Homeothermic Response to Reduced Ambient Temperature in a Scarab Beetle

Abstract. *Elephant beetles (*Megasoma elephas*; Scarabaeidae) weighing from 10 to 35 grams, respond homeothermically when ambient temperature is reduced below about 20°C in the laboratory. This metabolic response is not associated with locomotion or any other overt activity. Warming is initiated when the body temperature reaches an apparent set point of 20° to 22°C. Unlike the case for euthermic birds and mammals, energy metabolism and body temperature in these beetles are conspicuously oscillatory, with a given cycle in oxygen consumption peaking before the corresponding cycle in body temperature.*

During flight, insects belonging to many different orders attain thoracic temperatures (T_{th}) greater than ambient temperature (T_{a}). In some species endogenous heat production can be independent of flight or preparation for flight, and body temperatures (T_{b}) are elevated during activities such as sound production, terrestrial locomotion, and brooding (*1*). Endogenously elevated T_{b} in beetles was first reported 40 years ago in *Geotrupes stercorarius* that were preparing for flight (*2*). Elevated T_{b} in scarabs is also associated with terrestrial activity (*3*). Male rain beetles (*Pleocoma* sp.) warm to flight temperature (38°C) and maintain a T_{b} as high as 32°C during terrestrial activity, at air temperatures of 3°C (*4*).

We report here enhanced heat production and regulation of T_{b} in a large neotropical scarab beetle (*Megasoma elephas*) during exposure to decreasing T_{a}. This phenomenon is not associated with flight, preparation for flight, terrestrial locomotion, or any other overt activity.

We simultaneously measured T_{th}, abdominal temperature (T_{ab}), and instantaneous rates of oxygen consumption ($\dot{V}_{\mathrm{O}_2}$) of freshly captured *Megasoma* at T_{a} values between 7° and 26°C. Behavior was monitored visually. We measured T_{b} with copper-constantan thermocouples (wires 0.13 mm in diameter) implanted dorsally at a depth of approximately 0.5 cm. The leads were attached to the surface of the beetle with beeswax and connected to thermocouple thermometers (Bailey Bat-12) whose outputs went to a microprocessor (AIM-65) via an automatic switch and an analog-to-digital converter. We measured T_{a} with a thermocouple inside the respirometer.

We measured the instantaneous $\dot{V}_{\mathrm{O}_2}$ in an open-flow system (*5*), using an oxygen analyzer (Applied Electrochemistry S3A) connected to the microprocessor. The effective volume of the system used for smaller beetles was 94 cm^3 and for larger beetles was 390 cm^3. The flow rates of dry, $\mathrm{CO_2}$-free air were 116 and 145 cm^3 min^{-1}, respectively.

The T_{a} was controlled to within 0.5°C with a portable refrigerator equipped with a blower, a heating element, an observation window, and a thermostat. This system cooled the Lucite respirometer chamber containing a beetle at a rate of 0.3°C min^{-1}.

Megasoma ranging in mass from 10.8 to 34.8 g were captured at ultraviolet night-lights on Barro Colorado Island, Republic of Panama (*6*). Thermocouples were implanted on the day after capture. The beetle was placed in a respirometer chamber in the dark at a T_{a} of 25° to 26°C; T_{th}, T_{ab}, T_{a}, $\dot{V}_{\mathrm{O}_2}$, and behavior were monitored continuously. After the beetle had quieted down and T_{th} was stable and equal to T_{a}, body temperatures and $\dot{V}_{\mathrm{O}_2}$ were recorded for 30 to 35 minutes; then T_{a} was reduced by decrements of 5° to 8°C. After each reduction, T_{a} was held steady and T_{th} was allowed to stabilize. Thereafter, T_{th}, T_{ab}, T_{a}, and $\dot{V}_{\mathrm{O}_2}$ were recorded for 16 to 35 minutes.

