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HIBERNATION AND DAILY TORPOR IN TWO PYGMY POSSUMS (CERCARTETUS SPP., MARSUPIALIA)¹

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The physiology of torpor was investigated in the pygmy possums *Cercartetus concinnus* (18 g) and *C. lepidus* (12 g). Body temperatures (T_b) during torpor remained within 1 C of air temperature (T_a) and showed a minimum of about 5 C in both species. Oxygen consumption ($\dot{V}O_2$) during torpor was reduced to about 0.05 liters O_2 /kg h, which amounts to only 1% of the rate of normothermic animals. Below T_a of 5 C, the metabolism during torpor increased with a further decrease in T_a , while T_b was regulated at about 5 C. Rates of arousal were faster than predicted for endothermic vertebrates of comparable size. Duration of torpor bouts ranged from less than a day to a week, with the longest bouts occurring at $T_a < 10$ C. The physiological characteristics of torpor in these two marsupial species are qualitatively and quantitatively similar to those of placental hibernators.

INTRODUCTION

Pygmy possums, small (<50-g) marsupials of the family Burramyidae, are found in Australia and New Guinea. Seven species are recognized, with *Distoechurus pennatus* occurring only in New Guinea. The taxonomic membership of the two feathertail possums (*Acrobates pygmaeus* and *Distoechurus pennatus*) to burramyids is currently under review (Archer 1984), and the remaining species belong to the genera *Cercartetus* and *Burramys*.

Torpor has been observed in all Australian burramyids and is qualitatively similar to hibernation in placental mammals (Bartholomew and Hudson 1962). It has been suggested, however, that quantitative differences do exist between the two groups. Such differences appear to be a less pro-

nounced reduction of body temperature and mass-specific oxygen consumption during torpor (Bartholomew and Hudson 1962), a shorter duration of torpor (Hickman and Hickman 1960; Strahan 1983), and a slower rewarming from torpor (Bartholomew and Hudson 1962; Fleming 1985a, 1985b) than in placental mammals. Furthermore, there are no experimental data on the thermoregulatory ability of pygmy possums during torpor and thus no indication that the reduction in T_b is a controlled process. Some of these quantitative differences led to the conclusion that torpor in burramyid marsupials may be less "refined" than in the "perfect" model of hibernating rodents (Lyman 1982).

Physiological data are available for three of the six Australian burramyids (Bartholomew and Hudson 1962; Fleming 1985a, 1985b). Because large interspecific differences in the pattern of thermoregulation have been observed in rodent families that may contain "deep" hibernators and species that enter shallow, daily torpor (Lyman 1982), it was of interest to investigate whether such specific differences in the thermal physiology also occur in the burramyids. I also examined in greater detail the suggested differences in the physiology between placental hibernators and the marsupial family Burramyidae by studying temporal and thermal aspects of torpor in *Cercartetus concinnus*, the western pygmy possum, and *C. lepidus* (syn. *Eudromicia lepida*), the little pygmy possum.

¹ I wish to thank Meredith Smith for her loan of several pygmy possums and John Coventry for allowing me to use his pitfall traps in the Big Desert and partake of his dinkum bush chooks. Bronwyn McAllan helped me to set up and check trap lines. Russell Baudinette provided many helpful suggestions during the experimental period, and Sara Hiebert, Jim Kenagy, and two anonymous referees constructively criticized the manuscript. The study was supported by a Flinders University Research Scholarship and the paper was compiled while the author held an Alexander von Humboldt-Lynen Research Fellowship at the University of Washington.

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MATERIAL AND METHODS

THE ANIMALS

Cercartetus concinnus is found in South Australia and Western Australia and occurs in mallee heath and dry sclerophyll forest. It is nocturnal, uses tree hollows as daytime shelters, eats insects, pollen, and nectar, and stores fat in its prehensile tail (Smith 1983). Three males and two females were live trapped at various locations on the southeastern coast of South Australia and the Eyre Peninsula and kept in the laboratory at T_a 22 C under natural photoperiod. In autumn (March) they were transferred to a constant T_a of 19 C with a photoperiod of 12L:12D, a condition similar to the natural photoperiod at that time of the year, and held for 3 wk before the experiments commenced. All experiments were performed in autumn between March and May 1984 and 1985. The mean body mass during the experimental period was 18.6 ± 1.8 g (SD) (range 16–22 g).

