

Ecological correlates of locomotion speed, morphometrics and body temperature in three Namib Desert tenebrionid beetles

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In closely related tenebrionid beetles (tribe Adesmiini) in the Namib Desert, locomotion speeds and body temperatures are correlated with the ecology of different species. We measured average running speeds of 90 cm/s for *Onymacris plana*, 23 cm/s for *Physadesmia globosa* and 3 cm/s for *Epiphysa arenicola*. The speed achieved by *O. plana* is probably the highest yet recorded for any pedestrian insect. Relative speeds of the three tenebrionids are related to leg length and muscle mass, and to behavioural thermoregulation. The beetles are flightless and ectothermic, and exercise does not elevate their body temperature.

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In naverwante spesies van die familie Tenebrionidae, is die spoed van beweging en liggaamstemperatuur met die ekologie van die verskillende spesies gekorreleer. Die volgende gemiddelde snelhede van beweging is gemeet: 90 cm/s vir *Onymacris plana*, 23 cm/s vir *Physadesmia globosa* en 3 cm/s vir *Epiphysa arenicola*. Die snelheid wat deur *O. plana* bereik is, is waarskynlik die hoogste wat ooit vir 'n landbewegende insek gemeet is. Daar bestaan ook 'n verwantskap tussen die snelheid van beweging van die drie verskillende spesies en die lengte van hulle ledemate asook hulle spiermassa en gedragstermoregulering. Die kewers kan nie vlieg nie, hulle is ektotermies en die aktiwiteit van beweging het nie die liggaamstemperatuur verhoog nie.

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Flightless tenebrionid beetles are conspicuous and abundant in the Namib Desert of south-western Africa, and play an important role in the dune ecosystem (Koch 1961; Holm & Scholtz 1980; Seely & Louw 1980). Their adaptations to the desert environment have received considerable attention, especially with regard to water and temperature relations (see for example Edney 1971a, b; Hamilton 1975; Henwood 1975; Seely 1979).

The Namib tenebrionids occur in three major habitat types: lightly vegetated dunes, gravel plains and well-vegetated, dry river courses. Although many are similar in appearance, they exhibit very different patterns of activity and behaviour (Holm & Edney 1973). We have examined this differentiation in terms of locomotion speed and body temperature for three species which occupy the three habitats listed above: *Onymacris plana* (Péringuey), *Epiphysa arenicola* Penrith and *Physadesmia globosa* (Haag). These species all belong to the same tenebrionid tribe, the Adesmiini (Penrith 1979), and are similar in size and appearance (Figure 1). They are relatively large (0.5–1.2 g), black and flightless, with fused elytra enclosing a subelytral cavity into which the abdominal spiracles open. All are active throughout the year, but whereas *O. plana* and *P. globosa* are strictly diurnal, *E. arenicola* is mainly nocturnal. It may, however, be active during unusually cool, overcast days. The energy metabolism and respiratory patterns of these beetles have recently been examined (Bartholomew, Lighton & Louw 1984).

Materials and Methods

This study was carried out during late May 1983 at the Namib Research Institute at Gobabeb, SWA/Namibia. The Institute is situated next to the Kuiseb River, which separates the southern dune sea from the northern gravel plains. *P. globosa* and *O. plana* were abundant in the dry river bed and on the adjacent high dunes respectively. However, *E. arenicola*, an inhabitant of the river edge and gravel plains, is less common and was therefore collected beforehand and maintained in the laboratory.

