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Endothermy During Terrestrial Activity in Large Beetles

Abstract. *The large tropical American beetles* Strategus aloeus *(Scarabaeidae) and* Stenodontes molarium *(Cerambycidae) can endogenously maintain metathoracic temperatures 5° to 7°C or more above ambient temperature for many hours. During such periods, their activity is exclusively terrestrial and their oxygen consumption equals that of active mammals of the same size. Before and during flight they elevate metathoracic temperatures by an additional 8° to 10°C.*

Insects belonging to at least five different orders can attain thoracic temperatures 10° to 20°C above ambient temperature by retaining some of the heat produced by the contraction of the flight muscles (*1*). The primary functional result of these elevated temperatures is an increase in the power output and the frequency of wingbeat. However, heat produced by the wing muscles can also be important in processes not involved with flight, for example, brooding in bees and stridulation in katydids (*2*). The endogenous heat production of beetles has received less attention than that of bees and moths, but preflight warm-up was demonstrated 35 years ago in a scarabaeid, *Geotrupes stercorarius* (*3*), and the role of high pterothoracic temperatures in large beetles has been critically examined (*4*). We report here prolonged, endothermically supported, elevated body temperatures during terrestrial activity as well as during preflight warm-up in *Strategus aloeus* (Scarabaeidae; Dynastinae) and *Stenodontes molarium* (Cerambycidae; Prioninae).

We measured the energy metabolism of both resting and strenuously active animals in a closed system with a paramagnetic oxygen analyzer (*5*). To measure oxygen consumption during activity we rotated the glass respirometer chambers manually so that the beetles were either continuously walking or continuously attempting to right themselves. We made instantaneous measurements of thoracic temperatures by inserting a thermocouple probe 0.2 mm in diameter into the metathorax anteriorly through the fold of thin chitin at the base of the third walking leg. We obtained continuous records of body temperatures from 40-gauge copper-constantan thermocouples inserted laterally or dorsally into the abdomen, metathorax, and prothorax. The signals from the implanted thermocouples were either read from a thermocouple thermometer or recorded on the servo channel of a polygraph. The activity of the implanted beetles included walking about freely in a tabletop enclosure, attempting to walk on the table surface while tethered by threads attached to the mesothoracic legs, or walking on a running wheel rotated by hand at a speed which kept the beetle climbing uphill or walking horizontally. The frequencies of respiratory pumping were counted by eye and timed with a stopwatch. All measurements were made in an air-conditioned room (air temperature 22° to 25°C) illuminated by fluorescent lights.

The body temperatures of *Strategus* and *Stenodontes* were indistinguishable from ambient temperature, but during activity each showed two different patterns of endothermic temperature elevation. One pattern, a preflight warm-up, consisted of a rapid and sustained rise in body temperature that continued until flight temperature (38° to 41°C, depending on the species) was attained and the animal took wing. The other pattern did not involve flight and consisted of an initial rise followed by sustained maintenance of body temperatures at a level intermediate between resting and flight temperatures.

The preflight warm-up of *Strategus* and *Stenodontes* (Fig. 1B) is generally similar to that for *Geotrupes stercorarius* (Scarabaeidae) (*3*) and *Acilius sulcatus* (Dysticidae) (*6*) and resembles preflight warm-up in moths (*7*). In view of the heavy wing loading of both *Strategus* and *Stenodontes*, it is to be expected that they, like heavily wing-loaded moths and bees, require high thoracic temperatures for flight (*8*). Under laboratory conditions immediately after flight, metathoracic temperatures ranged from 39.0° to 40.2°C in *Strategus* and from 38.2° to 40.6°C in *Stenodontes*. However, these beetles not only warmed up as a prelude to flight but also frequently maintained metathoracic temperatures 5° to 7°C or more above ambient for several consecutive hours during which they made no attempt to fly but remained continuously active and in almost constant motion. During these periods of sustained endothermy, metathoracic temperatures oscillated over a range of several degrees Celsius, sometimes with great regularity (Fig. 1A). In both species the oxygen consumption during activity was many times that at rest; in a 6-g *Strategus*, oxygen consumption increased to more than 100 times the resting level (Table 1). The dependence of metathoracic temperature on the rate of energy metabolism is shown by the strong correlation between increases in metathoracic temperature and specific metabolic scope (Fig. 1C). However, our data do not allow us to as-