Cercartetus lepidus occurs in Tasmania and two areas of southeastern Australia. It is the smallest of all possums. It is mainly nocturnal and has been found sheltering in hollow logs and birds' nests (Green 1983). It appears to feed primarily on invertebrates and stores fat in its tail. One male and one female were live trapped in the Big Desert, Victoria, in September and transferred to the laboratory, where they were kept at T_a 19 C and a photoperiod of 12L:12D (similar to natural photoperiod at the time of capture) for 5 wk before measurements commenced. Experiments with these two individuals were conducted in spring and early summer (October to beginning of December) 1984. Another male was caught at Messent Conservation Park, South Australia, and was kept in the laboratory at T_a 22 C and natural photoperiod. In autumn (March) it was transferred to T_a 19 C and a photoperiod of 12L:12D and was kept under these conditions for 3 wk before the experiments began. The mean body mass was 12.6 ± 1.9 g (range 10–15 g).

The animals were fed with Heinz canned baby food (fruits), a mixture of Heinz high-protein cereal and honey, and apples. Because pygmy possums held in captivity become extremely fat, their weight was controlled by feeding them only apples on

certain nights. Food was exchanged daily in the afternoon.

EXPERIMENTAL DETAILS

Diurnal fluctuations in oxygen consumption ($\dot{V}O_2$) were determined at T_a 6–31 C for 30 periods of 21.1 ± 2.1 h (range 15.5–29.25 h, *C. concinnus*) and for 20 periods of 22.0 ± 2.3 h (range 17.25–25.75 h, *C. lepidus*). These experiments began in the late afternoon. Food and water were not available during measurements of $\dot{V}O_2$. To determine whether burramyids regulate their T_b during periods of torpor at a specific "set point," torpid animals were cooled (<0.05 C/min), and the $\dot{V}O_2$ was continuously monitored. Additional measurements during shorter periods were used to determine the $\dot{V}O_2$ of postabsorptive, normothermic, inactive animals at T_a around and above thermoneutrality. The $\dot{V}O_2$ of one *C. lepidus* was measured during prolonged torpor over a 7-day period. Flow rates of air in the open flow system were between 0.15 and 0.30 liters/min and were adjusted and measured with calibrated rotameters. Measurements of $\dot{V}O_2$ were used to determine the metabolic rate of normothermic, inactive animals measured when a variation of less than 5% over at least 15 min occurred within an inactivity period of at least 30 min; the metabolic rate of torpid animals was determined at times of constant $\dot{V}O_2$ over at least 30 min. Furthermore, the duration of torpor and the time that was required to arouse from torpor to normothermia were determined from these measurements (the $\dot{V}O_2$ peak during arousal was assumed to be the end point of the arousal period). In some instances the displacement of sawdust from the animal's back was used to determine the duration of torpor. All measurements were conducted in a quiet controlled-temperature room ($T_a \pm 0.5$ C) that was acoustically insulated from the recording equipment. A video camera was used to observe the animals during the experiments.

A Servomex Model OA 184 paramagnetic oxygen analyzer was used for the $\dot{V}O_2$ measurements together with a Rikadenki potentiometric recorder. The $\dot{V}O_2$ was determined from the difference between the oxygen content in two parallel open-flow circuits, one being a room air reference and

the other containing the animal. All gas volumes were corrected to dry standard temperature and pressure (STPD). The T_a was measured continuously in the respiratory chamber (volume 3 liters) with calibrated thermocouples. The T_b was measured with calibrated 0.5-mm diameter thermocouples inserted 20 mm into the rectum. Esophageal temperature during torpor was also determined occasionally. During induced arousal the rate of re-warming was determined by taping the thermocouple wire of the rectally inserted thermocouple probe to the animal's tail.

A Student's t -test was used for comparisons of paired observations. Straight lines were fitted by linear regression analysis. Differences in slope and elevation were determined using the derived t - and F -values. Means of samples are expressed \pm SD. N = number of individuals, n = number of determinations.