Body temperatures (T_b) of free-ranging beetles were measured to the nearest 0.1 °C with copper-constantan thermocouples connected to a Bailey Bat digital thermometer. We measured prothoracic temperatures (T_{pth}) with 40-gauge thermocouples threaded through hypodermic needles and inserted dorso-laterally into the prothorax to a depth of 3 mm. Beetles were captured with gloved hands and their T_{pth} measured within 5 s of capture. Prothoracic temperatures were selected as a measure of T_b in order to avoid the thermocouple entering the subelytral cavity. Temperatures of the sand surface (T_s)

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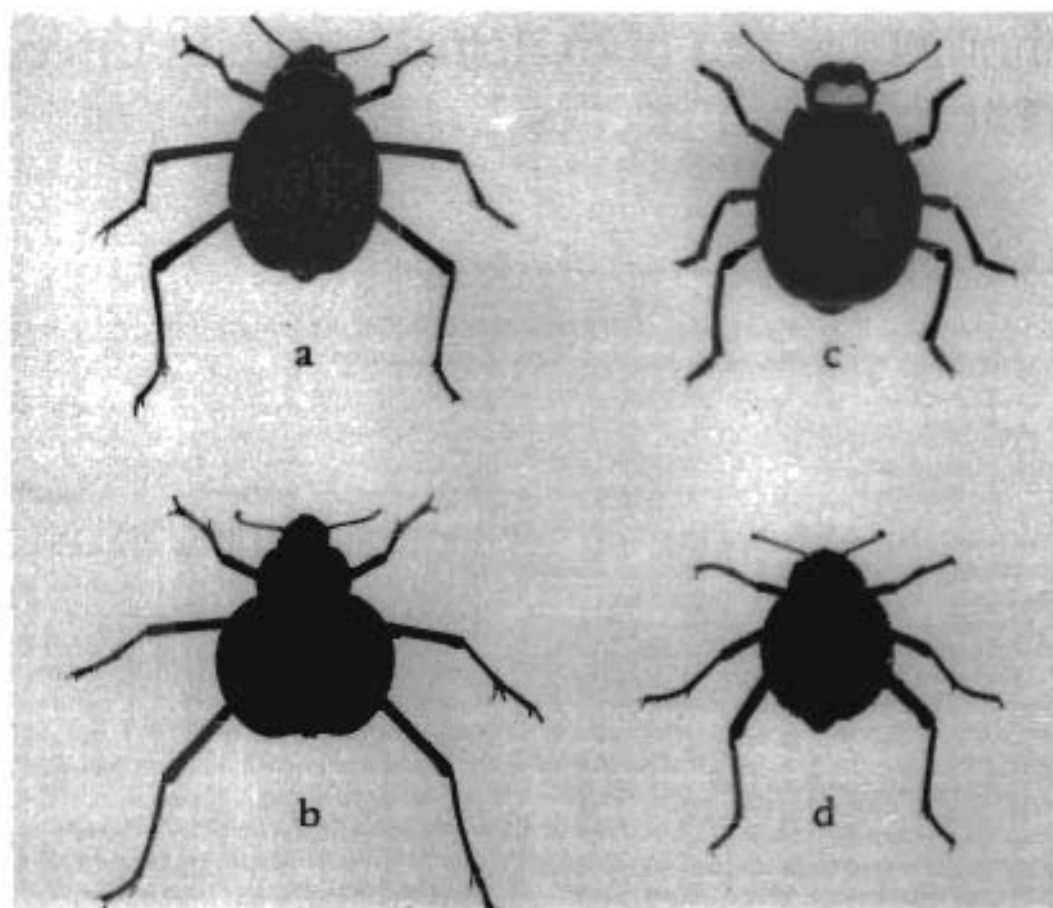


Figure 1 Tenebrionid beetles from the Namib Desert used in the present study: a, female *Onymacris plana*; b, male *O. plana*; c, *Epiphysa arenicola*; d, *Physadesmia globosa*. All to the same scale.

and shaded air temperatures (T_a) at approximately beetle height (1 cm) were also recorded.

Running speeds were timed with a stopwatch to the nearest 0,1 s. The distance travelled was measured to the nearest cm by laying a flexible metal tape measure along the distinctive tracks left by the beetles. This distance was usually about 10 m but sometimes as much as 20 m. The locomotion speed of each beetle was measured three times in succession, normally over the same route, and then averaged. Body temperatures of *O. plana* and *P. globosa* were determined immediately after the final run, together with sand and air temperatures. Body lengths and hind leg lengths were measured to the nearest 0,1 mm with calipers. Masses of individual beetles and of their thoracic musculature were determined to the nearest 0,1 mg, only males being used because the body mass of females fluctuates with egg production.

