TEMPERATURE REGULATION, ENERGY METABOLISM AND MATE-SEARCHING IN RAIN BEETLES (*PLEOCOMA* SPP.), WINTER-ACTIVE, ENDOTHERMIC SCARABS (COLEOPTERA)

By KENNETH R. MORGAN

Department of Biology, University of California, Los Angeles, CA 90024, USA

SUMMARY

Male rain beetles (*Pleocoma*; Scarabaeidae) of western North America engage in intense mate-searching activity at night during the winter. They may achieve a temperature excess greater than 35°C in flight, even though their thoracic pile is ineffective as insulation. Males also maintain thoracic temperature at high levels while walking on the ground in search of females. Female *Pleocoma* are flightless and are non-endothermic. In the laboratory, males maintained elevated body temperatures for as long as 4·2 h while walking in a respirometer chamber at an ambient temperature of 9°C. Energy metabolism and body temperature during these periods of sustained endothermy oscillated. Walking speed increased exponentially with body temperature. Male rain beetles compete (scramble competition) for opportunities to mate. It is likely that their mating success and ability to avoid predators depend on flight and rapid walking, which in turn depend on their having a high internal temperature.

INTRODUCTION

Endogenously elevated body temperatures in beetles were first reported more than 40 years ago in *Geotrupes stercorarius* that were preparing for flight (Krogh & Zeuthen, 1941). The requirement for a high body temperature for flight in many large insects has since been well documented (see Kammer, 1981, for a review). Many neotropical beetles elevate body temperature during terrestrial locomotion (Bartholomew & Casey, 1977a,b). African dung beetles maintain high body temperatures while making and rolling dung balls (Bartholomew & Heinrich, 1978; Heinrich & Bartholomew, 1979). Elephant beetles (*Megasoma elephas*) respond to reduced ambient temperature by maintaining body temperature at high levels (Morgan & Bartholomew, 1982). Green fig beetles (*Cotinis mutabilis*) elevate body temperature above ambient temperature while foraging in fruiting trees (Chappell, 1984). In contrast, flower scarabs (*Pachynotus sinuata*) warm up only prior to flight and maintain body temperature near ambient temperature while foraging even

though they have a well developed capacity for endothermic heat production (Heinrich & McClain, 1986).

The genus *Pleocoma* (family Scarabaeidae) includes approximately 33 species distributed through the coastal ranges and Sierra Nevada of western North America (Linsley, 1938; Hovore, 1977). The larvae feed on plant roots and are sometimes orchard pests. Adult males weigh 0·6–1·7 g, whereas the flightless females weigh 4·0–8·0 g. Male rain beetles undertake aerial and terrestrial searches for females at night during the autumn and winter. They are apparently attracted to the female's burrow by a pheromone (Rivers, 1890; Davis, 1935; Ellertson & Ritcher, 1959). When the males are searching, ambient temperatures range from −1 to 15 °C. There is one report of males flying during a snowstorm (Van Dyke, 1933). Adult rain beetles do not eat and therefore the intense activity of the males depends on energy stored by the larvae prior to metamorphosis. Previous studies indicated that heavy-bodied insects like these beetles require a high thoracic temperature for flight. However, the earlier studies concerned tropical and temperate species active at relatively warm ambient temperatures. I have examined thermal adaptations and energetics pertinent to activity in the cold.

MATERIALS AND METHODS

I studied rain beetles of the following taxa from October to February (1979–1985) during winter rains in the coastal mountains of California: *Pleocoma australis* Fall, *P. puncticollis* Rivers, *P. badia badia* Fall, *P. badia hirsuta* Davis, *P. conjungens* Horn and *P. linsleyi* Hovore. They all have localized distributions at altitudes ranging from 100 to 2400 m in chaparral or montane forest. Although I gathered field data (body temperatures and behaviour) for all of them, I concentrated my field efforts on *P. australis*, which is abundant in the San Jacinto Mountains. This species is sometimes active during the late afternoon on rainy days making it poss-ible to observe flight behaviour and terrestrial activity. Laboratory measurements (warming and cooling rates, walking speed and metabolic rates) were made only on *P. australis*. Beetles used in laboratory experiments were stored in airtight vials at 5 °C. Laboratory measurements were completed within 2 weeks of capture.

Field measurements

Body temperature measurements

Male *Pleocoma* were captured with an insect net. Battery powered ultraviolet lights were used to attract flying beetles after dark. Thoracic and abdominal temperatures (T_{th} and T_{ab}) were measured with copper-constantan thermocouples (0·03 mm in diameter) threaded through 30-gauge hypodermic needles with the thermocouple junctions glued in place. Beetles were grasped by the legs to minimize hand contact and measurements were completed within 3–6 s. Ambient temperature (T_a) was measured at the site of capture immediately after T_{th} and T_{ab} had been

measured. Temperatures were read to the nearest $0.1\,°C$ on a Bailey Bat-12 thermo-couple thermometer which had been calibrated against a mercury thermometer traceable to the US Bureau of Standards.

Laboratory measurements

Rates of endothermic warm-up

Thermocouples ($0.03\,mm$ in diameter) were implanted in the thorax of freshly captured male *P. australis*. Similarly sized individuals were chosen to avoid size effects. The leads were fixed in position with beeswax and the beetles were placed in an open container at $6–9\,°C$. Endothermic warm-up was induced by rapping the chamber on the bench top and T_{th} and T_a were recorded by a microcomputer at 0.5-min intervals. Ventilation rate during warm-up was determined visually by counting abdominal contractions.

