

Thermoregulation and torpor in the Kultarr, *Antechinomys laniger* (Marsupialia: Dasyuridae)

Fritz Geiser*

School of Biological Sciences, Flinders University, Bedford Park, Adelaide, S.A. 5042, Australia

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Summary. 1. Body temperatures (T_b), rates of oxygen consumption (\dot{V}_{O_2}) and the loss in body mass of the small insectivorous dasyurid marsupial *Antechinomys laniger* were determined at different ambient temperatures (T_a).

2. Most animals entered torpor below T_a 27 °C when food was withheld. Spontaneous torpor was observed frequently at T_a 19 and 12.5 °C.

3. An increase in \dot{V}_{O_2} and ΔT ($T_b - T_a$) was observed during torpor below a T_a of about 11 °C. The lowest individual T_b measured was 11.0 °C.

4. The linear increase in \dot{V}_{O_2} during torpor below T_a 11 °C was parallel to the T_a related increase in metabolism of normothermic resting, active, and arousing animals.

5. Torpor lasted between 2 and 16 h and the longest durations were observed at T_a 13–20 °C; below and above this temperature range torpor bouts were shorter.

6. The lowest relative weight loss was observed at the T_a of the longest torpor bouts and lowest metabolism during torpor.

7. Both the time of the activity peaks and onset of torpor were dependent on T_a and were observed later in the night at higher T_a . Torpor commenced before the onset of light.

8. Arousal rates were rapid and the arousal times increased exponentially with decreasing T_a .

ly accepted, there is little experimental evidence which would support the argument by Wallis (1979) that marsupial torpor, like in placentals, is an advanced and adaptive rather than a primitive feature. Since information about thermoregulation in heterothermic marsupials which would allow such a conclusion is scant, a study investigating the thermal strategies of *Antechinomys laniger*, in which torpor has not been previously described, was conducted.

Antechinomys laniger is a small insectivorous marsupial of the family Dasyuridae. It is a rare species which inhabits the arid desert plains of south and central Australia and has been found sheltering in logs, beneath spinifex tussocks or in burrows of other animals (Valente 1983). Apart from these observations its field biology is largely unknown.

Materials and methods

Four adult *A. laniger* were obtained from the Evolutionary Biology Unit, South Australian Museum. They had been wild caught in Betoota Queensland, 25°52' S 140° 45' E, and kept in the laboratory at an ambient temperature (T_a) of 22 °C under a natural photoperiod. In autumn (March) they were transferred to a constant temperature room (T_a 19 °C), with a photoperiod of LD 12:12 (light from 0600 to 1800 h), a condition similar to the natural photoperiod at that time of the year, and were held under these conditions for three weeks before the experiments commenced. All measurements were taken in autumn (March/April/May).

Animals were individually housed in cages provided with wood shavings and boxes containing nesting material. Water and a mixture of canned ('Whiskas' Jellymeat) and dried ('Harper's' Dog chow) pet food were available ad libitum, and *Tenebrio* larvae and an egg gelatine mixture were provided every two weeks. Under these conditions body weight remained constant at a mean value of the four animals of 27.4 ± 1.4 g (standard deviation).

Body temperatures were measured by inserting a 0.5 mm thermocouple probe rectally for 30 mm and reading from a Kane-May Digital Thermometer. All thermocouples were cali-

Introduction

Torpor in marsupials was once considered to be the expression of a primitive thermoregulation (e.g. Eisentraut 1956). While this view is no longer wide-

* Present address: Department of Zoology, University of Washington, Seattle, WA 98195, USA

brated against a precision mercury thermometer traceable to a National Standard. The daily fluctuations of T_b of two animals kept for one week in outside enclosures under natural photoperiod and temperature fluctuations with food ad libitum were determined by staggering the measurements of T_b over a five day period. Body temperatures were measured in intervals of more than 12 hours.