Results are expressed as means \pm S.D., and statistical significance was determined by the Student's *t* test.

Results

Body temperatures of free-ranging beetles

As expected for ectothermic insects, prothoracic temperatures did not differ by more than 0,2 °C from meso- or metathoracic temperatures measured immediately before or after T_{pb} by insertion of thermocouples at the leg bases ($N = 10$). Prothoracic temperatures of free-ranging *O. plana* were measured at mid-day in clear sunny weather. The beetles were running over the hot sand or sheltering in the shade of nara bushes (*Acanthosicyos horrida*). Mean sand temperature was 42,3 °C and air temperature at a height of 1 cm was 32,8 °C (Table 1). Prothoracic temperatures of beetles caught on the open sand

did not differ from those of beetles resting temporarily in the shade. Nor was there any difference between the sexes ($p > 0,1$). The range of T_{pb} was narrow: 35,8 – 38,9 °C for males and 35,0 – 37,9 °C for females.

P. globosa was most commonly found among the leaf litter beneath *Acacia erioloba* and *Acacia albida* in the dry bed of the Kuiseb River. We measured T_{pb} of this species on two days in late May. The first of these days was characterized by a fog which did not clear until about noon. Because of the cool conditions the beetles remained motionless and partially buried in the leaf litter until temperatures at the sand surface, and thus T_{pb} of the beetles, reached about 21 °C (Table 1). On the second day of measurements *P. globosa* was active in

Table 1 Body temperatures of free-ranging tenebrionid beetles*

Species	Activity	N	T_{pb}		
			Mean \pm S.D.	T_s	T_a
<i>O. plana</i>	Active males	14	36,8 \pm 0,9	42,4	32,9
	Active females	7	36,9 \pm 1,0	41,9	32,6
<i>P. globosa</i>	Inactive	12	19,4 \pm 0,8	18,8	16,9
	Slightly active	23	21,2 \pm 2,2	21,2	19,4
		3	21,5 \pm 0,8	22,9	23,0
	Day 2	Active males	17	29,3 \pm 2,4	27,2
Active females		6	30,0 \pm 2,3	27,5	25,9

* T_{pb} , T_s and T_a denote temperatures of prothorax, sand and air (at 1 cm) respectively.

dappled shade with body temperatures averaging 29–30 °C for both sexes ($p > 0,1$; Table 1).

Running speeds

The running speeds of 20 *O. plana* were measured on level, open sand at the base of the dunes. Sand temperatures and body temperatures of the beetles were measured concurrently. All recordings were made between 11h20 and 15h30 on a clear sunny day, and meteorological readings from the weather station at Gobabeb showed for this period a relative humidity of 16–18%, air temperatures of 30–31 °C and a north-westerly wind of 20–24 km/h. The beetles frequently ran in the depressions between ripples in the sand, i.e. they ran perpendicular to the direction of the prevailing wind, and individual beetles tended to run in the same preferred direction on the three successive runs.

Locomotion speeds of *O. plana* were extremely high (Table 2), averaging 90,2 cm/s or 3,24 km/h. Two of the beetles averaged 115 cm/s. There was no difference in running speeds between the sexes ($p > 0,1$). Body temperatures, measured immediately after the final run, were almost identical to the temperatures of free-roaming beetles measured previously under similar conditions ($p > 0,1$ for both sexes). Exercise, therefore, apparently does not cause any significant elevation in prothoracic temperature in *O. plana*.