Cooling rates

Cooling rates were determined using freshly killed male *P. australis* with thoracic thermocouples as described above. Similarly sized individuals were chosen to eliminate size effects. The insects were heated to $42\,°C$ using an incandescent lamp and were then allowed to cool while T_{th} and T_a were recorded at 2-s intervals by a microcomputer. In the first set of experiments, beetles were positioned in walking posture and cooling rate was measured first on the intact animal and then after removal of the wings and elytra. The insects were then positioned in typical flight posture in a laminar-flow wind tunnel and cooling rate was measured at a wind speed of $3.8\,m\,s^{-1}$. A second group of beetles was mounted in flight posture and cooling rate was measured at a wind speed of $4.3\,m\,s^{-1}$, first with the pile intact and then with the pile removed from the thorax. Thermal conductance ($W\,°C^{-1}$) was calculated from cooling rates by assuming a specific heat of $3.4\,J\,g^{-1}\,°C^{-1}$ (May, 1979). Air speeds in the wind tunnel (measured with a hot wire anemometer) were selected to be similar to flight speeds timed in the field.

Effect of body temperature on walking speed

Walking speed at a T_a of $4\,°C$ was measured by timing *P. australis* males on a 1-m linear track 5 cm wide. Body temperature increased during the trials by no more than $3\,°C$. Accordingly, T_{th} was measured before and after each trial and averaged to provide an estimate of mean T_{th} during the trial. The beetles walked spontaneously at all temperatures.

Resting oxygen consumption

Oxygen consumption ($\dot{V}_{O_2}$) of inactive *P. australis* was measured by placing individuals into airtight 50 ml syringes for 30–300 min. Measurements were made between 09.00 and 18.00 h in a dark, controlled-temperature room maintained at 5, 15 or 25 °C. The syringes containing beetles were allowed to equilibrate at a given temperature for 2 h and were continuously flushed with fresh air (20 ml min^{-1}) until

measurements began. At the beginning of a measurement the respirometer was sealed and an initial sample of air was collected. At the end of the measurement period, a 30-ml air sample was transferred through three-way valves from the syringe respirometer to a third syringe. The fractional concentration of oxygen was measured using an infusion pump to push sample gas through a scrubbing train of Ascarite and Drierite and then through the sensor of an Applied Electrochemistry S3A oxygen analyser. Gas volumes were corrected to STPD after accounting for the volume of the beetle.

Oxygen consumption during warm-up and sustained endothermy

The $\dot{V}_{O_2}$ during warm-up and sustained endothermy was measured in an open-circuit respirometry system using the instantaneous method of Bartholomew, Vleck & Vleck (1981). The effective volume of the system was 83 ml. T_a averaged 9 °C and was controlled to within 1 °C with a temperature cabinet. A beetle (*P. australis*) was placed in a Lucite respirometer chamber through which air was pumped at a rate of 60 ml min^{-1}. A second pump pulled a subsample (30 ml min^{-1}) of the gas leaving the respirometer through a scrubbing train of Ascarite and Drierite and then through the oxygen sensor. T_{th}, T_{ab}, T_a and $\dot{V}_{O_2}$ were recorded simultaneously by a microcomputer at 30- to 60-s intervals.

RESULTS

Behaviour

The mating activity of male and female rain beetles was closely synchronized by autumn and winter rains. Male *P. australis* emerged from underground and were most abundant during light drizzle at dusk and just after dark. In other *Pleocoma* species, peak male activity occurred during similar weather just before dawn. Males searched for females by flying upwind in a meandering path within 1–2 m of the ground. Flight speeds ranged from hovering to as high as 4·5 m s^{-1}. Flying males were wary and often avoided capture by climbing to heights of 5 m or more. Aerial searching ended when the males landed downwind of the female (usually in a burrow and partially covered by soil). Ground searchers appeared agitated and crawled rapidly. Unlike flying beetles they did not seem to orientate to the burrow but instead appeared to search randomly. If they failed to find the burrow they usually took wing and resumed aerial searching. Upon reaching the burrow entrance they began to dig down to the female who was usually several centimetres or more beneath the surface. Often several males were present near an occupied burrow and although they did not fight they clearly interfered with each other in their efforts to reach the female.

Field measurements

Body temperatures

The T_{th} of male *Pleocoma* during flight ranged from 33·7 to 40·6 °C at T_a ranging from 2·4 to 15·0 °C (Fig. 1A). On one occasion I observed *P. linsleyi* males in flight at $T_a < -1$ °C but was unable to measure T_{th}. The slope of the regression of T_{th} of