The T_{th} remained stable near 20°C for at least as long as 3 hours at T_{a} as low as 7.0°C (Fig. 1A). Mean $\dot{V}_{\mathrm{O}_2}$ increased linearly with the difference between T_{th} and T_{a} (Fig. 1B). The $\dot{V}_{\mathrm{O}_2}$ of two female *Megasoma* (mass, 10.8 and 22.3 g) with T_{th} equal to T_{a} (26°C) averaged 0.19 and 0.21 cm^3 min^{-1}, respectively. These values are substantially greater than those predicted on the basis of mass for resting beetles at similar temperatures, but they are only 1/5 to 1/10 the rates characteristic of vigorous terrestrial activity at those temperatures (*7*). Thus, under the experimental conditions, the *Megasoma* we measured cannot be characterized as resting even though they were motionless at room temperature. At a T_{a} of 26°C, $\dot{V}_{\mathrm{O}_2}$ was steady. At lower T_{a}, $\dot{V}_{\mathrm{O}_2}$ oscillated markedly; at a T_{a} of 15°C, the maximum value for $\dot{V}_{\mathrm{O}_2}$ during a given oscillation was as much as 14 times the

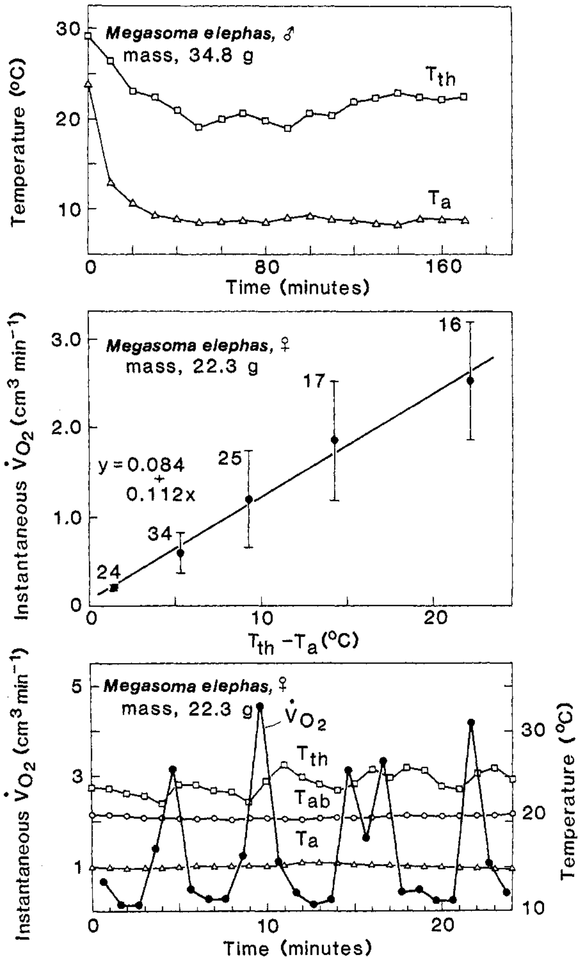

Fig. 1. (A) The response of the thoracic temperature (T_{th}) of *Megasoma elephas* to reduced ambient temperature (T_{a}). (B) The regression of oxygen consumption ($\dot{V}_{\mathrm{O}_2}$) on ΔT ($T_{\mathrm{th}} - T_{\mathrm{a}}$). The points are mean values for $\dot{V}_{\mathrm{O}_2}$. The numerals are the number of measurements of $\dot{V}_{\mathrm{O}_2}$ made at 1-minute intervals at a given value of ΔT. The vertical bars indicate 2 standard errors around the mean. (C) The relation between $\dot{V}_{\mathrm{O}_2}$, T_{th}, abdominal temperature (T_{ab}), and T_{a} during homeothermy. Oscillations in $\dot{V}_{\mathrm{O}_2}$ and T_{th} are evident.

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minimum value during that cycle (Fig. 1C). The cycles of $\dot{V}_{O_2}$ were closely followed by oscillations in T_{th}, with the peaks in $\dot{V}_{O_2}$ slightly preceding the peaks in T_{th} (Fig. 1C). We assume that the cycles in $\dot{V}_{O_2}$ and T_{th} coincide with cycles of activity in the thoracic flight muscles. The T_{ab} values sometimes showed similar, but smaller oscillations which lagged behind those of the thorax. Our experiments usually lasted 2 to 3 hours, and during this interval the beetles were almost completely motionless and T_{th} was continuously elevated. We did not determine the maximum duration of the homeothermic response of *Megasoma*.