RESULTS

Both *Cercartetus concinnus* and *C. lepidus* showed a high tendency to enter torpor. In all but one experiment, *C. concinnus* entered torpor during measurements of $\dot{V}O_2$ when no food and water were provided and T_a was less than 20 C. All *C. lepidus* entered torpor under these conditions when T_a was less than 27 C. Apart from these induced torpor periods, the animals frequently entered torpor spontaneously in the laboratory when food and water were freely available (table 1). Spontaneous torpor at T_a 19 C was observed in the morning; in the afternoon animals usually were normothermic. *Cercartetus lepidus* showed a greater

tendency to enter torpor spontaneously than the larger *C. concinnus*.

Most entries into torpor in both species occurred between 2400 and 0600 hours, before the onset of light. The time of day when torpor commenced was not related to T_a . The nocturnal peaks of $\dot{V}O_2$ during activity of *C. concinnus* occurred between 1845 and 0130 hours, with a mean of 21.1 ± 2.1 h, and did not appear to be dependent on T_a . In *C. lepidus*, the nocturnal peaks of oxygen consumption associated with activity occurred between 1845 and 2200 hours (with two exceptions).

At temperatures above 15 C, both species usually entered torpor on a daily basis and aroused spontaneously in the afternoon. The longest torpor bouts of *C. concinnus* were 4 days at T_a 12 C and 8 days at T_a 8 C. In *C. lepidus*, torpor lasted for a maximum of 2 days at T_a 19 C (sawdust method) and about 6 days at T_a 8.7 C ($\dot{V}O_2$ measurement; fig. 1).

Periods of apnea lasting for about 5 min at T_a 10 C were observed in torpid *C. concinnus* and longer than 30 min at T_a 8.7 C in *C. lepidus*. These periods were punctuated by marked polypnea.

Body temperatures at rest were stable at T_a 3–32 C with a mean T_b of 34.4 ± 0.5 C (*C. concinnus*; $N = 5$, $n = 17$) and 33.7 ± 0.8 C (*C. lepidus*; $N = 3$, $n = 14$) (fig. 2). Higher T_b 's were observed at T_a 's > 32 C. During torpor, T_b decreased with decreasing T_a . The lowest ΔT values ($T_b - T_a$) of 0.3–2.5 C occurred between T_a 5 and 20 C, and most ΔT were less than 1.0 C in both species. Below T_a 4 C (*C. concinnus*) and T_a 5 C (*C. lepidus*), an increase in ΔT was

TABLE 1
SPONTANEOUS TORPOR IN *Cercartetus concinnus* AND *C. lepidus*

Species	T_a (°C)	n	Torpid	Normothermic	% Torpid
<i>C. concinnus</i> ($N = 5$) . . .	19	38	19	19	50
	11–13	60	42	18	70
	8	24	21	3	88
<i>C. lepidus</i> ($N = 3$) . . .	19	72	51	21	71

NOTE.—Food and water were available ad lib. Observations were made between 0800 and 1000 hours. N = number of individuals; n = number of observations.