flying *Pleocoma* on T_a was not significantly different from zero (*t*-test, $P = 0.659$), suggesting that *Pleocoma* regulates T_{th} during flight. The mean flight temperature was 37.6°C (S.D. = 1.56, $N = 83$). A minimum flight T_{th} of 34–35°C was estimated from the lowest flight temperatures measured in beetles in the field. One 1.0 g male had a temperature excess $(T_{th}-T_a)$ of 35.2°C. The T_{ab} in flight ranged from 11.9 to 28.4°C (mean = 16.8, S.D. = 4.01, $N = 58$; Fig. 2). The slope of the regression of
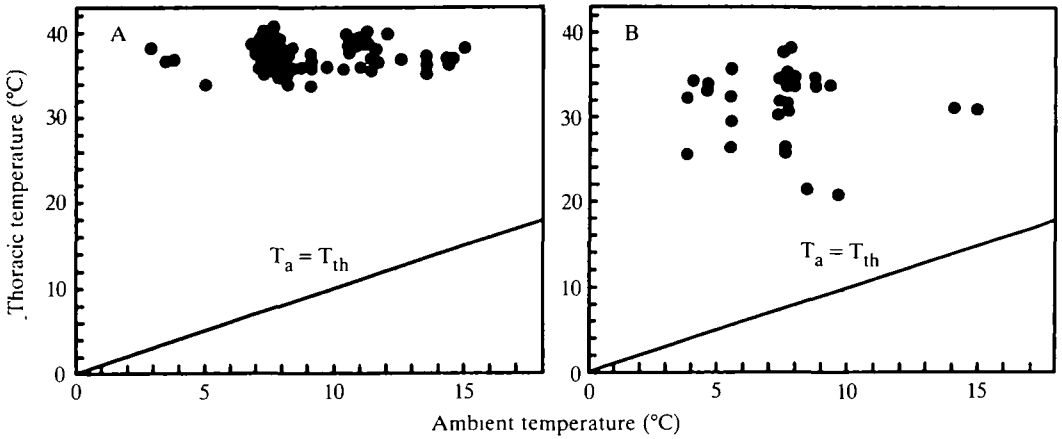
Fig. 1. The relationship between thoracic temperature (T_{th}) and ambient temperature (T_a) for (A) 83 males of five different species during mating flights and (B) 34 males of four different species during ground searching. The solid lines are isotherms where points would lie if thoracic temperature was equal to ambient temperature.
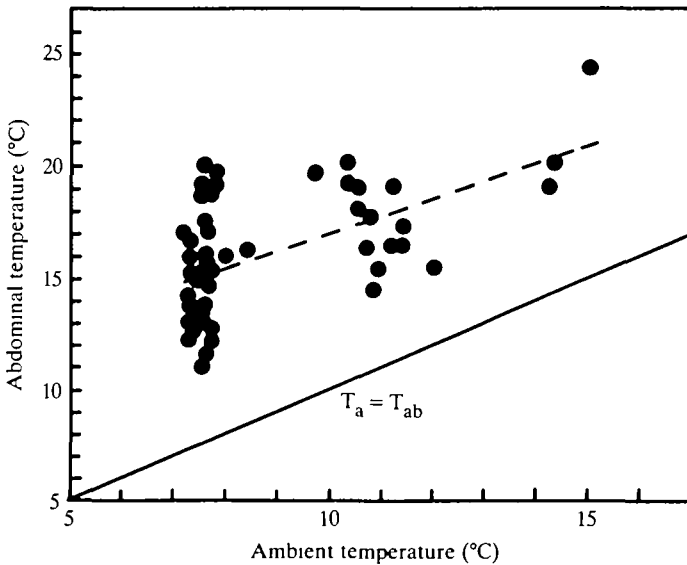

Fig. 2. The relationship between abdominal temperature (T_{ab}) and ambient temperature (T_a) for 58 *Pleocoma australis* males during mating flights. The dashed lines shows the least squares regression of abdominal temperature on ambient temperature. The solid line is the isotherm where points would lie if abdominal temperature was equal to ambient temperature.

T_{ab} on T_a was not significantly different from 1 ($T_{ab} = 9 \cdot 156 + 0 \cdot 777T_a$; $r^2 = 0 \cdot 292$, $N = 54$, $P = 0 \cdot 191$).

The T_{th} of male *Pleocoma* searching on the ground surface for females ranged from 20·7 to 38·1 °C (mean = 31·5, S.D. = 4·50, $N = 34$) at T_a ranging from 3·1 to 15·0 °C (Fig. 1B). The slope of the regression of T_{th} of searching males on T_a was not different from zero (*t*-test, $P = 0 \cdot 395$), suggesting that T_{th} is also regulated during ground searching. The T_{ab} ranged from 13·3 to 21·5 °C (mean = 16·7, S.D. = 2·01, $N = 24$) and was unrelated to T_a.

Male *P. australis* were occasionally found in their burrows just prior to the onset of flights. The T_{th} of six individuals was from 0·9 to 4·3 °C higher than ground temperature (which varied from 9·9 to 12·6 °C).

The T_{th} of female *Pleocoma* (three *P. australis* and one *P. linsleyi*) captured on or below the ground surface while males were flying ranged from 4·3 to 10·9 °C and was not different from the temperature of their immediate surroundings. Dissections of *P. australis* showed that the flight muscles, which are the site of endothermic heat production in males, are absent in females. In females the thorax and abdomen are filled with what appears to be fat.

Laboratory measurements

Endothermic warm-up

Male rain beetles were able to initiate endothermic warm-up from a T_{th} at least as low as 4·0 °C. There was considerable variation in rates of warm-up. At T_a between 6 and 9 °C, the increase in T_{th} was relatively linear and averaged 1·4 °C min^{-1} ($N = 20$, range = 0·7–2·1). There was no apparent relationship between body mass and warm-up rate, but the range of body masses was limited (0·90–1·45 g).