To determine the duration and depth of torpor without disturbance (measurements of T_b induced arousal), rates of oxygen consumption were measured over 20.7 ± 2.8 h (range 15.5–25 h) at constant ambient temperatures between 7 and 31 °C. These measurements were begun in the late afternoon. Additional measurements over several hours were conducted around and above thermo-neutrality. The effect of a reduction of T_a and \dot{V}_{O_2} during torpor was also determined. Food and water were not available during measurements of \dot{V}_{O_2} but animals were fed 1 g *Tenebrio* larvae 2 h before the experiments commenced. A Servomex Model OA 184 paramagnetic oxygen analyser was used together with a Rikadenki Potentiometric Recorder. \dot{V}_{O_2} was determined from the difference between the oxygen content in two parallel circuits, one a room air reference and the other containing the animal. The 31 metabolic chambers had ports for inhalant and exhalant air and two thermocouples one of which was continuously read with the second channel of the Rikadenki Recorder; the second thermocouple was used for point readings. Flow rates 0.2–0.4 l/min were maintained through calibrated rotameters. All gas values were corrected to dry volumes under standard conditions of temperature and pressure (STPD). \dot{V}_{O_2} was calculated using the equation 3a of Withers (1977). For the calculation of mass specific \dot{V}_{O_2} during the prolonged measurement periods, the animals were weighed before and after the experiments and body mass interpolated assuming a constant rate of loss (see Fig. 4 for weight loss). Measurements of \dot{V}_{O_2} were used to determine: (1) the metabolic rate of normothermic inactive animals measured when a variation in \dot{V}_{O_2} of less than 5% over at least 15 min occurred within an inactivity period of at least 30 min; (2) the metabolic rate of torpid animals determined at times of constant \dot{V}_{O_2} over at least 30 min; (3) the metabolism during the nocturnal \dot{V}_{O_2} maxima determined over at least 10 min; and (4) the metabolic rate at the peak of the arousal period, independent of the duration of the arousal peak. The latter two determinations do not represent steady state values, but were within 80% of equilibrium (Lasiewski et al. 1966). All measurements were conducted in a quiet controlled temperature room, that was acoustically insulated from the recording equipment. A video camera was used to observe the animals during the experiments. These observations and others taken during arousal form the basis for the temperature ethogram.

Arousal times of *A. laniger* at different T_a were determined from T_b and \dot{V}_{O_2} measurements. Arousal rates were determined from T_b measurements during which the thermocouples were taped to the tail. For the \dot{V}_{O_2} measurements the peak level of \dot{V}_{O_2} during arousal was assumed to be the endpoint of the arousal period.

The tendency to enter spontaneous torpor was determined at T_a 19 and 12.5 °C. The possible ability of *A. laniger* to undergo prolonged periods of torpor rather than daily torpor was investigated at T_a 12.5 °C (food and water ad libitum) using the 'sawdust method' (see Folk 1957). All animals used in the present study survived the experiments.

Body temperature and \dot{V}_{O_2} criteria ($T_b < 31$ °C; $\dot{V}_{O_2} < 75\%$ of normothermic inactive animals; Hudson and Scott 1979) were applied to define periods of torpor. Although 31 °C may appear a rather high value considering the relatively low normothermic T_b of this species, motor control below T_b 31 °C was clearly different from normothermic animals.

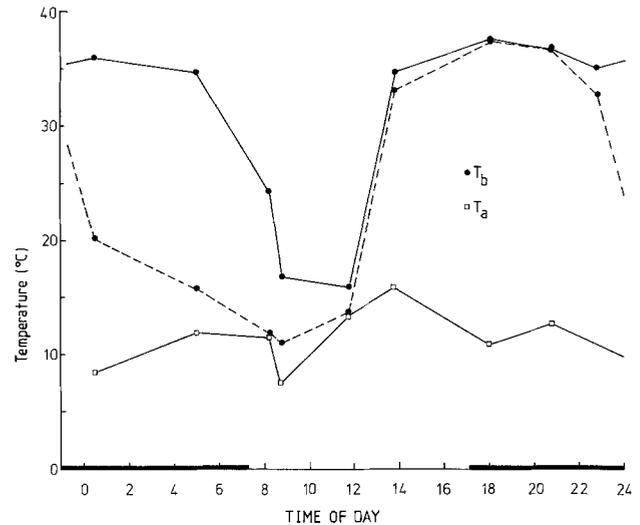


Fig. 1. Body temperatures of two *A. laniger* held under natural photoperiod and temperature fluctuations. Food and water were ad libitum. Measurements were staggered over a 5 day period. The abscissa represents the local time and the dark bar indicates the periods of darkness. Each point represents an individual measurement of T_b (●) and T_a (□)