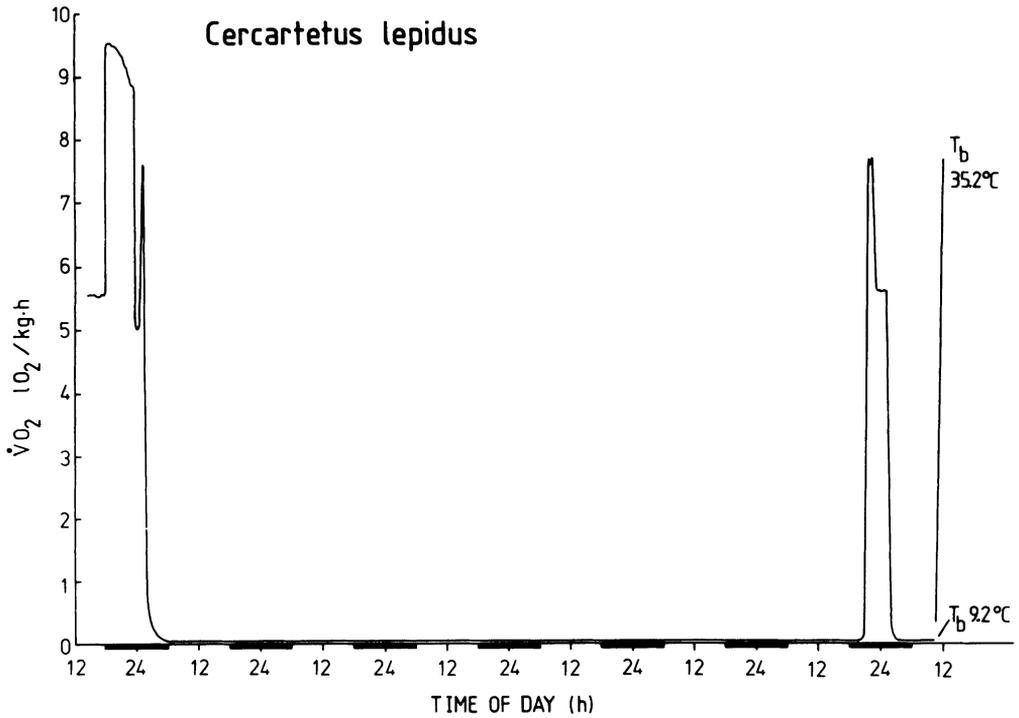


FIG. 1.—The fluctuation in the rate of oxygen consumption ($\dot{V}O_2$) of an individual *Cercartetus lepidus* measured over a 7-day period at T_a 8.7 ± 0.7 C. The abscissa represents the local time, and the dark bars indicate the periods of darkness. Body temperatures (T_b) are indicated at the end of the measurement.

observed. The lowest individual T_b 's measured during torpor were 4.7 C in *C. concinnus* and 5.9 C in *C. lepidus*. Esophageal temperatures during torpor at T_a 10 C were

indistinguishable from values measured rectally in *C. concinnus*. In torpid *C. lepidus*, the esophageal temperatures were at most 1.4 C above the rectal temperatures

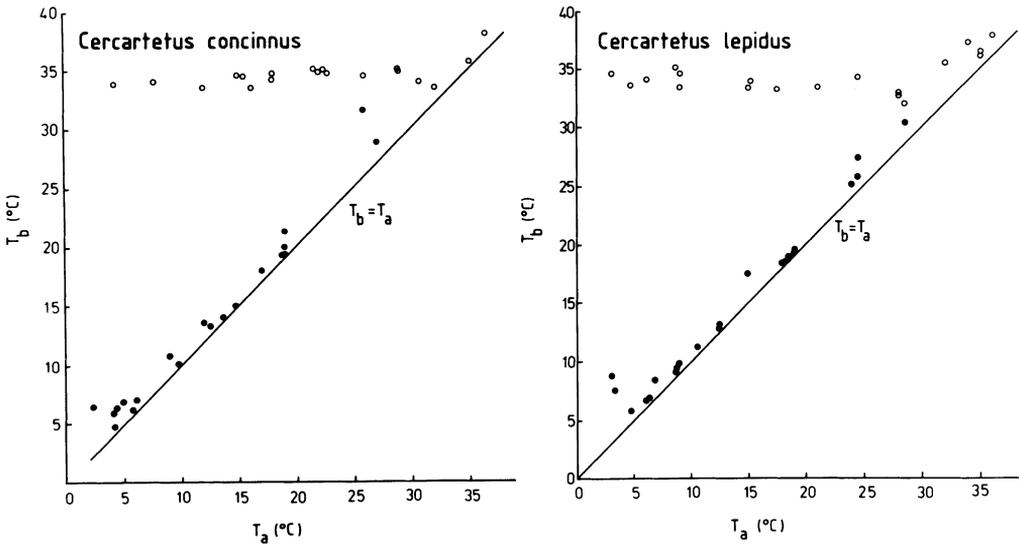


FIG. 2.—Body temperatures (T_b) of normothermic, inactive (O), and torpid (●) *Cercartetus concinnus* and *C. lepidus* as a function of air temperature (T_a). The solid lines represent $T_b = T_a$.

below T_a 's of 10 C; at T_a 19 C both temperatures were within 0.2 C.

