BODY TEMPERATURES IN SOME AUSTRALIAN MAMMALS

II. PERAMELIDAE

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Summary

Body temperature measurements on the short-nosed bandicoot (*Thylacis obesulus*) have shown a nocturnal cycle with a range of 1·2°C and a short active phase at 2200–0400 hr. The bilby or rabbit bandicoot (*Macrotis lagotis*) had a sharply defined temperature cycle, with a range of almost 3°C after several months of captivity, during which the day-time resting temperature was progressively lowered from 36·4 to 34·2°C. Forced activity raised the diurnal temperature substantially but not to the nocturnal level. Forced activity did not raise the nocturnal level which was similar in the two species (37·0°C). Both species could regulate effectively at an ambient temperature of 5°C, but only *Thylacis* showed regulation at ambient temperatures of between 30 and 40°C.

I. INTRODUCTION

The marsupials lie between the monotremes, with their clearly primitive thermoregulation, and the higher Eutheria, which are, as a rule, effectively homeothermic (Martin 1903). But despite a generally lower level of body temperature, the relation of marsupial thermoregulation to that in the higher mammals is by no means evident since, in certain aspects, it appears quite as effective. Within the order Marsupialia, the families form a fairly well-defined morphological sequence from the primitive Dasyuridae through the most specialized Macropodidae and show some interesting physiological parallels in their responses to heat stress (Robinson and Morrison 1957). This study concerns other facets of thermoregulation in two species from one of these families, the Peramelidae, a group on which there appears to be only a single previous temperature study in the literature (Robinson 1954).

II. MATERIAL AND METHODS

The Peramelidae or bandicoots are a small, syndactylous, and polyprotodont group standing between the generalized Dasyuridae and the more specialized Phalangeridae and Macropodidae. The species studied here were the short-nosed bandicoot (*Thylacis* (= *Isoodon*) *obesulus*) and the bilby or rabbit bandicoot (*Macrotis lagotis*). The former genus ranges widely over much of coastal Australia and is rather common along the north-eastern coastal region (Troughton 1941). These specimens were trapped in Brisbane. The general appearance is heavy-bodied and rat-like with a rather coarse, grisled, brown-black fur. Individuals were

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unamiable either with others of their kind or during experimental handling. Certainly in our hands the "cheerful assumption of goodfellowship with man" described by Wood-Jones (1924) was not noticeable. Their habit is nocturnal and they appear to be largely carnivorous, although they will sometimes eat vegetable material. These individuals were housed individually in ordinary wire animal cages and were fed principally on ground meat. Their weights ranged from 700 to 2600 g.

The bilby is a quite different animal, having been described without exaggeration as "among the most beautiful of the marsupials". It has a long, soft, blue-grey fur, which extends over the tail and the long rabbit-like ears. These animals are carnivorous, living on insects and mice. In captivity they were fed on grasshoppers and beef. In earlier days they were not uncommon, but of late they have become rare and confined to more isolated regions. Aboriginals helped dig this animal out of its burrow at Haast's Bluff, N.T. The burrow was of the "characteristic" form (Troughton 1941), descending through sandy soil along a spiral path about 6 feet in diameter until the nest chamber was reached some 5 feet below the surface and almost directly below the entrance of the burrow. In this instance, the animal was not found in the nest chamber but was located in a side passage only a few feet from the entrance. Its position was detected by an aboriginal who put his ear to the ground to locate it. The bilby was carried overland in our Landrover a distance of some 1500 miles to Brisbane, where the experimental observations were made.

The bilby proved an admirable experimental subject, offering minimal objection to handling, and often remained completely relaxed during experimental procedures. Body temperatures were measured with iron–constantan thermocouples using a 5-cm depth of insertion. The animals were never measured more frequently than twice a day, and usually only once, to avoid distortion of the daily cycle. Since they were kept in general animal quarters in the laboratory, they were by no means isolated and so may have been influenced to an unknown extent by outside disturbances. The bilby appeared quite immune to disturbance, but the short-nosed bandicoots were easily aroused.