Table 2 Running speeds of three species of tenebrionid beetles^a

Species	N	T _s	T _{pth}	Speed (cm/s)
			Mean ± S.D.	Mean ± S.D.
<i>O. plana</i>	20	40,2	36,7 ± 0,9	90,2 ± 13,5
<i>P. globosa</i>	29	33,1	30,5 ± 1,4	23,1 ± 5,7
<i>E. arenicola</i>	12	19,0		3,0 ± 0,8

^aT_s, sand temperature; T_{pth}, prothoracic temperature.

Running speeds of *P. globosa* were recorded on flat sand in the bed of the Kuiseb River, and it is possible that actual speeds among the dry leaf litter may be slightly lower. Prothoracic temperatures of running beetles were similar to those previously measured in active beetles under warm conditions (Tables 1, 2; $p > 0,05$), again showing that T_{pth} does not increase significantly during exercise. Running speeds of *P. globosa* were much lower than those of *O. plana*, averaging 23,1 ± 5,7 cm/s (Table 2). Again, running speeds of males and females were not significantly different ($p > 0,1$).

Locomotion speeds of *E. arenicola* were measured on flat sand in shade in the late afternoon (18h00). Air temperature at 1 cm was 19,2 °C, and the sand surface temperature was 19,0 °C. We did not measure T_b of *E. arenicola*, and assume it was close to the temperature of the surroundings. Running (walking?) speeds of this beetle averaged only 2,98 cm/s (N = 12; Table 2).

Absence of endothermy

As mentioned above, prothoracic temperatures measured immediately after running in *O. plana* and *P. globosa* were no higher than those of free-roaming beetles. We tested this further by forcing male *O. plana* to run continuously in the laboratory for periods of 3–5 min. At a substrate temperature of 17,7 °C these bouts of sustained activity increased the body temperature of the beetles by only 0,93 ± 0,19 °C (N = 7).

Morphometrics

Body lengths of all three species were similar (Table 3). The hind leg was longest in *O. plana* and shortest in *E. arenicola*, although the body mass of the latter was significantly greater ($p < 0,001$) than that of the other two species. Muscle masses of *O. plana* and *P. globosa* differed significantly ($p < 0,001$), and muscle mass as percent of body mass was significantly higher in *O. plana* than in *P. globosa* ($p < 0,001$, *t* test after arcsine transformation). Thus leg length and muscle mass appear to be correlated with running speeds in these tenebrionids. If allowance is made for the relatively heavy exoskeleton, the muscle mass of *O. plana* is impressively high for a flightless insect, and is no doubt related to the remarkable speed of 48,7 body lengths per second achieved by this species.

Table 3 Morphological data for three species of tenebrionid beetles

	<i>O. plana</i> Mean ± S.D.	<i>P. globosa</i> Mean ± S.D.	<i>E. arenicola</i> Mean ± S.D.
Total body mass (mg)	770,0 ± 185,1	625,8 ± 124,5	1154,3 ± 188,6
Muscle mass (mg)	107,7 ± 35,3	49,7 ± 18,7	
Muscle mass as % of body mass	13,81 ± 1,99	7,75 ± 1,66	
Body length (mm)	18,5 ± 1,6	15,3 ± 0,9	19,4 ± 1,2
Length of hind leg (mm)	26,7 ± 2,0	23,7 ± 1,1	19,0 ± 1,4
N	10	10	10

Discussion

Locomotion speed and body temperatures correlate well with the ecology of the three tenebrionids. *Onymacris plana* is an ultrapsammophilous species living on the slope of the dunes in association with sparsely distributed, perennial plants which provide it with food, shelter and shade. We found that the beetles regulated their T_{pth} around 37 °C, running swiftly over the hot sand from one plant to another. This species of *Onymacris* shows a distinct sexual dimorphism, the males having a broader, flattened shape (Figure 1). Although this difference in shape could conceivably affect both T_{pth} and running speed, we found no difference between the sexes.