A Student's *t*-test was used for comparisons of paired observations. Straight lines and curves were fitted by regression analyses. Differences in slope, elevation and y-intercepts of the straight lines were determined using the derived *t*- and *F*-values. Means of samples are expressed \pm the standard deviation (SD).

Results

Antechinomys laniger showed strong diurnal fluctuations in body temperature when held under natural conditions of photoperiod and ambient temperature. As shown in Fig. 1 the T_b maxima 36.8–37.7 °C were observed during the activity period between 1800 and 2000 h. Both animals entered torpor spontaneously (food ad libitum) and the duration of torpor estimated from this five day period was 7.5 and 15.0 h. The lowest individual T_b measured was 11.0 °C.

The T_b at rest (normothermic inactive animals) and in torpor as a function of T_a are shown in Fig. 2. Resting animals showed no significant variation in body temperature at T_a 8–30 °C, and had a mean value of 34.8 ± 0.9 °C. Body temperatures were slightly increased above T_a 30 °C. During torpor, a steady decrease in T_b with decreasing T_a was observed above T_a 11 °C. The lowest ΔT values ($T_b - T_a$) of 0.5–0.8 °C occurred between T_a 12–20 °C. Above 20 °C and below 11 °C an increase in ΔT was observed in all cases but in some individuals ΔT had already increased below 14 °C. The mean T_b minimum determined for the four individuals was 11.6 ± 0.4 °C.

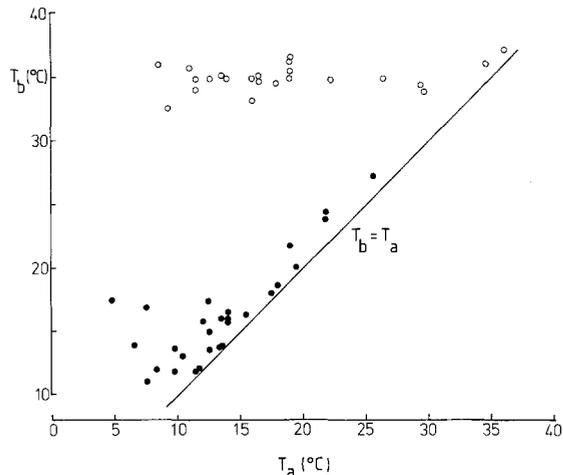


Fig. 2. Body temperatures (T_b) of normothermic, inactive (○) and torpid (●) *A. laniger* as a function of ambient temperature (T_a)