Cooling rates

Cooling data ($T_{th} - T_a$) linearized by semilogarithmic plotting were accurately described by least squares linear regressions (all r^2 were greater than 0·997). Representative cooling data for a 1·2-g male are shown in Fig. 3. In the absence of forced convection, the conductance of three male *Pleocoma* (mean mass 1·17 g, S.D. = 0·042) averaged 0·0231 W °C^{-1} (S.D. = 0·0026). During terrestrial activity, the air spaces under the wings and elytra insulate the thorax and abdomen. After removal of the wings and elytra, conductance increased by about 15 % to 0·0271 W °C^{-1} (S.D. = 0·0020). At a wind speed of 3·8 m s^{-1} (equivalent to flight speed) conductance averaged 0·0411 W °C^{-1} (S.D. = 0·0119), a 44 % increase over conductance of the intact beetle in still air. Although *Pleocoma* have thoracic pile, cooling rates of males with the pile removed were not significantly different from those of intact beetles.

Effect of body temperature on walking speed

Walking beetles responded to handling by warming endothermically from $T_{th} = T_a = 4$ °C to T_{th} as high as 34 °C. Two or three speed measurements were made on each individual as T_{th} gradually increased. This method could potentially introduce
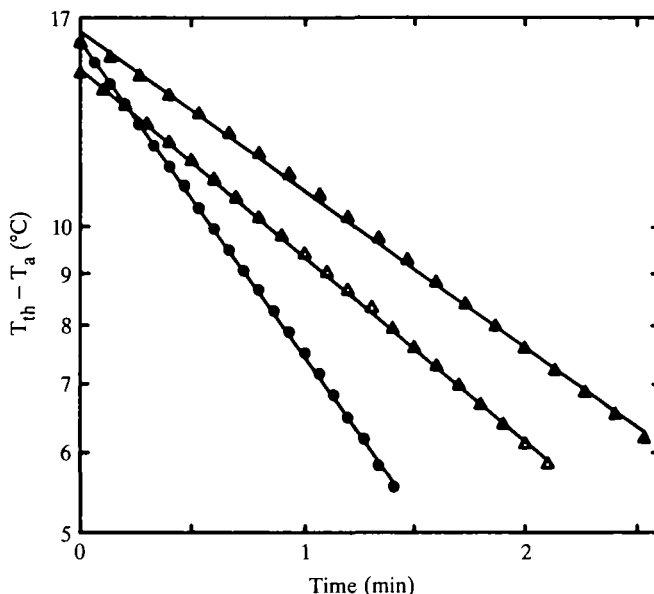
Fig. 3. Representative cooling curves for a male *Pleocoma australis* weighing 1·2 g. The solid triangles represent the intact beetle in still air. The open triangles represent the beetle with its wings and elytra removed in still air. The solid circles represent cooling with the wings and elytra removed and a wind speed of 380 cm s^{-1}. The lines are least squares regression lines. T_{th}, thoracic temperature; T_a, ambient temperature.

a training effect in the successive trials. However, the insects walked with very little prompting in all of the trials, suggesting that training effects were unimportant. Walking speed increased exponentially with T_{th} from a low of 0·22 cm s^{-1} at 7°C to a high of 5·35 cm s^{-1} at 33°C (Fig. 4). The mean Q_{10} between 6 and 34°C was 2·5. Male rain beetles walked in a coordinated fashion at T_{th} as low as 2°C, but by maintaining T_{th} at 34°C they were able to walk more than 12 times faster than at a T_{th} of 6°C.

Non-endothermic oxygen consumption

The $\dot{V}_{O_2}$ of resting beetles increased exponentially with body temperature (Fig. 5). The mean Q_{10} between 5 and 15°C, and between 15 and 25°C was 2·6. Mean body masses of beetles used in these measurements were as follows: 5°C, 1·06 g, S.D. = 0·218, $N = 44$; 15°C, 1·00 g, S.D. = 0·220, $N = 20$; 25°C, 0·94 g, S.D. = 0·113, $N = 21$.

Endothermic oxygen consumption

T_{th} and $\dot{V}_{O_2}$ usually rose steadily during endothermic warm-up preceding sustained endothermy (Fig. 6). Performance during sustained endothermy varied in duration and in the level at which T_{th} was maintained. Bouts of sustained endothermy lasted for 0·15–4·17 h. The mean T_{th} during these bouts ranged from 10·1 to 30·3°C at a T_a of 9·0°C. T_{th} and $\dot{V}_{O_2}$ during sustained endothermy oscillated with a
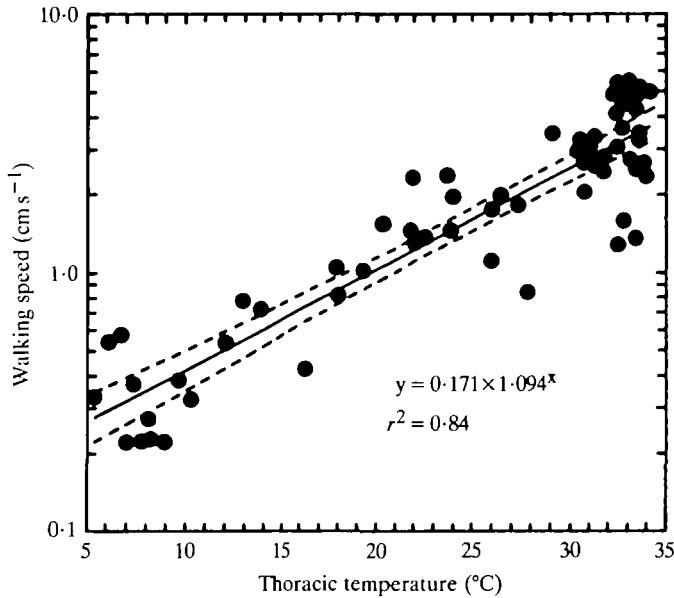
Fig. 4. The relationship between walking speed and thoracic temperature for *Pleocoma australis* in the laboratory. The solid line represents the least squares regression of the log transformed values of walking speed on thoracic temperature. The dashed lines are the 95 % confidence limits for the regression line.
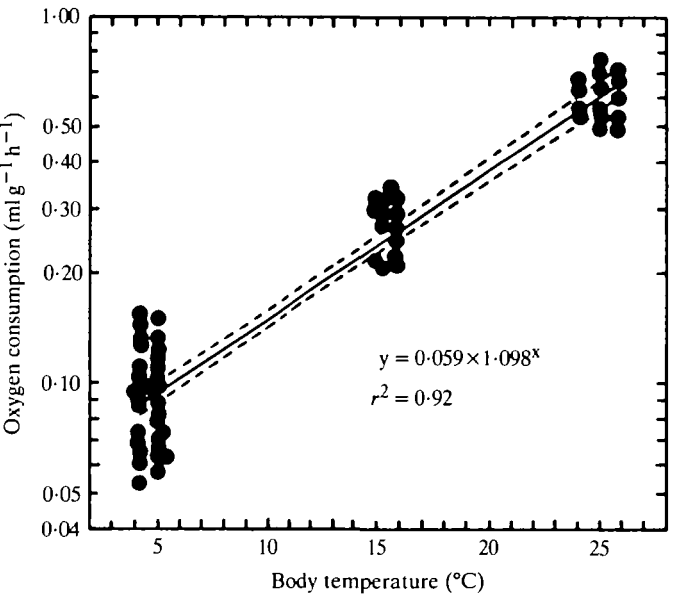