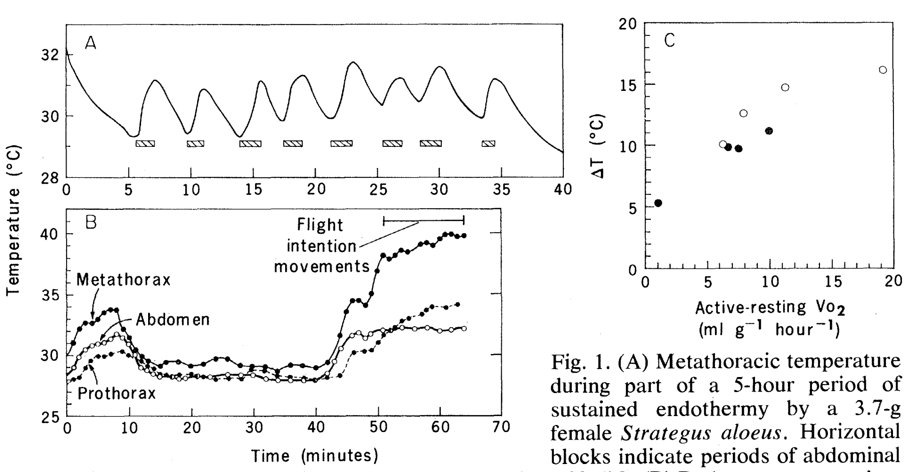

Fig. 1. (A) Metathoracic temperature during part of a 5-hour period of sustained endothermy by a 3.7-g female *Strategus aloeus*. Horizontal blocks indicate periods of abdominal respiratory pumping. Ambient temperature (T_a) = 23.0° to 23.5°C. (B) Body temperatures in a 2.8-g male *Stenodontes molarium* during a period of sustained endothermy followed by preflight warm-up and take-off: T_a = 22.6° to 23.0°C. (C) The relation of elevated body temperature to increased oxygen consumption ($\dot{V}_{O_2}$) for *Stenodontes molarium* (closed circles) and *Strategus aloeus* (open circles); ΔT = metathoracic temperature minus ambient temperature; T_a = 22.3° to 25.0°C.

sess the extent to which the level of body temperature is regulated under different or changing environmental conditions. In the individuals we measured, the metathoracic temperature after 3 to 5 minutes of activity was not significantly dependent on body mass.

The oscillatory pattern of sustained endothermy shown by *Strategus* and to a lesser extent by *Stenodontes* is reminiscent of the on-off shivering responses in moths that are prevented from flying (*9*), but the prolonged elevation of body temperatures in these beetles appears to be completely unrelated to flight preparation—they often maintained high temperatures for several hours without attempting to fly or making any flight intention movements.

During intervals of sustained endothermy the rates of specific energy metabolism of both species of beetles approached and sometimes exceeded that of active mammals of similar size at the same ambient temperature. For example, at 25°C the oxygen consumption of the smallest (mass, 3 to 4 g) North American mammal, the masked shrew (*Sorex cinereus*) ranges from 10 to 18 ml of O_2 per gram of body mass per hour (*10*), whereas that of active but nonflying *Strategus* with masses of from 4.8 to 6.3 g and body temperatures in the same range as that of the shrew (36° to 40°C) ranged from 7.9 to 19.3 ml g^{-1} $hour^{-1}$ (Table 1).

