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A test of the 'maxithermy' hypothesis with three species of tenebrionid beetles

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Hamilton invoked his 'maxithermy' hypothesis, which suggests that the high body temperatures of desert tenebrionid beetles are sustained because they lead to increased rates of many biological processes, and are therefore advantageous. I designed an experiment to test the validity of the 'maxithermy' hypothesis in three species of Namib desert beetles (*Onymacris plana, O. rugatipennis* and *Physadesmia globosa*) known to have high body temperatures. Moreover, this experiment examined the ability of these ectothermic beetles to reduce their metabolic rates in times of food shortage, by choosing lower environmental temperatures. None of the three species changed the selected environmental temperature with progressive food deprivation. This experiment rejects the 'maxithermy' hypothesis as an adaptive hypothesis to explain high body temperatures.

Introduction

The high body temperatures of Namib desert tenebrionid beetles (Insecta: Tenebrionidae) have attracted a great deal of attention among arid-zone biologists (e.g. Cloudsley-Thompson, 1962; El Rayah, 1970; Hamilton, 1971, 1973, 1975; Edney, 1971; Louw & Hamilton, 1972; Henwood, 1975; Nicolson *et al.*, 1984; McClain *et al.*, 1985; Seely *et al.*, 1988). These diurnal beetles, many of which are black, have the highest body temperatures of any ectotherm (30–43°C; Seely *et al.*, 1988). These high body temperatures are particularly remarkable because North American desert tenebrionids, which experience higher ambient temperatures (Seely *et al.*, 1988), have much lower body temperatures (21–27°C; Whicker & Tracey, 1987; Parmenter *et al.*, 1989).

A number of theories have been mooted to explain the high body temperatures of these insects (Hamilton, 1973; Heinrich, 1977; Seely *et al.*, 1988). The most prominent of these is Hamilton's (1973) 'maxithermy' hypothesis. Hamilton (1973) hypothesised that the high body temperatures of Namib desert beetles may increase the rates of many biological processes (the 'maxithermy' hypothesis). This may allow them to maintain higher metabolic rates. Following this adaptive hypothesis, beetles with higher body temperatures will have greater efficiency in foraging and other activities than those beetles that select lower body temperatures. Beetles selecting higher body temperatures will, therefore, be able to increase reproductive output or enhance survival, i.e. 'hotter' beetles have greater expected fitness.

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However, the increased metabolic rate of an animal following a maxithermic strategy is only of value if food is not limiting. At first sight, this appears a reasonable assumption for these generalist detritivores (Crawford, 1988). However, should food be limiting, an animal with a high metabolic rate incurs a greater energy cost than an animal with a low metabolic rate. Indeed, low metabolic rates are characteristic of animals living in nutrient-poor environments (Schmidt-Nielsen, 1975). Thus, if these desert tenebrionid beetles are adopting a maxithermic strategy one would expect them to select lower temperatures when deprived of food.

I predicted that if 'maxithermy' was operating, then beetles placed in a thermal gradient should choose progressively cooler parts of the gradient with time without food in order to minimise energy expenditure. Thus, I set out to test the 'maxithermy' hypothesis by depriving beetles of three black species (*Onymacris plana, O. rugatipennis* and *Physadesmia globosa*) of food over a period of weeks and examining their temperature preference in a thermal gradient.

Materials and methods

Temperatures selected by the beetles were measured in the laboratory using a circular gradient modified from that described by Kramm & Kramm (1972). Constructed of sheet metal, the gradient had an inside diameter of 0.8 m and an outside diameter of 1 m, creating a trough 100 mm wide. The gradient was established using a counter-current heat-exchange system, with hot and cold water running through adjacent copper tubes lining the floor of the trough. The tubes were covered by about 10 mm of sand. A gradient ranging from about 25 to 50°C was established. If at any time the beetle was found at either extreme of the gradient for more than 5 min, the range of temperatures was shifted until this behaviour was terminated. Sand-surface temperatures at the extremes of the gradient were measured at half-hourly intervals using 26 gauge copper-constantan thermocouples connected through a switchbox to a thermocouple thermometer (Bailey Bat-12). These thermocouples were calibrated against a standard mercury thermometer with an accuracy of ±0·1°C. The thermal gradient apparatus has several features: (1) cornering by the beetle was prevented; (2) the temperature gradient could be adjusted at any time; (3) the conductant heat source prevented confusion from phototaxic responses (evenly dispersed lighting was provided by fluorescent tubes directly above the gradient).

Beetles of three species (*Onymacris plana, O. rugatipennis* and *P. globosa*) were deprived of food and water for 6 weeks. These were collected, as adults, from the field within 5 km of the Desert Ecological Research Unit, Gobabeb, Namibia (23°34′S, 15°02′E). These beetles are capable of withstanding at least 2 months of food deprivation (M. K. Seely, pers. comm.). Ten beetles of each sex of each species were used in these experiments. The physiological status of the beetles was not examined as it was assumed that they represented a random sub-set of the populations. The beetles were placed in the temperature gradient once a week for 5 weeks, starting 1 week after the initiation of food deprivation. The beetles were placed in the gradient individually (at the high temperature end) and allowed 5 min each to settle in the part of the gradient they selected. Beetle body temperatures (T_b) were not measured in these experiments, relying rather on the temperature at the position in the gradient that the beetles selected for comparison among beetles and experimental periods. Copper-constantan thermocouples were placed at 10 cm intervals around the gradient, ±1–2 mm below the sand surface.