Fig. 5. The relationship between oxygen consumption and body temperature in resting *Pleocoma australis*. The solid line represents the least squares regression of log oxygen consumption on body temperature. The dashed lines are the 95 % confidence limits for the regression line.
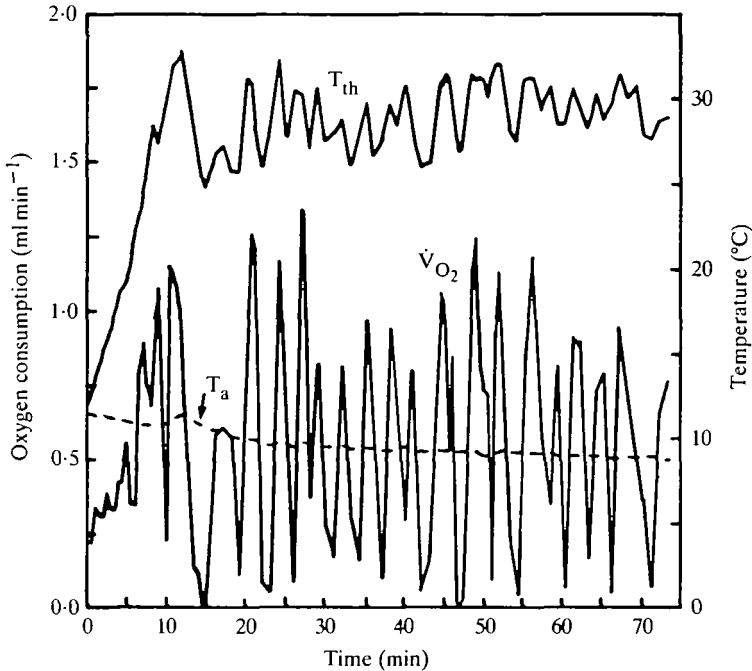
Fig. 6. The relationship between instantaneous rate of oxygen consumption ($\dot{V}_{O_2}$) and thoracic temperature (T_{th}) during endothermic warm-up and sustained endothermy in a male *Pleocoma australis* weighing 1.1 g. T_a, ambient temperature.

given cycle in $\dot{V}_{O_2}$ peaking before the corresponding cycle in T_{th} (Fig. 6). The magnitude of oscillations in T_{th} usually ranged from 1 to 3 °C. Maximum excursions in T_{th} during sustained endothermy in 11 beetles were from 1·3 to 6·3 °C. Oscillations in T_{ab} corresponding to those in T_{th} were sometimes detected but their amplitudes were small. During a warming cycle in one beetle, T_{th} changed by 6·2 °C but T_{ab} changed by only 0·8 °C. Oscillations in $\dot{V}_{O_2}$ were considerably larger than those in T_{th}. The $\dot{V}_{O_2}$ was often near zero but occasionally rose to as high as 1·3 ml min⁻¹. The mean $\dot{V}_{O_2}$ during sustained endothermy increased in a linear fashion with the temperature difference between the thorax and ambient air (Fig. 7). The frequency of warming cycles during sustained endothermy also increased with the temperature difference between the thorax and ambient air (Fig. 8).