III. Results

(a) Thylacis obesulus

Two groups of short-nosed bandicoots were used: one of a dozen individuals (5 females and 7 males) in the winter during July and August and a second group of four females during midsummer in January and February. Although the mean ambient temperature rose some 8°C between these experiments, there was no change in either the nocturnal or the day-time level of body temperature. Neither could a difference be related to the sex of the animals. Accordingly, the data were pooled for analysis of the diurnal temperature cycle and these values are shown in Figure 1. A modest amplitude of 1·10°C was observed, but the intractability of this species may have damped the cycle to some extent (i.e. by impeding

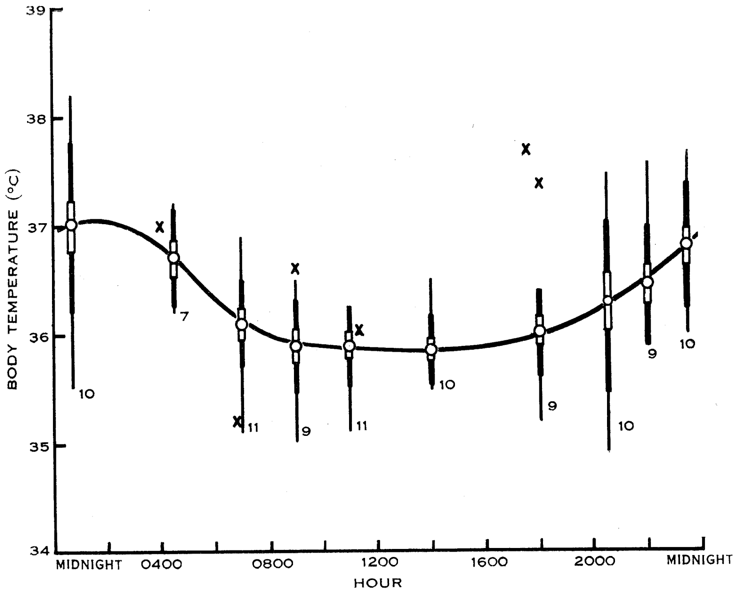

Fig. 1.—Body temperature in *Thylacis obesulus* as a function of time. Means of pooled values from summer and winter data grouped by hour. Boxes show standard error; bars, standard deviation; lines, range. × Single values for a 130-g young female.

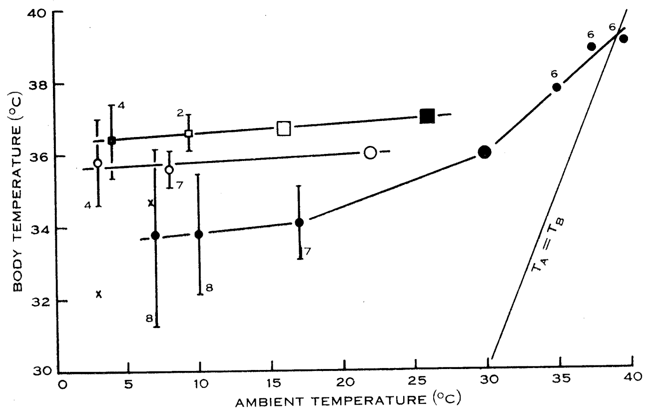

Fig. 2.—Body temperature (T_B) in *Thylacis obesulus* as a function of ambient temperature (T_A) after 2- or 4-hr exposures. Circles, day; squares, night; open symbols, winter observations; closed symbols, summer observations. Larger symbols are means for caged (not closely confined) animals. Lines show standard deviations for confined exposures. × Values for 1-hr exposures for a 130-g young female.

the day-time fall). The cycle was distinguished by the length of the inactive phase (0800–2100 hr) as compared to the much shorter active phase (2300–0300 hr).

The response of these animals to low ambient temperatures is shown in Figure 2. Body temperatures were first measured after exposure for 2 hr and then again after an additional 2 hr. Although differences were noted between any pair of values, there was no systematic trend, and the 2-hr average values were the same as the respective 4-hr averages. Accordingly, those values represent maintenance conditions and all were pooled for each ambient temperature. It