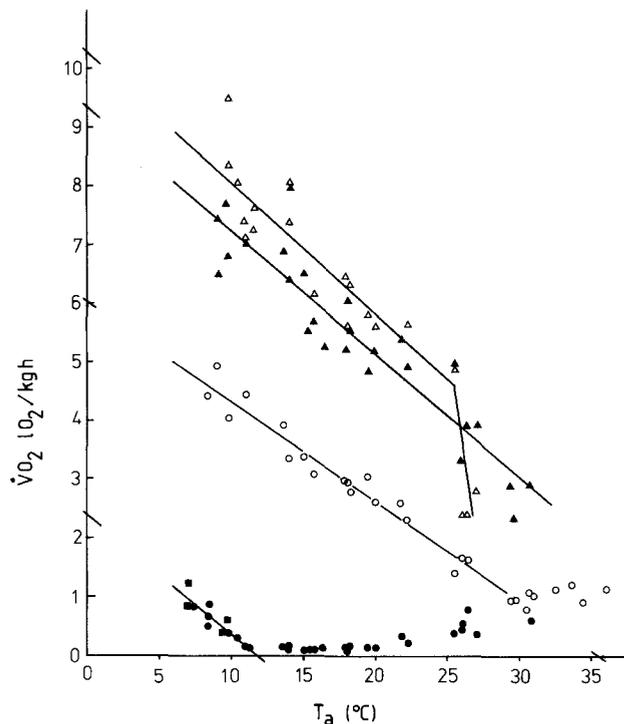


Fig. 3. Rates of oxygen consumption (\dot{V}_{O_2}) of *A. laniger* as a function of ambient temperature (T_a). The symbols indicate: arousal peaks (Δ); nocturnal activity peaks (\blacktriangle); normothermic, inactive (○); and the \dot{V}_{O_2} minima at a constant T_a (●) or after T_a had been lowered (\blacksquare). Straight lines were fitted by linear regression analyses. The equations are: arousal peaks $y = 10.29 - 0.22x$; $r = 0.89$. Activity peaks $y = 9.32 - 0.21x$; $r = 0.92$. Normothermic, inactive $y = 6.02 - 0.169x$; $r = 0.97$. In torpor $y = 2.39 - 0.20x$; $r = 0.88$

Like the body temperatures, the rate of oxygen consumption of *A. laniger* showed strong diurnal variations. The effect of T_a on \dot{V}_{O_2} of *A. laniger* is summarised in Fig. 3 which compares the resting metabolic rate with the nocturnal maxima, the

arousal peaks and the daily minima as determined from measurements of \dot{V}_{O_2} on individual animals. The resting \dot{V}_{O_2} below thermo-neutrality increased in a linear manner as T_a decreased ($r = 0.97$) and the line relating these variables intersects the abscissa at 35.6 °C a value 0.8 °C higher than the mean resting T_b . The metabolic rate of normothermic resting animals at T_a 29.3–31.0 °C was 0.98 ± 0.12 l O_2 /kg·h ($n = 5$), a value slightly lower than predicted for dasyurids (MacMillen and Nelson 1969). A slight increase in \dot{V}_{O_2} was observed above T_a 32 °C (mean 1.11 ± 0.13 l O_2 /kg·h; $n = 4$). The lower critical temperature of the thermo-neutral zone was between 29 and 30 °C.

The \dot{V}_{O_2} maxima measured during activity at night also increased with decreasing T_a . These values were significantly lower in elevation ($p < 0.01$; F-test) than the arousal peaks below T_a 26 °C (Fig. 3), but the slopes for both linear regressions were not significantly different. Above 26 °C, the values of \dot{V}_{O_2} measured for the arousal peaks were lower than those determined during nocturnal activity.

For the daily \dot{V}_{O_2} minima determined at steady state over at least a 30-min period, a continuous decrease was observed from about 0.6–1.0 l O_2 /kg·h at T_a 25–27 °C, to values between 0.07 and 0.26 l O_2 /kg·h (mean: 0.14 ± 0.04 l O_2 /kg·h) at T_a 11–20 °C (Fig. 3). At T_a 11 °C, the \dot{V}_{O_2} during torpor was only about 4% of the value observed at rest and between 2–3% of the activity and arousal peak values. Below T_a 11 °C, a linear increase in \dot{V}_{O_2} occurred during torpor ($r = 0.88$). The line relating T_a and \dot{V}_{O_2} intersects the abscissa at 11.9 °C. At T_a above 29 °C the minimal values of \dot{V}_{O_2} were not below 75% of the resting values (boundary value for torpor), but below 27 °C, all \dot{V}_{O_2} minima represent animals in torpor.

\dot{V}_{O_2} of torpid animals increased when they were cooled below a critical temperature (data not shown). This elevated metabolic rate was similar to that during torpor at constant T_a . The mean T_a where an increase in \dot{V}_{O_2} followed cooling was 10.5 ± 0.5 °C ($n = 4$).