As long as T_b remains constant, heat production is necessarily equal to heat loss. Heat loss is proportional to the difference between T_b and T_a (ΔT); in the case of endothermic insects T_b refers to T_{th}. A mammal with a T_b of 37°C at a T_a of 23°C should have the same heat loss as a *Megasoma* of the same mass with a T_b of 27°C at a T_a of 13°C. (This parity requires that the mammal and beetle have similar thermal conductances.) It is instructive to compare the $\dot{V}_{O_2}$ (which is proportional to heat production) of a homeothermic *Megasoma* with that of placental mammals of similar mass experiencing the same ΔT (Fig. 2). For comparative purposes we have selected two small rodents whose metabolic rates were measured with an open-flow respirometry system smiliar to that used for *Megasoma* (*8*). The rodents, a kangaroo mouse (*Microdipodops pallidus*) and a pocket mouse (*Perognathus californicus*) have lower $\dot{V}_{O_2}$ than *Megasoma* of the same mass when ΔT is greater than 5° to 7°C (that is, at T_a below the thermal neutral zone of the mammals). Below thermoneutrality, the mass-specific thermal conductances of the mammals did not change with T_a, whereas the mass-specific thermal conductances of the beetles decreased linearly with T_a. For example, the conductance of an 11-g beetle was 0.42 ml of O_2 per gram per hour per degree Celsius at a T_a of 26°C but was only 0.30 ml of O_2 per gram per hour per degree Celsius at a T_a of 8°C. The decrease was apparently caused by a decline in T_{ab} from 27.1° to 15.5°C while T_{th} remained constant. Consequently, heat loss from the abdomen decreased with decreasing T_a.

The dearth of information on the natural history of *Megasoma elephas* makes ecological interpretation of the homeothermic metabolic response problematic. We assume that when T_b is regulated above T_a during terrestrial activity, the pattern of T_b regulation is the same as the pattern we observed in the laboratory at T_a below 20° to 22°C; that is, that variation in heat production rather than variation in heat loss to the abdomen is the primary mechanism of control of T_b. *Megasoma* is certainly capable of supporting normal activity levels by regulating a high T_b at T_a below 20° to 22°C (T_a values as low as 15°C have been recorded on Barro Colorado Island), but we do not know whether the beetles could fuel the metabolic increase required, should T_a remain low for more than a few hours.

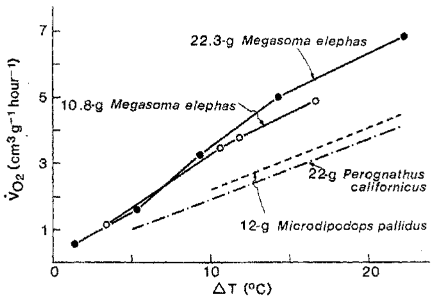

Fig. 2. A comparison of the relation of mass-specific $\dot{V}_{O_2}$ to ΔT in scarab beetles and heteromyid rodents of similar size. The curves for rodents are the regressions of their euthermic energy metabolism below the thermal neutral zone (*8*). The points for the beetles are the means of 16 or more measurements taken while T_{th} was constant at a given T_a.

To our knowledge, among insects, a homeothermic metabolic response to decreases in T_a in the absence of locomotor activity has only been reported in worker honey bees (*9*) and in incubating queen bumble bees (*10*). The homeothermic responses of the beetles reported here were not as fine-tuned as those of birds and mammals. In the beetles, T_b declined to about 20° to 22°C before there was any regulation. Thereafter, their metabolic response to a decrease in T_a was qualitatively similar to that of birds and mammals. However, instead of maintaining T_b constant, there was an oscillation over a range of 3° to 4°C with the frequency but not the amplitude of the oscillations increasing with ΔT. The beetles appear to have a definite set point below which they "defend" T_b. The greater the ΔT, the more rapid the heat loss and the more rapid the oscillations in $\dot{V}_{O_2}$ and T_b.

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Indoor Airborne Asbestos Pollution: From the Ceiling and the Floor

Abstract. *Electron microscopic measurements of the concentrations of airborne asbestos were carried out inside and outside an office building having ceilings sprayed with a crocidolite-containing material and floors covered with vinyl-chrysotile tiles. Under normal conditions in this building, constructed 10 years ago, the two asbestos-containing materials released fibers into the air. This is the first measurement of elevated (up to 170 nanograms per cubic meter) concentrations of indoor airborne asbestos associated with the weathering of asbestos floor tiles during their service life. Asbestos flooring is used in a large number of buildings and represents the third largest use of asbestos fibers in the United States and in Europe, ranking after roofing and asbestos-cement pipe.*

The potential hazard arising from exposure to airborne asbestos inside buildings sprayed with asbestos-containing materials is currently the subject of much concern. The Environmental Protection Agency has undertaken a large-scale program to control friable asbestos-containing materials in school buildings (*1*). The Conseil Supérieur d'Hygiène Publique de France has recommended controlling the concentrations of airborne asbestos inside buildings sprayed with asbestos (*2*). Since 1975, analytical facilities for the measurement