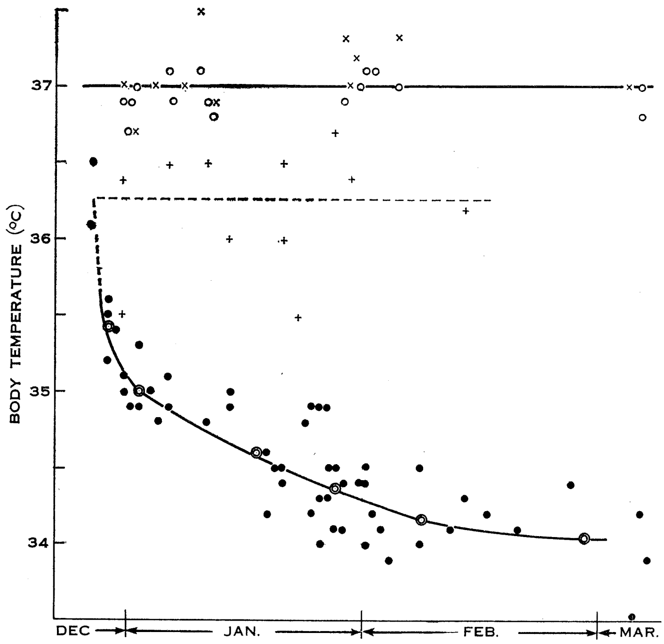

Fig. 3.—Body temperature in *Macrotis lagotis* as a function of time. Double circles show group means for day values. ●, ○ Natural activity at day- and night-time respectively. +, × Induced activity at day- and night-time respectively.

may be seen from the top curve that at night during the active phase, cold has a negligible effect (slope $= 0 \cdot 03$). A similar response is seen for the day-time values in the winter group, in which the values at 3–8°C are very close to the values at room temperature (slope $= 0 \cdot 03$). However, following day-time exposures to cold, the summer animals showed a substantial fall which averaged 2°C (slope $= 0 \cdot 12$). But there was great variability in this response, with values ranging from 30°C to almost 37°C, so that some individuals were regulating while others were not.

The ordinary day-time value was the same in summer as in the winter, even though the average surrounding temperature was about 8°C higher. But exposures to warmer environments elevated the body temperature sharply to

39°C at an ambient temperature of 39°C (slope $=0\cdot3$). Regulation by evaporative cooling under these conditions has been described previously (Robinson and Morrison 1957).

One young bandicoot was available for testing, a 130-g female of unknown age. Values during the day are shown as crosses on Figure 1 and fit in well with those of the adults, except that the evening rise appears somewhat earlier. But its response to cold was definitely less effective, with a 1-hr exposure to 3°C reducing the body temperature to 32°C (Fig. 2).

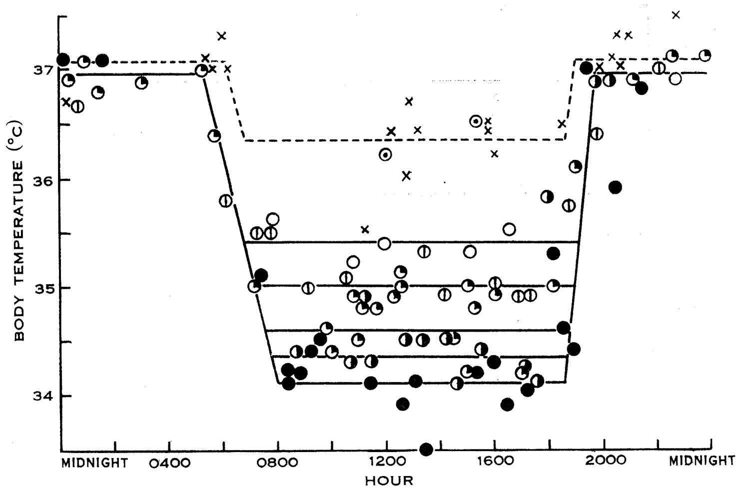

Fig. 4.—Nocturnal temperature cycle in *Macrotis lagotis* with points grouped according to date (see Fig. 3): ⊙ December 26–27; ○ December 28–30; ⦶ December 31–January 4; quarter-filled circles, January 5–25; half-filled circles, January 28–31; ● February 1–March 7. Horizontal lines show average values for groups. Crosses and dotted line show response to induced activity.