Physadesmia globosa avoids extensive activity in the open (Wharton & Seely 1982), and its river-bed habitat offers shade and a variety of microenvironments. Body temperatures and running speeds of this species were lower than those of *O. plana*. Both species are able to burrow in sand to avoid extremes of temperature. In contrast, *E. arenicola* is nocturnal, does not appear to thermoregulate behaviourally, and walks very slowly. Its hard cuticle may be an important defence against predators (Wharton & Seely 1982), so that it need not escape by burrowing or running.

Our measurements of T_b in *O. plana* are lower than those reported by Henwood (1975), who found at the same time of year that this species regulated its T_b near 40 °C by means of a bimodal activity rhythm and microhabitat selection. Henwood, however, measured T_b by inserting a thermistor probe between head and thorax. Moreover, his observations were made during warm weather, whereas our study took place during a week with cool mean temperatures. Neither set of observations falsifies Hamilton's (1975) 'maxithermy' hypothesis that many desert insects attempt to maximize the time spent with their T_b at 37–41 °C. Kenagy & Stevenson (1982) measured T_b of tenebrionids in an arid but cooler environ-

ment, and found that beetles were active within a lower range of T_b (10–30 °C) at all seasons. This was interpreted as allowing increased activity at times of greater food availability.

Rates of oxygen consumption during rest and activity have recently been measured in the same Namib tenebrionids used in the present study (Bartholomew *et al.* 1984). Resting rates of oxygen consumption for *O. plana*, *P. globosa* and *E. arenicola*, measured during the evening at a T_a of 22 °C, were indistinguishable. Maximum rates of oxygen consumption, measured while the beetles were running on a treadmill at speeds of up to 22 cm/s and at a T_a of 35 °C, were 7,8 ml/g/h for *O. plana* and 3,8 ml/g/h for *P. globosa*. At all velocities the oxygen consumption of *P. globosa* was substantially less than that of *O. plana*, despite the fact that the treadmill speeds were closer to the running speeds of *P. globosa* under natural conditions.

Running speeds of *O. plana* are probably the highest yet recorded for any pedestrian insect. Table 4 compares locomotion speeds obtained in the present study with data for some other insects. Only the cockroach *Periplaneta* approaches the speed of *O. plana* (McConnell & Richards 1955). Another fast beetle is the predatory tiger beetle *Cicindela* (Evans 1977). Running speeds show little relationship with body size, as exemplified by the similar speeds attained in laboratory studies by the 5-g cockroach *Gromphadorhina portentosa* and the 5-mg ant *Formica fusca* (Herreid, Full & Prawel 1981; Jensen & Holm-Jensen 1980). Different species of the desert ant *Cataglyphis* attain maximum speeds of 33–83 cm/s in the field (Harkness & Wehner 1977).

Table 4 Comparative running speeds of some pedestrian insects^a

Species	Speed (cm/s)	T_a	T_b	Reference
<i>Onymacris plana</i>	90	–	37	Present study
<i>Physadesmia globosa</i>	23	–	30	Present study
<i>Epiphysa arenicola</i>	3	19	~19	Present study
<i>Cicindela</i> sp.	~40	20–23	–	Evans 1977
<i>Periplaneta americana</i>	74	25	–	McConnell & Richards 1955
<i>Gromphadorhina portentosa</i>	3,3	25	~25	Herreid <i>et al.</i> 1981
<i>Cataglyphis albicans</i>	34	–	–	Harkness & Wehner 1977
<i>Formica</i> sp.	2,3	21	–	Jensen & Holm-Jensen 1980

^a T_a , ambient temperature; T_b , body temperature.

Running did not significantly elevate thoracic temperature in either the Namib tenebrionids or in flightless cockroaches (Herreid *et al.* 1981). There are other large beetles which maintain high thoracic temperatures during terrestrial activity (Bartholomew & Casey 1977; Bartholomew & Heinrich 1978), but these are winged, endothermic insects, and their flight muscles are the principal source of heat production. The flightless

Namib tenebrionids show no evidence of endothermy, and the high thoracic temperatures maintained by the diurnal species during activity and running are a result of behavioural thermo-regulation.

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