Ventilation rate

Ventilatory movements (abdominal contractions) were not observed in resting *Pleocoma*. The onset of endothermic warm-up was accompanied by periodic abdominal contractions which continued throughout warm-up and sustained endothermy. Ventilation rate increased exponentially ($Q_{10} = 2·2$) with the $T_{th} - T_a$ difference from a low of 20 min⁻¹ at a $T_{th} - T_a$ of 2·2 °C to a high of 112 min⁻¹ at a $T_{th} - T_a$ of 22·7 °C (Fig. 9). In one individual, abdominal contractions were noticeably deeper and slower than was typical, although the rate of warm-up was normal.
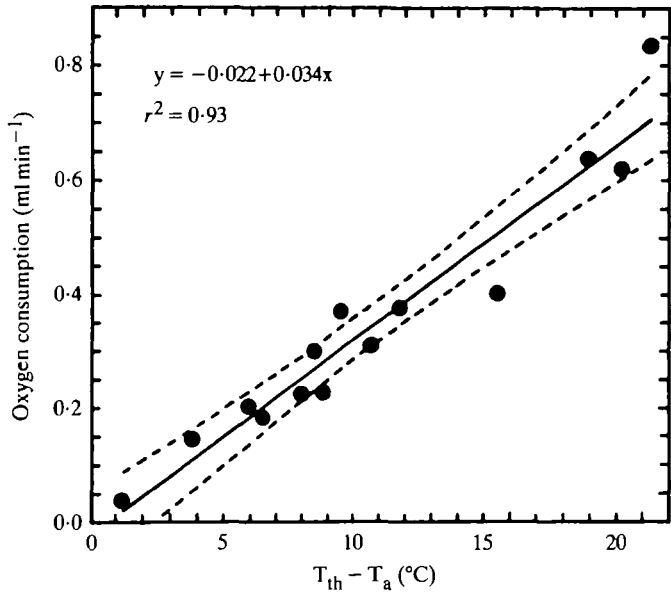
Fig. 7. The relationship between mean oxygen consumption during bouts of sustained endothermy and the difference between thoracic temperature (T_{th}) and ambient temperature (T_a) in *Pleocoma australis*. The solid line shows the least squares regression of oxygen consumption on the difference in temperature between the thorax and ambient air. The dashed lines are the 95 % confidence intervals for the regression line.
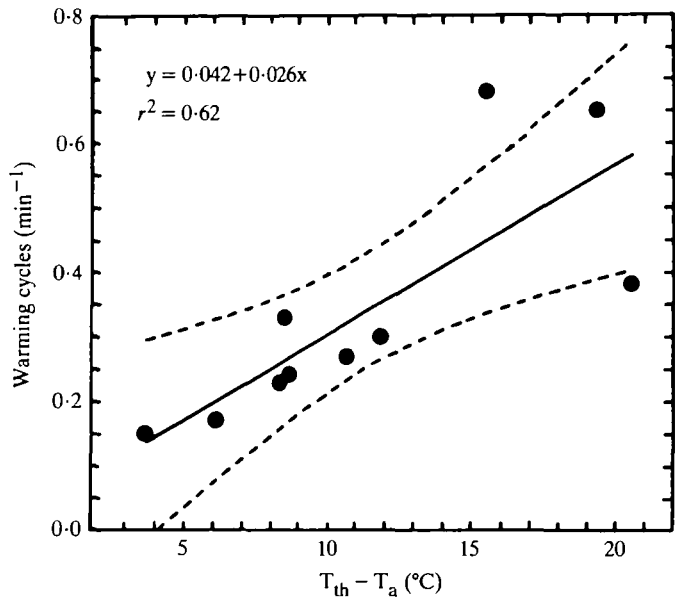

Fig. 8. The relationship between the frequency of warming cycles during sustained endothermy and the difference in temperature between the thorax (T_{th}) and ambient air (T_a) in *Pleocoma australis*. The solid line represents the least squares regression. The dashed lines are the 95 % confidence intervals for the regression line.
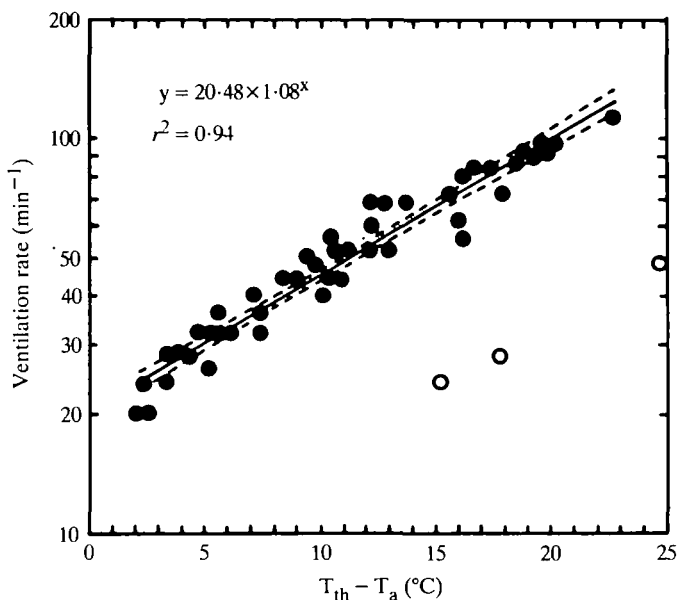
Fig. 9. The relationship between ventilation rate and the difference in temperature between the thorax (T_{th}) and ambient air (T_a) during endothermic warm-up in *Pleocoma australis*. The solid line represents the least squares regression. The dashed lines are the 95 % confidence intervals for the regression line. The three points located below the regression line were not included in the regression and represent an individual that showed normal warm-up but had an unusually slow ventilation rate.

DISCUSSION

Body temperature regulation

Despite low environmental temperatures, flying male *Pleocoma* maintain a T_{th} similar to that of other endothermic insects of comparable size (e.g. sphinx moths, bees and other scarabs). The temperature excess (as high as 35·2°C) maintained by male *Pleocoma* during flight is among the greatest yet reported for an insect, even though the thoracic pile is apparently ineffective as insulation. Moths and bees are covered with dense pile which may reduce their thermal conductance by as much as 50 % (Church, 1960*a*,*b*). The cooling rate of male *Pleocoma* in still air averages 44 % more than that of well-insulated sphinx moths of the same body size [0·347 *versus* 0·195°C min^{-1}°C^{-1} (data for moths taken from Bartholomew & Epting, 1975)].