The muscle contractions associated with walking and respiratory pumping necessarily produce heat. However, the principal source of heat production in *Strategus* and *Stenodontes* appears to be contraction of the flight muscles, from which heat is transferred to the rest of the body by circulating hemolymph, by air movements in the respiratory passages, and by conduction in a manner similar to that found in other endothermic insects (*1*). During episodes of heating, the temperature in the metathorax in both *Strategus* and *Stenodontes* was always higher than in either the abdomen or the prothorax. Although neither the wings nor the elytra of either species showed any visible movements during periods of increasing body temperature, each time the body temperature rose the leads from the thermocouple implanted in the thorax vibrated at high frequency whereas the leads from the thermocouples in the prothorax and abdomen did not. These vibrations were also readily detectable by touch. Increases in body temperature in both species were always accompanied by respiratory pumping, during which the abdomen throbbed strongly in close synchrony with thrusting movements of the head. During the sustained endothermy shown in Fig. 1A, strong abdominal pumping (mean rate, 73.4 per minute; standard deviation, 8.6) coincided with each of the cyclically recurrent intervals of increasing body temperature. In the endothermic episode shown in Fig. 1B the respiratory pumping of *Stenodontes* was continuous but varied in rate from 48 to 115 per minute with the higher rates occurring at the higher temperatures. We cannot quantify the heat produced by abdominal respiratory pumping, but, because of the small mass of the abdominal muscles relative to those of the thorax, it should be of minor importance. We assume that the abdominal pumping we observed functioned primarily to supply oxygen to support the contractions of the flight muscles (*11*). Whether the individual was walking or not had no apparent effect on thoracic temperature. For example, the *Strategus* for which temperatures are plotted in Fig. 1A walked continuously during every period of decreasing body temperature and during about a third of the periods of increasing body temperature, whereas the *Stenodontes* for which data are presented in Fig. 1B walked continuously throughout the period of measurement prior to the onset of flight intention movements and walked intermittently thereafter.

Table 1. Oxygen consumption ($\dot{V}_{O_2}$) during rest and during 3 to 5 minutes of sustained terrestrial locomotion. The metathoracic temperature (T_m) was measured at the end of the activity period; T_a, ambient temperature.

Beetle	Mass (g)	Resting $\dot{V}_{O_2}$ (ml g^{-1} $hour^{-1}$)	Active $\dot{V}_{O_2}$ (ml g^{-1} $hour^{-1}$)	T_m (°C)	T_a (°C)
Strategus aloeus	3.7	0.14	6.41	34.4	24.2
Strategus aloeus	4.8	0.20	11.50	38.8	23.3
Strategus aloeus	5.4	0.17	7.90	36.6	24.0
Strategus aloeus	6.3	0.17	19.27	40.2	22.8
Stenodontes molarium	1.0	0.28	7.82	32.0	22.3
Stenodontes molarium	3.8	0.17	6.81	33.0	23.2
Stenodontes molarium	3.8	0.28	1.35	29.3	25.0
Stenodontes molarium	4.1	0.30	10.32	33.7	22.5

Strategus aloeus and *Stenodontes molarium* are primarily nocturnal. They have little opportunity to elevate body temperature by behavioral thermoregulation of the sorts shown by diurnal desert tenebrionids (*12*). Consequently, they can obtain the advantages that accrue from high body temperatures only by endogenous heat production. The advantage of preflight warm-up and elevated flight temperature in increasing the frequency and power of wingbeats is clear. In large beetles high metathoracic temperatures also appear to be important in matching the frequency of muscle contraction to the passive mechanical resonance of the wing-flight muscle system (*4*). However, the specific functional utility of sustained nonflying endothermy is not known. Beetles do not brood eggs or larvae. Neither *Strategus* nor *Stenodontes* stridulates loudly, and neither is an active predator. Minimizing the duration of preflight warm-up, which is one result of maintaining body temperatures 5° to 7°C above ambient, may be selectively advantageous. It is possible that the increased power and speed of terrestrial locomotion associated with a modest elevation of body temperature has been favored by natural selection. Elevated body temperatures may offer reproductive advantages by increasing the effectiveness of intraspecific aggressive behavior, particularly between males—both *Strategus* and *Stenodontes* show conspicuous sexual dimorphism. However, evaluation of the specific functional role or roles of sustained nonflying endothermy in beetles must await further information, as must evaluation of the extent to which the elevated temperatures represent a regulated state.

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