(*b*) Macrotis lagotis

The bilby is an unusual animal, both in appearance and in behaviour, and demonstrated most interesting temperature responses as well. The daily temperature cycle was well developed. During the 7-hr active period (2000–0500 hr), a level of $37\cdot1$°C was maintained with great precision (S.D. $=0\cdot13$°C); and there was a sharp transition between activity and inactivity. But during the 12-hr inactive period (0700–1900 hr), contrastingly great variability was observed (S.D. $=0\cdot43$°C). This variability was perplexing, since the bilby showed the most regular behavioural response of almost any animal that we have encountered. Throughout the day it maintained a profound sleep despite even gross disturbance, and its only movement was an occasional twitch. However, it was noted that during the course of these observations progressively lower day-time values were recorded. This is shown in Figure 3, where body temperatures are plotted against date.

Over a 2-month period, the mean day-time level fell by more than 2°C from above 36°C down to 34°C, although there was no visible change in behavior. By contrast, the night-time values showed no change whatsoever and maintained an average of 37·0°C. If the animal was disturbed during the day and forced into activity, its temperature could be elevated considerably to 36–36·5°C. There was no trend in this elevated level over the 2-month period. By contrast, forced activity during the normal active period produced no significant rise in temperature. These relations are shown more effectively in Figure 4, which plots the daily temperature

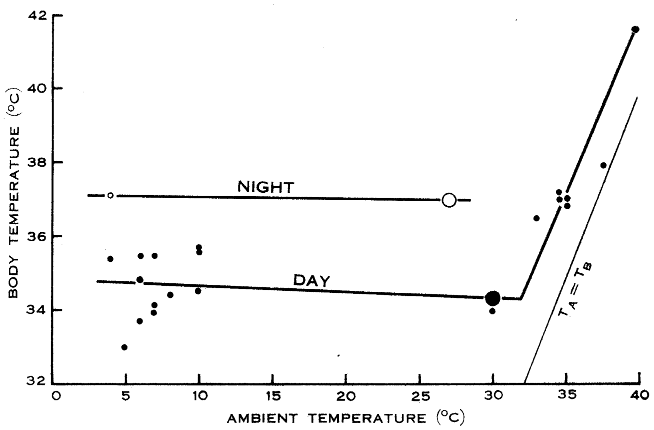

Fig. 5.—Body temperature (T_B) in *Macrotis lagotis* as a function of ambient temperature (T_A). Larger symbols are as defined in legend to Figure 2.

cycle while separating the data into groups by date. By this means, the dispersion of the day-time points around the mean is reduced to about half (S.D. $=0·23$°C), still somewhat greater than that of the active night values. The dotted line in this figure indicates the average temperature level during forced activity.

The influence of ambient temperature is shown in Figure 5. Most of these observations were made after the middle of January, when the day-time level had fallen to the lower plane (Fig. 3). It may also be seen that most of these experiments were carried out by day. Under these conditions, exposure to cold resulted in no reduction of body temperature. The small elevation seen is probably attributable to the disturbance incident in removal from the nesting cage and confinement in a small holding cage during cold exposure. A single experiment at night showed exact maintenance of the normal night-time level. By contrast, *Macrotis* proved very heat-sensitive, showing almost no regulatory capacity at ambient temperatures above 30°C ($dT_B/dT_A = 0·88$). Of all the marsupials studied under heat stress (Robinson and Morrison 1957), *Macrotis* was the least able to withstand this stress, and it was necessary to remove the animal from the hot room after only 2 hr at 40°C, after achieving a body temperature of almost 42°C.

IV. Discussion

At first glance, the daily cycles in the two species appeared quite different; but superposition, as in Figure 6, brings out some similarities. First, the maximum or active levels are identical; and second, the phasing of the cycles is very similar. And the differences in the minimum or sleeping levels and in the sharpness of the transition between active and resting states may merely reflect the adjustment of the animal to captivity. Thus, the early day-time values on *Macrotis* were not far from those on *Thylacis* and it was only after adjustment to captivity that much lower values were seen. *Thylacis* maintained a truculent, uncooperative attitude throughout and never did really adjust itself to captivity, which may account for both the higher day-time values and the more diffuse transition between activity states.