The T_b of torpid pygmy possums was regulated above a specific minimum. In the typical case, shown in figure 3, T_a was decreased from 10.5 C, the temperature at which the *C. concinnus* had entered torpor. As T_a decreased to 4.1 C, $\dot{V}O_2$ remained stable at a level of about 0.06 liters O_2 /kg h. At T_a 3.6 C, $\dot{V}O_2$ increased to a new plateau of 0.24 liters O_2 /kg h. An increase in T_a to 4.2 C resulted in a decrease in $\dot{V}O_2$ to 0.16 liters O_2 /kg h, and T_b was 4.7 C. Manipulations during measurement of T_b at 1445 hours induced arousal. The mean T_a at which an increase in $\dot{V}O_2$ followed cooling was 4.4 ± 0.4 C ($N = 3$) in torpid *C. concinnus* and 5.3 ± 0.6 C ($N = 3$, $n = 4$) in *C. lepidus*. In all but one experiment, where cooling induced arousal, the pygmy possums remained torpid but had an increased metabolic rate.

Reduction in T_a resulted in a parallel increase in $\dot{V}O_2$ during rest and torpor at T_a below the minimum T_b (fig. 4). The $\dot{V}O_2$ of normothermic, inactive animals below thermoneutrality increased linearly as T_a decreased in both species; the lines relating

these values extrapolated to the abscissa at 35.0 C (*C. concinnus*) and 36.5 C (*C. lepidus*). These intercepts were 0.6 and 2.8 C, respectively, above the mean resting T_b . The lower critical temperature of the thermoneutral zone was between 28 and 30 C in both species. The mean metabolic rate at T_a 28.8–31 C was 1.20 ± 0.3 liters O_2 /kg h ($N = 4$; *C. concinnus*) and 1.49 ± 0.2 liters O_2 /kg h ($N = 3$, $n = 8$; *C. lepidus*), and both values were slightly greater than the predicted standard metabolic rate for a marsupial of the respective body mass (Dawson and Hulbert 1970).

For the daily $\dot{V}O_2$ minima (fig. 4), a steady decrease with T_a was observed above T_a 5 C. The $\dot{V}O_2$ of torpid *C. concinnus* was 0.046 ± 0.02 liters O_2 /kg h ($N = 5$, $n = 16$; T_a 5–13 C and 0.052 ± 0.01 liters O_2 /kg h (*C. lepidus*, $N = 3$, $n = 17$; T_a 6–11 C). Below T_a 5 C, a linear increase in $\dot{V}O_2$ during torpor occurred in both species. Extrapolation of these lines intersected the abscissa at 4.9 C (*C. concinnus*) and 5.6 C (*C. lepidus*). The $\dot{V}O_2$ during torpor at the T_a below which an increase in metabolism was observed during torpor was 0.7% and 0.8%, respectively, of the values observed

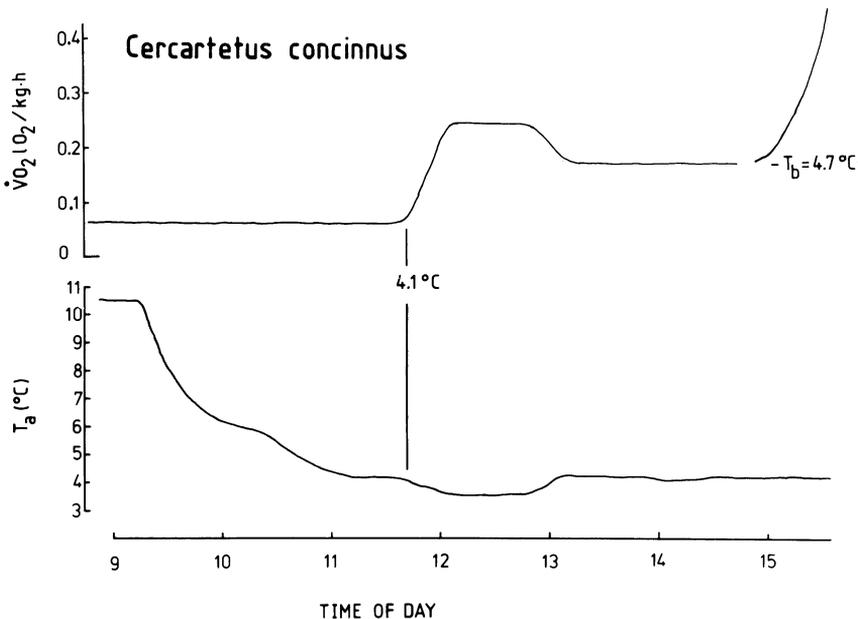


FIG. 3.—The rate of oxygen consumption ($\dot{V}O_2$) of an individual torpid *Cercartetus concinnus* exposed to changing air temperature (T_a). The body temperature (T_b) is indicated; handling during this measurement induced arousal. The abscissa represents the local time.