In Fig. 4, the \dot{V}_{O_2} minima as a function of T_a are compared with the duration of torpor and the relative weight loss. The duration of torpor determined from the measurements of \dot{V}_{O_2} was dependent on T_a (Fig. 4b). The longest torpor bouts occurred at temperatures between 13 and 20 °C with a maximum duration of 16 h seen in two individuals. Below T_a 11 °C and above T_a 22 °C a reduction in the length of the torpor periods was observed. A parabolic fit to the data resulted in a coefficient of multiple correlation of 0.65; a rela-

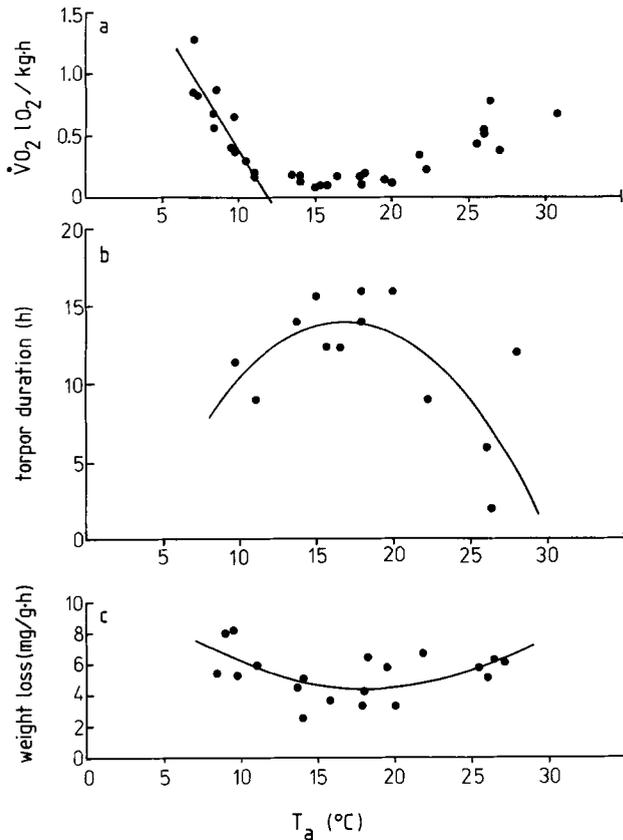


Fig. 4. The daily minima of \dot{V}_{O_2} (a), the duration of the torpor bouts determined from the measurements of \dot{V}_{O_2} (b), and the relative weight loss in mg/g·h (c) as a function of ambient temperature (T_a). The \dot{V}_{O_2} minima are the same data as in Fig. 3 but the \dot{V}_{O_2} during constant T_a measurements and where T_a was decreased were not distinguished. **b** Shows only those measurements where spontaneous arousal (no T_b measurement) was observed; in **c** only measurements at constant T_a and where torpor occurred were included; thus the different numbers of data points between the three variables. Both the length of torpor and the relative weight loss were fitted by a parabola using regression analyses. The equations are: **b** $y = -7.72 + 2.59x - 0.077x^2$; coeff. mult. corr. = 0.65 **c** $y = 12.36 - 0.87x + 0.024x^2$; coeff. mult. corr. = 0.46

relationship more appropriate than a straight line fit ($r = 0.46$).

The relative loss in body mass (mg/g·h) for animals that entered torpor, appears to be related to the pattern observed for the \dot{V}_{O_2} minima and the durations of torpor, although the scatter was considerable (Fig. 4c). Significantly lower values (4.34 ± 1.28 mg/g·h) were observed at T_a 13.6–20 °C than at T_a 8.3–11 °C (6.56 ± 1.43 mg/g·h) and T_a 21.8–30.8 °C (5.97 ± 0.59 mg/g·h). A parabolic fit to the data resulted in stronger correlation than a straight line.