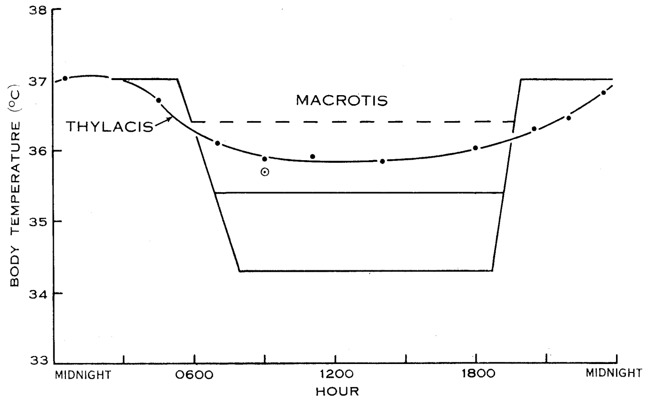

Fig. 6.—Comparison of body-temperature cycles of *Thylacis* and *Macrotis*. ⊙ Represents value for *Perameles nasuta* (from data of Robinson 1954).

The controlled (?) lability in the resting temperatures shown by *Macrotis* was a striking phenomenon which has not been previously seen. Since the animal's overt activity was always the same—namely zero—we appeared to have observed a shift in the regulated level of the body temperature, a value which is usually considered as fixed. By contrast, the night-time level was maintained without change over the whole period.

In regulation against cold, the two species also appear similar in their capacity for effective regulation down to below an ambient temperature of 5°C (Fig. 7). However, the reduction in the summer day-time temperature for *Thylacis* was distinctive. Data on the very similar *Perameles nasuta* by Robinson (1954) closely parallel the measurements on *Thylacis*, although the ambient range is more limited (14–21°C).

By contrast, *Macrotis* showed no defence against heat ($dT_B/dT_A = 0 \cdot 88$), while *Thylacis* and *Perameles* showed rather effective regulation at ambient temperatures between 30 and 40°C ($dT_B/dT_A = 0 \cdot 34$ and $0 \cdot 28$ respectively). These differences do not correspond to the environments, since the severity of heat stress in the *Macrotis* habitat in the central regions of Australia exceeds that of the two coastal species. However, this problem may be resolved by recalling the habits of the respective animals. *Macrotis* evades heat stress during the day in the subterranean microclimate of his burrow, while both *Thylacis* and *Perameles* have only an indifferent shelter of loose brush. Further, the reluctance of a species to dissipate water for heat regulation may reflect the paramount importance of water conservation in a desert animal, i.e. a higher or more critical level of homeostasis. Thus, the dehydrated camel allows its body temperature to rise rather than to make use of its quite adequate capacity for evaporative cooling (Schmidt-Nielsen *et al.* 1957). *Macrotis* would appear to be more rigidly set in a pattern of a desert life where water is *always* minimal, not just seasonally.

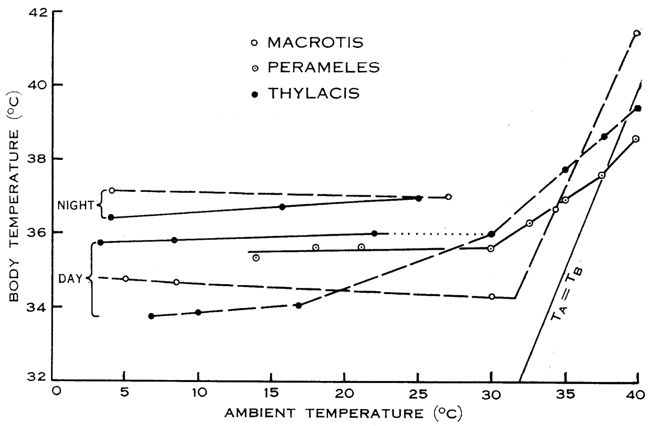

Fig. 7.—Regulation of body temperature in Peramelidae. Data on *Perameles nasuta* (⊙) taken from Robinson (1954). – – – Summer observations. ——— Winter observations.

Among the marsupials, these Peramelidae occupy a thermoregulatory position which corresponds to their taxonomic position, i.e. between the Dasyuridae and the Phalangeridae. Their regulation to heat is more effective than that of the smaller marsupial "rats" and "cats", but not so effective as in the possums and gliders. Their regulation to cold appears quite adequate for the conditions which they encounter in nature and exceeds that found in some tropical rodents. Their regulation to heat also can be as effective as some higher eutherian mammals.

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