Among insects, sustained endothermy at low T_a is known in worker honey-bees (Heusner & Roth, 1963; Heusner & Stussi, 1964; Southwick & Mugaas, 1971; Cayhill & Lustic, 1976), incubating queen bumble-bees (Heinrich, 1974*a*) and in the scarab beetle *Megasoma elephas* (Morgan & Bartholomew, 1982). Whereas *Pleocoma* usually walks steadily during warm-up and sustained endothermy, *Megasoma* is stationary. Otherwise, the patterns of body temperature regulation in *Pleocoma* and *Megasoma* are qualitatively similar. However, *Pleocoma* and *Megasoma* differ markedly in the temperature-dependence of their ability to initiate endothermic warm-up. *Megasoma* was incapable of initiating the endothermic response if T_{th} fell

below about 18°C. In contrast, *Pleocoma* was able to initiate warm-up at a T_{th} below 4°C. In tropical flower scarabs (*Pachynotus sinuata*), the temperature threshold for endothermic warm-up is about 20°C (Heinrich & McClain, 1986).

The main functions of thermoregulation during flight are to ensure that the flight muscles produce adequate power, while preventing overheating of the thorax (Heinrich, 1974*b*). *Pleocoma* clearly regulates T_{th} during flight, but the mechanism of regulation is unclear. If, like other insects, *Pleocoma* has a constant flight $\dot{V}_{O_2}$ at all T_a values, thermoregulation must be accomplished behaviourally (by varying flight duration) or physiologically (by evaporating water or adjusting thermal conductance). At present, only honey-bees are known to use evaporative cooling which they accomplish by regurgitating a droplet of honeycrop fluid onto their tongue (Heinrich, 1979). This mechanism is not possible in *Pleocoma* because the adults have no mouth. A variety of insects control T_{th} by pumping warm haemolymph from the thorax to the abdomen which acts as a heat exchanger (e.g. see Heinrich, 1970, 1971, 1976; Heinrich & Casey, 1978; Chappell, 1982; Willmer, 1982; Morgan, Shelly & Kimsey,ʼ 1985). However, there is no evidence that *Pleocoma* or any other beetle controls T_{th} in this manner (e.g. see Bartholomew & Heinrich, 1978; Chappell, 1984; Heinrich & McClain, 1986). Although T_{ab} was greater than T_a in flying *Pleocoma* (Fig. 2), there is no indication that this situation arises other than from passive heat transfer from the thorax to the abdomen. Although much heat is produced by the flight muscles of *Pleocoma* during flight, the T_a is always below 15°C so that heat loss is rapid. Regulation of T_{th} in flying rain beetles may depend on intermittent flight. However, I have no field observations which support or refute this idea. It is noteworthy in this regard that flower scarabs (*Pachynotus sinuata*) also show no evidence of active heat transfer to the abdomen and suspend flight when T_{th} exceeds 41°C (Heinrich & McClain, 1986).

Variation in heat production is the primary mechanism for control of T_{th} during sustained terrestrial endothermy in *Pleocoma*. Males maintained T_{th} at a fairly constant high level by initiating heat production whenever T_{th} fell below an apparent lower temperature set point (Fig. 6). They responded to the increased rate of heat loss at greater $T_{th}-T_a$ differences by increasing the frequency of heating cycles (Fig. 8).

Energy metabolism

Male rain beetles showed distinct ectothermic and endothermic patterns of $\dot{V}_{O_2}$ in the laboratory. When allowed to rest quietly the beetles had a low $\dot{V}_{O_2}$ that increased in a regular fashion with temperature between 5 and 25°C (Fig. 5). The $\dot{V}_{O_2}$ of inactive males at 25°C is similar to that of the green fig beetle (*Cotinis mutabilis*), another temperate scarab of about the same size (Chappell, 1984). In contrast, above 25°C, or when disturbed at low T_a, beetles began walking, increased $\dot{V}_{O_2}$ to as high as $1 \cdot 3 \, \text{ml min}^{-1}$ and often maintained body temperature considerably above T_a by periodic heat production. The maximum $\dot{V}_{O_2}$ during these intervals of heat production was as much as 13 times the minimum (Fig. 6).
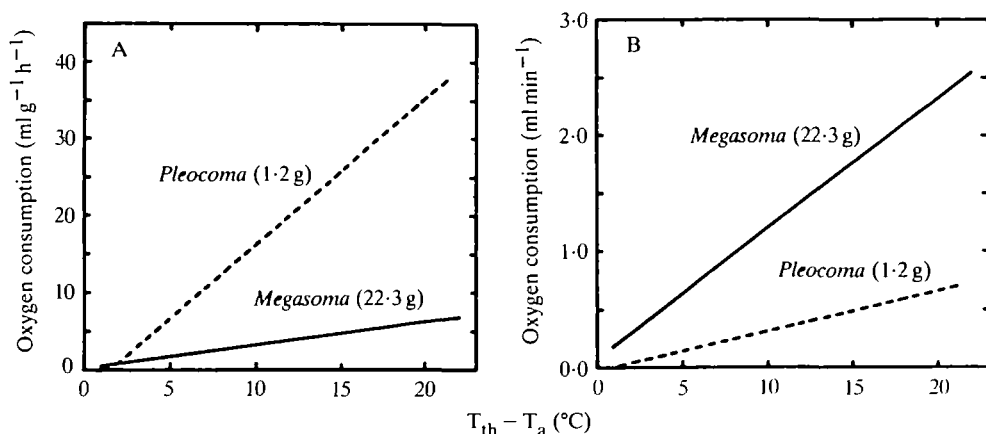
Fig. 10. (A) The relationship between the regressions of mass-specific oxygen consumption and the difference between the thoracic (T_{th}) and ambient (T_a) temperatures during sustained endothermy in scarabs of different sizes. (B) The relationship between the regressions of whole body oxygen consumption and the difference between the thoracic and ambient temperatures during sustained endothermy in the same insects. Data for *Megasoma elephas* were taken from Morgan & Bartholomew (1982).

