Absence of endothermy in flightless dung beetles from southern Africa

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Body temperatures of the large, flightless dung beetle *Circellium bacchus* have been measured during walking, ball making and ball rolling, but were not significantly different from black bulb temperatures. *Circellium* is thus strictly ectothermic, unlike winged dung beetles, which are endothermic during terrestrial activity as well as in flight.

Liggaamstemperature van die groot, vlugtelose miskruier *Circellium bacchus* is tydens stap en die vervaardiging en vervoer van misballe gemeet. Hierdie temperature het nie betekenisvol van swartbol temperature verskil nie. *Circellium* is dus streng ektotermies en verskil van vlieënde miskruiers, wat endotermies is gedurende landaktiwiteit en gedurende vlug.

Endothermy in insects is normally associated with flight but has been observed during strictly terrestrial activity in beetles (Bartholomew & Casey 1977a, b). A study by Bartholomew & Heinrich (1978) in Kenya showed that dung beetles are conspicuously endothermic during flight, ball making and ball rolling, and sometimes while walking. Endothermy during terrestrial activity is probably advantageous when competing for fresh dung: this was clearly demonstrated in *Scarabaeus laevistriatus,* a large, nocturnal species which is involved in intense competition for elephant dung (Heinrich & Bartholomew 1979).

Some interesting flightless dung beetles (Coleoptera: Scarabaeinae) occur in southern Africa. Ten flightless species of the genus *Scarabaeus* (formerly assigned to the separate genus *Pachysoma)* occur along the west coast between the Cape and the Namib Desert (Mostert & Holm 1982). The unrelated genus *Circellium* is endemic to South Africa and consists of a single species, *Circellium bacchus,* once widely distributed but now abundant only in the Addo Elephant Park. Body temperatures of this large, diurnal, ball-rolling dung beetle were measured in the present study to find whether they are maintained at elevated levels as in the winged dung beetles already studied.

Observations were made in the field at Addo Elephant Park on 27 and 28 January 1981, when the beetles were active after rain. Body masses were measured to the nearest 0,1 g with Pesola spring balances. Body temperatures were measured with calibrated copper-constantan thermocouples threaded through 22-gauge hypodermic needles and connected to a Bailey BAT 4 thermometer. Beetles were captured with gloved hands and body temperatures measured within 5 s of capture, to the nearest 0,1°C. For metathoracic temperatures (Tmth) the thermocouple was inserted to a depth of 5 mm between the coxae of the second and third pairs of legs. In some cases prothoracic temperatures (Tpth) were recorded with thermocouples inserted ventrally into the approximate centre of the prothorax. Air temperatures (Ta) at approximately beetle height were also recorded, and black bulb temperatures (Tbb) were measured with a thermocouple enclosed in a metal cylinder about the size of a beetle and painted matt black.

Metathoracic temperatures of *Circellium bacchus* engaged in various activities are shown in Table 1. Irrespective of whether the beetles were walking, making dung balls or rolling balls, there were no significant differences between Tmth and Tbb, although both were several degrees Celsius higher than Ta. These measurements were made in sunny, windless conditions and show that body temperatures of *Circellium* were elevated by solar radiation and not by endothermy. The highest Tmth recorded was 38,9°C, and a beetle which had just emerged victorious in a fight over a dung ball had a Tmth no higher than 35,0°C.

There was no difference between pro- and metathoracic temperatures of the same beetles (n = 7; $P > 0,1$), as would be expected from the similar influence of solar radiation on different parts of the black cuticle. Figure 1 shows that body temperature remained between Ta and Tbb in a beetle whose Tpth was recorded during 20 min of continuous walking (via a dorsally implanted thermocouple held in place by clotted haemolymph). Control of body temperature is apparently achieved by behavioural means as the beetle moves between sun and shade.

Body masses of the beetles ranged from 3,7 to 11,0 g (mean ± SE = 7,3 ± 0,4 g; n = 24). *Circellium* is larger than all the ball-rolling dung beetles examined in the Kenyan study (Bartholomew & Heinrich 1978). In the tropical beetles studied by Bartholomew & Casey (1977b), the extent of endothermy during forced activity was positively correlated with body mass. However, in spite of its size, *Circellium* is strictly ectothermic. Bartholomew & Heinrich (1978) found that when the diurnal species were rolling dung balls their Tmth was increased by endothermic means and then further elevated by solar radiation. However, these beetles still

Table 1 Metathoracic temperatures of *Circellium bacchus* during various activities

Activity	Walking	Ball making	Ball rolling
Ta (range)	23,0 – 28,1	24,3 – 27,2	25,5 – 29,8
Tbb (mean ± *SE*)	30,9 ± 1,1	33,0 ± 0,4	34,4 ± 0,6
Tmth (mean ± *SE*)	29,3 ± 0,8	32,4 ± 0,6	34,8 ± 1,0
n	9	5	7
P	>0,1	>0,1	>0,1

Ta, ambient temperature; Tbb, black bulb temperature; Tmth, metathoracic temperature. All measurements made between 10h00 and 14h00. Beetles were utilizing dung of elephant, buffalo, eland and bush pig. Probabilities refer to paired t tests comparing Tbb and Tmth.