The time of day when *A. laniger* entered torpor (as determined from the \dot{V}_{O_2} measurements), was linearly related to T_a ($r = 0.76$). As shown in Fig. 5,

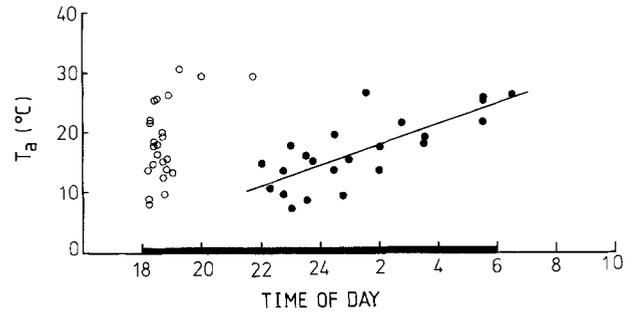


Fig. 5. The time of peak activity (o) and entrance into torpor (●) for *A. laniger* as a function of ambient temperature (T_a). These values were derived from the \dot{V}_{O_2} measurements. The abscissa represents the local time and the dark bar indicates the period of darkness

Table 1. Arousal rates of *Antechinomys laniger*

T_a (°C)	T_b initial (°C)	T_b end (°C)	Overall arousal (°C/min)	Fastest arousal (°C/min)	Food
7.5	11.0	33.1	0.17	0.52	+
9.7	13.7	36.6	0.19	0.37	—
9.7	11.8	37.7	0.21	0.58	—
11.0	11.7	35.7	0.24	0.61	+
11.0	16.4	34.8	0.36	0.67	+
11.5	11.8	35.5	0.24	0.50	+
12.5	15.0	36.4	0.35	0.68	+
15.5	16.3	35.3	0.40	0.64	—
19.0	21.8	33.1	0.57	n.d.	+
20.0	23.4	36.8	0.67	0.80	—
23.0	24.3	37.0	0.75	0.84	—

The fastest arousal rates were determined over periods of at least 10 min at T_b 's above T_a . n.d. not determined

at $T_a < 12$ °C torpor commenced between 2215 and 0045 h while at $T_a > 25$ °C animals entered torpor after 0500 h (apart from one exception). In all but one of the measurements torpor commenced during the period of darkness. The nocturnal activity peaks of \dot{V}_{O_2} occurred within one hour after the lights switched off (1800 h) below T_a 27 °C. At around 30 °C these values were observed 1.25–3.75 h after darkness commenced.

The increase of T_b during arousal of *A. laniger* was dependent on T_a (Table 1). The overall arousal rates varied between 0.17 °C/min (T_a 7.5 °C) and 0.75 °C/min (T_a 23.0 °C). The fastest arousal rate determined over a period of 10 min was 0.84 °C/min and was measured at T_a 23 °C. The availability of food during the night before arousal was measured did not appear to have a strong influence on the arousal rates.

For the overall time which was required to arouse from torpor to normothermia an exponential increase with decreasing T_a was observed

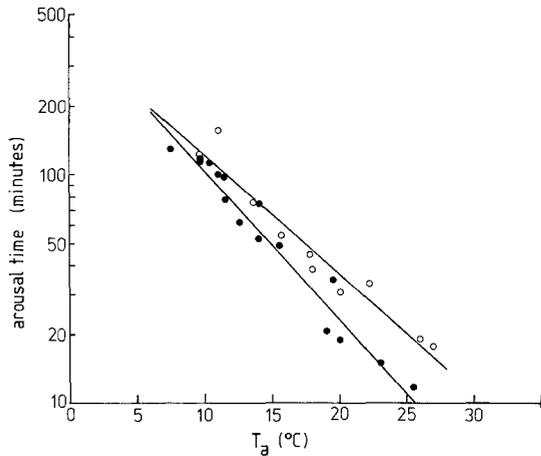


Fig. 6. Semi-log plot of the arousal times of *A. laniger* as a function of ambient temperature (T_a). Spontaneous arousal (○) was slower than induced arousal (●). The equations are: spontaneous $\log y = 2.61 - 0.052x$; $r = 0.97$. Induced $\log y = 2.67 - 0.065x$; $r = 0.98$