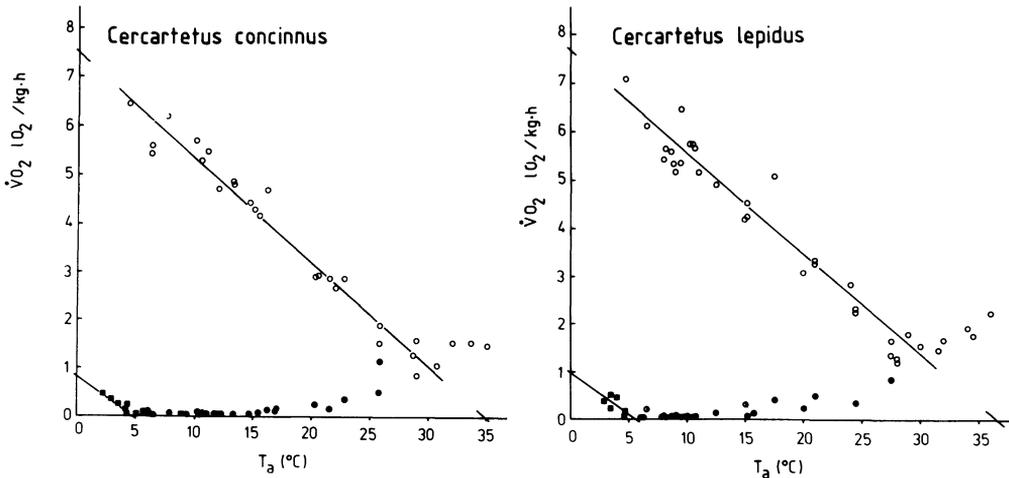


FIG. 4.—Rates of oxygen consumption ($\dot{V}O_2$) of *Cercartetus concinnus* and *C. lepidus* as a function of ambient temperature (T_a). The symbols indicate: normothermic inactive (O), and the $\dot{V}O_2$ minima at constant T_a (●) or after T_a had been lowered (■). The equations for the lines are: *C. concinnus*, normothermic inactive: $y = 7.5 - 0.21x$, $r = -0.98$; in torpor: $y = 0.83 - 0.17x$, $r = -0.93$. *Cercartetus lepidus*, normothermic inactive: $y = 7.7 - 0.21x$, $r = -0.97$; in torpor: $y = 0.98 - 0.17x$, $r = -0.64$.

in normothermic, resting animals and only 3.8% and 3.5% when compared with the basal metabolic rates.

The relative weight loss was 4.6 ± 1.5 mg/g h (*C. concinnus*) and 4.9 ± 1.6 mg/g h (*C. lepidus*) for animals that had entered torpor. Weight loss (WL, mg/g h) was inversely related to torpor duration (TD, in hours) in both species (WL = $6.4 - 0.21$ TD, $r = -0.60$, *C. concinnus*; WL = $5.6 - 0.04$ TD, $r = -0.69$, *C. lepidus*) (data not shown).

The rate of increase in T_b during arousal was directly related to T_a in both species (table 2). The fastest overall arousal rate was 0.65 C/min in *C. concinnus* and 0.81 C/min in *C. lepidus*. The fastest arousal rate determined over a period of 10 min was 0.79 and 0.90 C/min, respectively. The availability of food during the night preceding arousal did not influence the arousal rates. Initial differences (0.2–1.4 C) between esophageal and rectal temperature in *C. lepidus* observed at low T_a were gradually reduced during arousal.

The time required to arouse from torpor to normothermia increased exponentially with decreasing T_a (fig. 5). No significant differences between induced and spontaneous arousal were observed in either species.