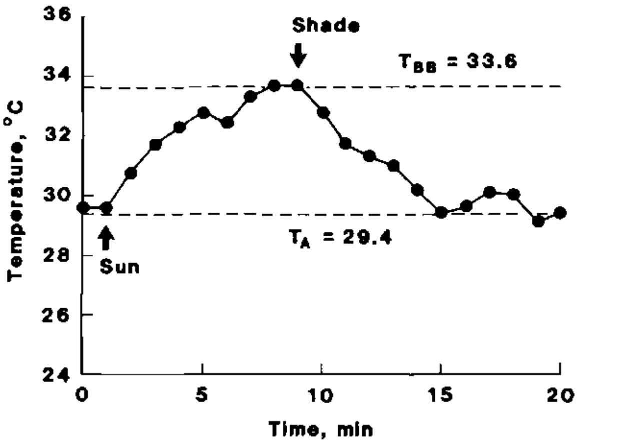

Figure 1 Record of prothoracic temperature in a beetle walking continuously for 20 min, first in sun and then in shade. Body mass = 4,6 g. Ambient (Ta) and black bulb temperatures (Tbb) shown by dashed lines.

worked in a leisurely manner when compared to the nocturnal *S. laevistriatus* in which endothermy is better developed (Heinrich & Bartholomew 1979). *Circellium* also moved rather slowly, even with body temperatures around 35°C. Another flightless dung beetle which shows no evidence of endothermy is *Scarabaeus rodriguesi* from the Namib dunes. This species is very active at Ta of 40°C and sand temperatures exoeeding 60°C, but uses its burrow as a thermal refuge (McClain & Nicolson, unpublished observations). Thoracic and abdominal temperatures of individual beetles were the same, usually around 40°C. Similar abdominal temperatures have been measured in the smaller *Scarabaeus denticolle* by Holm & Kirsten (1979).

Dissection of *Circellium* preserved in alcohol showed that the beetles possess tiny vestigial wings with greatly reduced venation. The large prothorax is densely packed with muscle associated with the powerful first pair of legs (used as shovels in forming dung balls and in excavating soil to bury them). The remaining leg musculature is less well developed and fibrillar flight muscle is not apparent. Smith (1964) made a detailed study of flightless Coleoptera, and found that exoskeletal modifications and gross reduction in size of all the fibrillar flight muscles often occurred before any reduction in wing size. It is to be expected that the capacity for endothermic heat generation is progressively lost in beetles with the atrophy of their flight muscles. In the male silkworm moth *Bombyx mori*, the loss of the ability to fly is accompanied by restricted thermoregulation (Ploye 1979).

Dung beetles, like carrion beetles, are nearly all strong fliers, because their food source is patchily distributed and temporary. When they do locate food the capacity for endothermy during terrestrial activity is of great importance in making dung balls quickly and in winning contests over dung balls (Heinrich & Bartholomew 1979). It is obvious that *Circellium* would fare badly in competition with winged dung beetles, and this, together with its preference for coarse dung and its reduced mobility, may be an explanation for its present restricted distribution. In the Addo Elephant Park competition for dung appears to be minimal, and *Circellium* is able to pursue its energetically less expensive way of life.

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References

BARTHOLOMEW, G.A. & CASEY, T.M. 1977a. Endothermy during terrestrial activity in large beetles. *Science* 195: 882–883.

BARTHOLOMEW, G.A. & CASEY, T.M. 1977b. Body temperature and oxygen consumption during rest and activity in relation to body size in some tropical beetles. *J. thermal Biol.* 2: 173-176.

BARTHOLOMEW, G.A. & HEINRICH, B. 1978. Endothermy in African dung beetles during flight, ball making, and ball rolling. *J. exp. Biol.* 73: 65–83.

HEINRICH, B. & BARTHOLOMEW, G.A. 1979. Roles of endothermy and size in inter- and intraspecific competition for elephant dung in an African dung beetle, *Scarabaeus laevistriatus*. *Physiol. Zool.* 52: 484–496.

HOLM, E. & KIRSTEN, J.F. 1979. Pre-adaptation and speed mimicry among Namib Desert scarabaeids with orange elytra. *J. arid Environ.* 2: 263–271.

MOSTERT, L.E. & HOLM, E. 1982. Notes on the flightless Scarabaeina (Coleoptera: Scarabaeidae) with a description of a new species. *Cimbebasia* (A) 5: 273–284.

PLOYE, H. 1979. Endothermy and partial thermoregulation in the silkworm moth, *Bombyx mori*. *J. comp. Physiol.* 129: 315–318.

SMITH, D.S. 1964. The structure and development of flightless Coleoptera: a light and electron microscopic study of the wings, thoracic exoskeleton and rudimentary flight musculature. *J. Morphol.* 114: 107–184.