Table 2. Spontaneous torpor in *Antechinomys laniger*

	<i>n</i>	torpid	normo-thermic	% torpid
T_a 19 °C				
0830–1000 h	24	9	15	38
1330–1700 h	9	3	6	33
T_a 12.5 °C				
0830–1000 h	20	17	3	85
1430–1700 h	22	0	22	0

n = number of observations

Table 3. A temperature ethogram for *Antechinomys laniger*

T_b range (°C)	Characteristics, behaviour
11.0–11.8	critical arousal temperature
11.0–21.0	lies on side
17.2–21.5	can sit
17.2–21.5	body on floor
19.0–23.0	body elevated from floor
27.0–29.6	moves slowly, clumsy
31.0–34.0	'normal' movements
11.0–18.0	shivers weakly, breathes heavily
18.0–28.0	strong shivering

(Fig. 6). The shortest periods of less than 20 min were observed at $T_a > 25$ °C. All arousal times measured at $T_a < 11$ °C were longer than 100 min. During induced arousal (T_b measurement) smaller values (elevation $p < 0.01$; F-test) than during spontaneous arousal were observed. The difference in slope was not significantly different (F-test).

Apart from the induced torpor periods observed during the \dot{V}_{O_2} measurements, or when held at low T_a in the outdoor facility, *A. laniger* frequently entered torpor in the laboratory when food and water were supplied ad libitum. In Table 2, the numbers of animals in torpor and in normothermia at T_a 19 and 12.5 °C are compared. Torpor periods determined by observing the displacement of sawdust from the animals' backs (T_a 12.5 °C) or by the measurement of \dot{V}_{O_2} never lasted overnight.

Periods of apnoea which lasted for about 1 min were observed in torpid *A. laniger* and were followed by periods of polypnoea. Other observations were made of arousing animals with the television monitor. A temperature ethogram for *Antechinomys laniger* is given in Table 3. The animals could not right themselves below T_b 17 °C and 'normal' movements were not observed below T_b 31 °C.

Discussion

Torpor in *Antechinomys laniger* is qualitatively similar to that observed in other dasyurid marsupials (for review Wallis 1982), however, considerable differences were observed from quantitative comparisons. The minimum T_b of 11.0 °C is lower than in any other dasyurid measured to date (T_b 13.5–24 °C; Wallis 1982; Geiser et al. 1984; Geiser 1985a; Geiser and Baudinette 1985; Geiser et al. 1986). Only in marsupials of the family Burramyidae have lower T_b 's been reported (for review Geiser 1985b). Similarly the \dot{V}_{O_2} minima during torpor of *A. laniger* (0.14 l O₂/kg·h; 4% of the resting metabolic rate) are considerably lower than in other dasyurid species with \dot{V}_{O_2} minima between 0.2–0.5 l O₂/kg·h (Wallis 1976; Morton and Lee 1978; Dawson and Wolfers 1978; Geiser 1985a; Geiser and Baudinette 1985; Geiser et al. 1986), or in rodents and shrews entering daily torpor (Hudson 1965; Nagel 1977; Hudson and Scott 1979; Vogt and Lynch 1982). Even for some hibernating placental mammals which generally have the ability to effectively reduce their metabolism during periods of torpor (Kayser 1961), similar or higher metabolic rates than in torpid *A. laniger* have been observed (Johansen and Krog 1959; Kayser 1961; Wang and Hudson 1971). Furthermore, the maximum duration of torpor in *A. laniger* is longer than in most other dasyurids (for review Wallis 1982; Geiser et al. 1986) but there was no evidence for prolonged torpor in this species. In contrast, Pygmy Possums (*Cercartetus concinnus*) held under identical conditions entered torpor for several days (unpublished observations).

However, the possibility of prolonged torpor in *A. laniger* cannot be ruled out totally. *Antechinomys laniger* frequently entered spontaneous torpor at T_a 19 and 12.5 °C, but most animals investigated entered torpor below T_a 27 °C when no food was provided.

The maximum arousal rate from torpor in *A. laniger* (0.84 °C/min) is greater than reported for other dasyurids, although most of the investigated species were considerably smaller (see Wallis 1982). It is also about 55% above the predicted arousal rates for mammals and birds (Heinrich and Bartholomew 1971). Like in many heterothermic placental mammals arousal was accompanied by a massive overshoot in oxygen consumption. The main increase in T_b during arousal occurred during periods of intense shivering and animals had the appearance of a shaking bellows. The exponential increase in the arousal time with decreasing T_a and consequently T_b indicates that at even lower T_a arousal would no longer be possible or extremely expensive if T_b was still lowered with T_a .