The energy cost of walking in beetles is small relative to the cost of maintaining a temperature excess during sustained endothermy (Bartholomew & Casey, 1977*b*). Therefore, despite the differences in behaviour between endothermic *Pleocoma* and *Megasoma* (rain beetles walked while elephant beetles remained stationary), the energy costs of sustained endothermy can be compared to examine the influence of body size. On a per gram basis, $\dot{V}_{O_2}$ of *Pleocoma* and *Megasoma* increases in a linear fashion with the $T_{th}-T_a$ difference (Fig. 10A). However, the slope of the regression of $\dot{V}_{O_2}$ on the $T_{th}-T_a$ difference is 1·91 in *Pleocoma* and only 0·30 in *Megasoma*. At a $T_{th}-T_a$ difference of 20°C *Pleocoma* uses almost six times more energy on a per gram basis (35·36 *versus* 6·25 ml $O_2 g^{-1} h^{-1}$). In contrast, *Pleocoma* uses only one quarter as much on a whole animal basis to maintain the same $T_{th}-T_a$ difference (39·42 *versus* 139·38 ml $O_2 g^{-1} h^{-1}$; Fig. 10B). These relationships suggest, paradoxically, that for an endothermic insect in a cold environment where energy stores are slow to accumulate or cannot be replenished there is, within limits, an energetic advantage to being smaller. Despite its more rapid heat loss, an insect the size of male *Pleocoma* can remain endothermic on a given amount of energy for a longer time than can a larger insect. That energy stores accumulate slowly in *Pleocoma* is apparent from the extended duration of the larval period. *Pleocoma* larvae that have been studied moult once per year and pupation is preceded by 9–13 larval instars (Ellertson, 1958). To my knowledge, no other scarab is known to have more than three larval instars.

Although I was unable to measure the energy cost of flight in *Pleocoma*, it may be calculated from thermal conductance measured at a wind speed equivalent to flight speed. A 1·2-g *P. australis* flying with $T_{th}-T_a=30·5$°C (the average for this species) has an estimated metabolic rate of 1·5 W. The metabolic rate of a 1·2-g

sphinx moth in flight is 0.5 W (Bartholomew & Casey, 1978). Assuming that one-tenth to one-quarter of the body mass of *Pleocoma* is stored fat used for flight, the maximum estimated flight duration should range from 0.9 to 2.2 h (1 g fat $= 39.7$ kJ).

The larval life history adaptations of rain beetles allow for gradual accumulation of energy from relatively non-nutritious food until adequate stores are available for pupation and mating activity. The large size of female *Pleocoma* has presumably evolved because females are free from constraints on weight placed by flight, and because by being larger they can produce more eggs. The adult life history of male *Pleocoma* allows for energy conservation until conditions are appropriate for mating, and then energy stores are expended in an all-or-nothing effort when conditions are optimum for mating success.

In view of the high energy cost of activity and the fact that adult *Pleocoma* do not eat, it is hardly surprising that a male is active for only a few days and that the activity of males and females is closely synchronized. Females must have some indication when to burrow to the surface and disperse pheromone if the males are to find them. In western North America, seasonal rainfall (which occurs during the late autumn and winter) may be the only available environmental stimulus that is precise enough to synchronize mating activity. However, it is unclear whether *Pleocoma* responds directly to the rain or to some associated stimulus (e.g. falling barometric pressure).

Ecological importance of high body temperature

Although endothermy in *Pleocoma* is energetically costly, it releases the beetles from physiological constraints on activity that would otherwise be imposed by low T_a. As in many other large insects a high T_{th} is required for flight in *Pleocoma*. Flight is clearly important during the initial phase of mate-searching when males must search a large area to locate a female. The presence of many males at a single female's burrow suggests that intermale competition is keen during the terrestrial phase of the search. As many as nine males have been excavated from the burrow of a single female, many having been damaged by the persistent digging efforts of males arriving later (Davis, 1935; Ellertson, 1956). Sustained endothermy increases the speed of terrestrial locomotion in male *Pleocoma*. Presumably it enhances the efficiency of terrestrial searching for the female and ultimately enhances mating success.

Male rain beetles are highly vulnerable to vertebrate predators during above-ground activity (reviewed in Ellertson, 1958). The problem is acute in daylight when even flying beetles are easily caught by birds. It seems likely that natural selection has favoured crepuscular and nocturnal activity to avoid visual predators. Even at night, active males are noisy and are vulnerable to foxes, coyotes and owls. The ability to locate a female quickly and thus reduce the amount of time spent on the ground surface, and to initiate flight on demand to avoid terrestrial predators, may be important additional advantages of endothermy.

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