Ten additional beetles of each sex of each of the three species were used as controls. The control beetles were maintained on *ad libitum* food (rolled oats, fresh cabbage and apple) in environmental conditions close to those prevailing in the ambient environment during the experimental period. Each week, these fed individuals were put into the gradient immediately after the unfed beetles of their respective species and their selected temperatures determined. All experiments started at 0900 h. The beetles in this experiment were not individually marked.

The distribution of the temperature-selection data for each of the three species was not significantly different from normal (Kolmogorov-Smirnov one-sample tests, $p > 0{\cdot}05$), so all statistical analyses were conventional analyses of variance (ANOVA).

Results

There was no significant difference in selected temperature between the sexes of any of the three species (ANOVA, $p > 0{\cdot}05$) in any time period (control and experimental animals). Therefore, the data for the sexes were pooled in all further analyses.

There was no significant change in the selected environmental temperatures of food-deprived and fed *O. plana, O. rugatipennis* and *P. globosa* over the experimental period (ANOVA, $p > 0{\cdot}05$). There was no significant difference between the selected temperatures of fed and unfed beetles of any of the three species during any experimental period (two-way ANOVA, $p > 0{\cdot}05$) [Fig. 1(a)–(c)]. There was no significant difference among species in temperature selected. The mean ±S.E. temperatures selected by fed beetles were 41·9 ± 1·55°C, 40·7 ± 1·41°C, and 40·3 ± 1·21°C by *O. plana, O. rugatipennis* and *P. globosa*, respectively. The mean ±S.E. temperatures selected by unfed beetles were 41·3 ± 1·29°C, 41·8 ± 1·26°C, and 41·0 ± 1·62°C by *O. plana, O. rugatipennis* and *P. globosa*, respectively.

Discussion

Hamilton's (1973) 'maxithermy' hypothesis has been criticised by a number of authors (Kenagy & Stevenson, 1982; Pietruszka, 1988; Seely *et al.*, 1988) on the grounds that T_bs recorded in their study species were not highest possible relative to prevailing environmental temperatures. That is, the beetles could have maximised metabolic rates by being active at even higher environmental temperatures, which were still within their thermal critical zones. These criticisms are inappropriate, however, if one considers the 'maxithermy' hypothesis to be a form of optimal strategy (*sensu* Maynard Smith, 1978), i.e. the beetles maximise their body temperatures within the constraint of a certain temperature where metabolic activity is impaired. If the beetles choose an optimal temperature for activity then there may be no congruence between beetle temperature and maximum ambient temperature. However, an optimal thermal strategy would require the beetles to select lower body temperatures when deprived of food, as would 'maxithermy'.

Heinrich (1977) has criticised the 'maxithermy' hypothesis because "Hamilton (1973) appears to overemphasise Q_{10} while ignoring biochemical adaptation when he suggests that animals are attempting to attain the maximal possible body temperature ('maxithermy') in order to boost activity rates. The hypothesis does not explain why the animal's biochemical machinery has not evolved to do the same job at lower temperatures". Heinrich's (1977) criticism may be valid but, like those of the other authors mentioned above, does not provide a test of the 'maxithermy' hypothesis. The results of the experiments documented here indicate that 'maxithermy' does not function in the beetles tested, at least not as an adaptive strategy to maximise energetic efficiency. Similarly, these results are inconsistent with an optimal strategy of body temperature selection.

Alternative hypotheses

Heinrich (1977) has suggested that ectotherms subjected to high tissue temperatures have no choice but to have high temperature set points because it is more important to survive