Like in the marsupial *Sminthopsis macroura* (Geiser and Baudinette 1985) the body temperature of *A. laniger* during torpor is regulated at a lower "setpoint". There was no evidence of failure in temperature regulation at any T_a investigated and the other parameters associated with torpor such as the time of entrance into torpor or the duration of torpor also appear to be under precise control. Unlike in hibernating ground squirrels (Twente and Twente 1965) the logarithm of the durations of the torpor bouts in *A. laniger* was not linearly related with temperature, but in contrast with the present study no measurements at T_a below the minimum T_b were made. However, recent investigations on garden dormice (Pajunen 1983) showed a similar response (shorter torpor bouts at T_a below the minimum T_b) to that observed in *A. laniger*. This would support the view that the duration of torpor is somehow linked to the rate of metabolism.

The time of the peak activity and that of entrance into torpor showed interesting relationships with T_a . At low T_a the activity peaks were observed immediately after the onset of darkness while at high T_a a shift towards later hours was observed. A similar although more constant change with T_a was observed for the time of entrance into torpor. This behaviour appears to be adaptive, since a low T_a would most likely restrict insect (the possible food source) activity in the second half of the night when foraging would be most expensive for *A. laniger*. A similar shift of torpor onset has been obtained in *Perognathus californicus* by feeding differ-

ent amounts of food (Tucker 1962) rather than changing the ambient temperature. The time period ground squirrels remained normothermic during spontaneous arousal increased with increasing T_a (French 1982); an observation supporting the influence of ambient temperature on the timing of torpor reported herein.

The determination of T_b by extrapolating the linear segments of the line relating oxygen consumption at T_a below thermo-neutrality for both normothermic resting and torpid *A. laniger* resulted in slightly higher values than actually measured at rest. However, this appeal to the 'Scholander model' ($T_b = T_a$ when $\dot{V}_{O_2} = \text{zero}$) was very precise in predicting the minimum T_b during torpor. Resting metabolism was increased to 4 times the standard metabolic rate (SMR) at T_a 10 °C and about 6 times SMR when extrapolated to 0 °C. This pattern is similar to the considerably larger dasyurid *Dasyuroides byrnei* but higher than that of the similar sized rodent *Notomys cervinus* (Dawson and Dawson 1982). This would support the view of a steeper increase in metabolism with decreasing T_a in marsupials than in placentals (Hinds and MacMillen 1984).

The slopes relating T_a and \dot{V}_{O_2} were similar in four physiological states of the daily cycle. These states were (1) normothermic and inactive, (2) torpid at T_a below the minimum T_b , (3), active at night, and (4) arousing from torpor. Such a parallel increase in metabolism indicates that the overall coefficient of thermal conductance across the body surface was maximal, and that the cost of thermoregulation increases in a similar manner as T_a decreases.

Antechinomys laniger shows a lack of motor-coordination at low T_b ; a feature accentuated by their extremely elongate hindlegs. Full coordination in *Antechinomys laniger* is attained at higher T_b than in *Antechinus stuartii* (Wallis 1976).

Hayden and Lindberg (1976) pointed out that longevity in heterothermic *Perognathus longimembris* is much greater than in similar sized homeothermic rodents. In *Mesocricetus brandti*, an increase in longevity was observed with an increase in the percentage of life spent in hibernation (Lyman et al. 1981). *Antechinomys laniger* also shows a remarkable life span of up to 5 years in the laboratory (Aslin 1982) which correlates with a high tendency to enter torpor spontaneously. A long life span is important for species living in unpredictable environments that have to deal with the uncertainty of survival of their offspring.

The habitat of *A. laniger* is characterized by aridity and variation in energy availability. Torpor

appears to be important in the conservation of energy and water as shown by the significantly reduced weight loss at T_a of minimum metabolism and longest torpor bouts. Furthermore, torpor may correlate with an extended life span and thus appears to have importance in the survival of this species in a highly unpredictable environment.

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