to lower body temperature, as no data on their metabolic rate are available. If the aerodynamic form of male beetles is responsible for the low cost of locomotion, as suggested by Bartholomew, Lighton & Louw (1985), then female beetles may have a higher increase in energy expenditure on running than males. Also, the convective heat transfer coefficients of female *O.plana* are lower than those of males (Henwood, 1975a).

Although running is not as efficient at reducing body temperature as shading the body from direct solar radiation, it enables *O.plana* to be mobile on the sand surface during thermally stressful periods. Since vegetation occurs as small isolated clumps at the base of dunes, it is important for beetles to be mobile in order to forage and seek mates. Running at high speeds between clumps of vegetation allows the beetle to extend their activity period

into conditions that are otherwise potentially lethal; in this way, they may be active at times when other animals sharing the same habitat are unable to be active on the surface.

Acknowledgements

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Figure Legends

Fig. 1. *Onymacris plana*: (a) dorsal view of the male beetle, (b) frontal view of male, and (c) frontal view of female. The female beetles have slightly rounder body forms. (Drawings by Valerie Myburgh).

Fig. 2. Change in body temperature (measured with respect to air temperature; mean ± SE, $n=6$) induced by simulated running at different ambient wind speeds in four groups of beetles tested in the laboratory at different radiant fluxes: 900 W m^{-2} (**x**), 500 W m^{-2} (**o**), and 200 W m^{-2} (●).

Fig. 3. Ambient radiant flux (mean ± SE, $n=3$) measured in the dunes of the Namib Desert over three days during summer (●) and winter (O).

Fig. 4. Predicted rate of increase of body temperature for male (●) and female (O) beetles. Left panel: rate induced by various radiant fluxes, as calculated from absorption, mass and specific heat. Right panel: rate induced by metabolic heat production at different running speeds, as calculated from oxygen consumption (data of Bartholomew, Lighton & Louw, 1985), mass and specific heat.

Fig. 5. Activity of *O.plana* on a summer's (left) and a winter's day (right), and concurrent body temperature of dead *O.plana* (O), temperature excess of body temperature above air temperature (●), radiation (solid curve), and wind speed 15 mm above the sand surface (■).

Fig. 6. The temperature excess of body temperature of dead *O.plana* above air temperature measured 15 mm above the sand surface (mean ± SE, *n*=6) during summer (O) and winter (●).

Fig. 7. The measured difference in body temperature (mean ± SE) between a dead beetle in the sun and that of a live, running beetle (●, *n*=7) in the same environment, plotted against duration of exposure. Running beetles covered about 1 m s^{-1}. The broken line shows the predicted change in temperature when running at 1 m s^{-1} based on metabolic rates.

Fig. 8. The relationship between the minimum cost of pedestrian locomotion and mass for some insects, compared with a composite relationship calculated for mammals, birds, lizards, salamanders, crustaceans and insects (Full and Tullis, 1990). The data points are labelled: Op (*Onymacris plana*; Bartholomew, Lighton & Louw, 1985), Ps (*Pachysoma hippocrates*), Ph (*Pachysoma hippocrates*) and Af (*Anthia fabricii*) (all Lighton, 1985) are beetles; Ac (*Atta columbica*; Lighton, Bartholomew & Feener, 1987) is an ant; Gp is the locust, *Gromphadorhina portentosa* (Herreid, Full & Prawel, 1981); Bd is the cockroach *Blaberus discoidalis* (Full and Tullis, 1990).

Table 1. Morphological data (mean ± SD; n=29) for female and male Onymacris plana.

	Mass (g)	Elytral length (mm)	Elytral width (mm)	Dorso-ventral depth (mm)	Surface area (mm^2)*
Females	0.87± 0.23	15.4 ± 1.3	12.7 ± 1.5	8.2 ± 0.7	193 ± 40
Males	0.65 ± 0.18	13.5 ± 1.2	14.1 ± 1.9	6.9 ± 0.6	203 ± 44

* dorsal surface area only; n=10