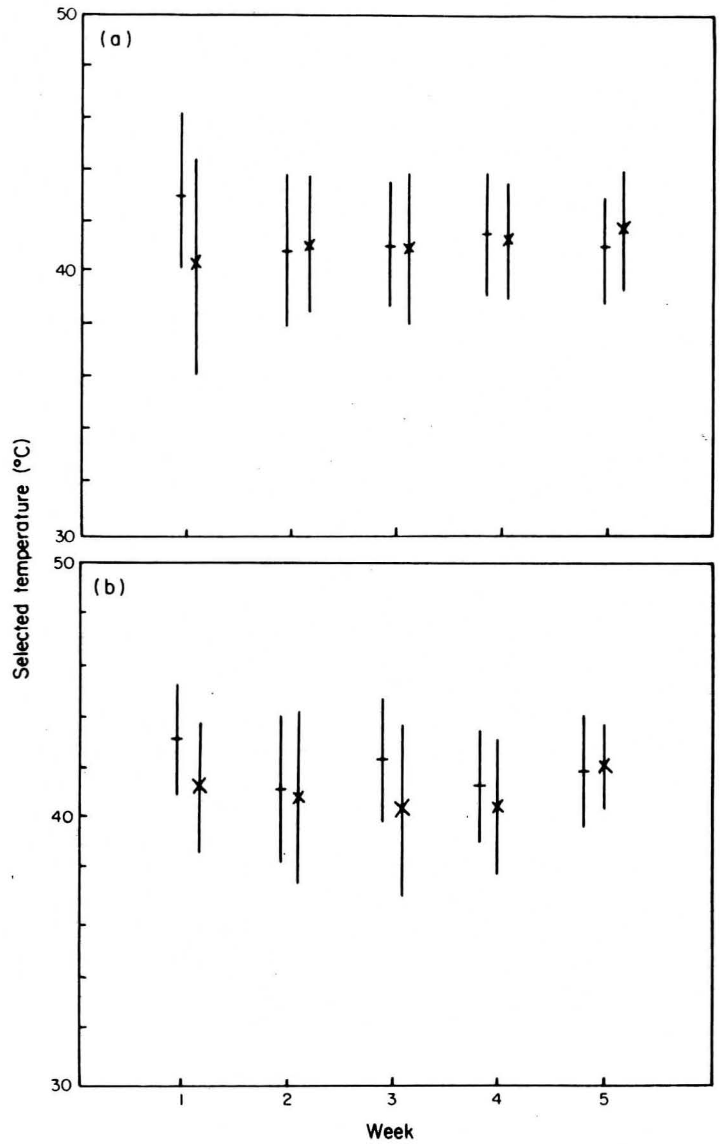

Figure 1. Temperatures in the gradient nearest to the position selected by the tenebrionid beetles, over 5 weeks. Means and 95% confidence limits are presented. The values for fed beetles are presented to the right of the unfed beetles each week. (a) *Onymacris plana,* (b) *O. rugatipennis,* and (c) *Physadesmia globosa.*

the high temperature bottlenecks than it is to have biochemical machinery that can operate efficiently at the low temperatures they experience. The lowering of body temperature much below ambient during sustained activity can be achieved only by the use of exorbitant supplies of water for evaporative cooling. Thus, the biochemical machinery of tissues is necessarily geared to operate at the upper temperatures encountered (Heinrich, 1977).

Heinrich's (1977) argument begs the question why these animals, whose food (detritus) is available at all times of the day and night, are not active during the cool night hours. That is, why have they not evolved the biochemical machinery to be active at the cool night

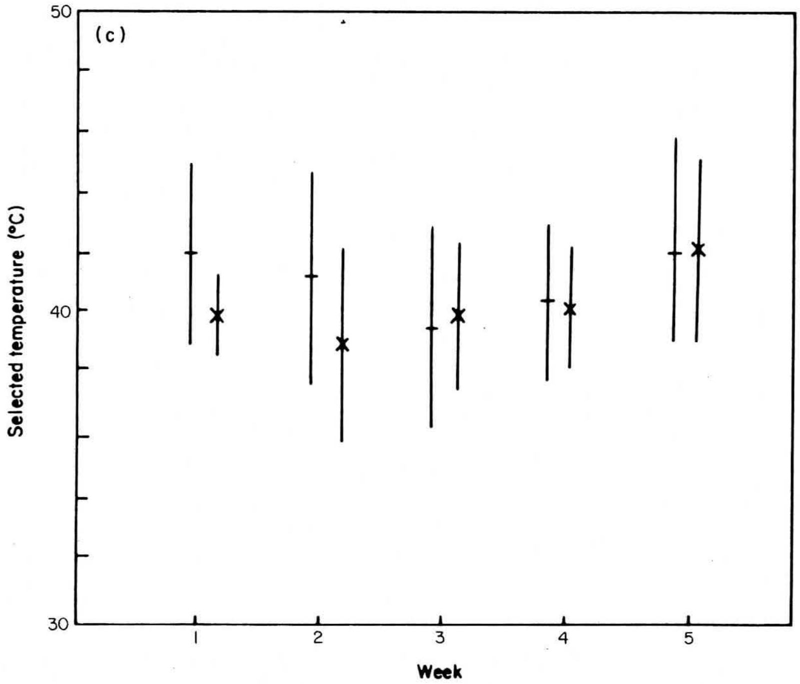

Figure 1. Continued.

temperatures? Heinrich's (1977) hypothesis is similar to that of Seely *et al.* (1988), who suggested that the high body temperatures of these beetles are an effect of: (1) the ease with which small diurnal invertebrates can maintain body temperatures higher than ambient; (2) the difficulty of attaining body temperatures lower than ambient without expending excessive amounts of water for evaporative cooling. That is, Seely *et al.* (1988) suggested that high body temperatures are passive effects of thermal loads imposed by prevailing environmental conditions. This hypothesis, like Heinrich's (1977), does not explain why these beetles are not nocturnal.

A more promising alternative hypothesis is the predation avoidance hypothesis (Seely, 1985). This hypothesis suggests that the beetles have evolved to select high body temperatures in order to escape predation. That is, the beetles avoid many nocturnal predators by being diurnal, and are able to withstand higher ambient temperatures than diurnal predators. In addition, as their metabolic rates increase they become faster and more adept at escaping.

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