DISCUSSION

The present study suggests that torpor in marsupials is under precise control and that their thermoregulation is not inferior to their placental counterparts. There appear to be no general physiological differences in the characteristics of torpor and hibernation in placental and marsupial mammals. Both groups contain species that show profound torpor while others enter shallow, daily torpor.

Minimum T_b 's around 5 C as in pygmy possums (table 3) have been reported in many placental "deep" hibernators (e.g., Strumwasser 1960; Pengelley 1964; Wang and Hudson 1971). However, the minimum T_b 's in the burramyids are much lower than those observed in marsupials of other families (Morrison and McNab 1962; Wallis 1976; Geiser 1985a, 1986).

The metabolic rate of torpid pygmy possums was reduced to less than 1% of the resting values (table 3). During activity of *Cercartetus concinnus* and *C. lepidus* at T_a 's below 10 C, oxygen consumption was increased about 200-fold in comparison to the torpor values. The low metabolic rate of pygmy possums was accompanied by ΔT 's that were usually less than 1 C (Fleming 1985a, 1985b; present study). Hiber-

nating placentals show a similar metabolic rate and ΔT during torpor (Kayser 1961; Lyman 1982; French 1985).

Body temperatures during torpor of burramyids are regulated to remain at or above a specific minimum similar to dasyurids (Geiser et al. 1986). However, the thermoregulatory increase in the metabolic rate occurred at a much lower T_a in burramyids (at $T_a = 5$ C) than in dasyurids ($T_a > 11$ C). The regulation of T_b at a specific minimum during torpor and the sensitivity to changes in T_a of less than 0.5 C show that torpor in pygmy possums is a controlled process.

In burramyid marsupials, the longest torpor bouts last from 2 to 13 days, with the possible exception of *C. caudatus*, which is found in Queensland rainforests and New

Guinea (for review, Geiser 1985b). In hibernating rodents rhythmical arousal also occurs about every week or two (Pengelley and Fisher 1961; Pohl 1961; Kenagy 1981; French 1982). However, in contrast to many placental hibernators, some pygmy possums appear to forage and feed during winter (Coventry and Dixon 1984). A less distinct seasonality in the torpor pattern of most pygmy possums is not surprising, considering the relatively mild winters in many parts of Australia. However, the mountain pygmy possum, *Burramys parvus*, which is exposed to strong seasonal fluctuations, appears not to emerge during winter (Mansergh 1984); nor do female *C. nanus* in parts of Victoria (A. K. Lee 1985, personal communication).

At high T_a , both *C. concinnus* and *C.*

TABLE 2
AROUSAL RATES OF *Cercartetus concinnus* AND *C. lepidus*

T_a (°C)	T_b Initial (°C)	T_b End (°C)	Overall Arousal (°C/min)	Fastest Arousal (°C/min)	Food
<i>C. concinnus</i> (N = 5)					
4.1	6.0	32.4	.11	.28	-
4.4	4.7	33.9	.13	ND	-
6.0	7.2	34.7	.18	.34	-
9.0	10.9	36.0	.28	.44	+
9.8	10.0	36.9	.30	.55	+
10.6	12.7	35.0	.31	.39	+
12.0	13.7	34.8	.33	.48	-
17.0	18.1	36.5	.46	.48	+
19.0	20.0	33.4	.56	.58	+
19.0	21.3	34.5	.60	.64	+
26.9	28.9	34.5	.59	ND	-
5 → 23	7.0	35.0	.56	.71	-
19 → 22	19.4	35.0	.65	.79	+
<i>C. lepidus</i> (N = 3)					
6.0	6.9	35.1	.19	.47	-
8.7	9.2	35.2	.34	.62	-
18.3	18.5	34.8	.71	.77	+
18.5	18.9	36.0	.81	.88	+
19.0	19.5	36.0	.71	.80	+
24.0	25.2	35.5	.81	.90	-
3.4 → 20	7.7	35.9	.67	.83	-
19 → 23	19.3	36.0	.73	.80	+

NOTE.—The fastest arousal rates were determined over time periods of at least 10 min at T_b 's above T_a . Arrows indicate that the animals were transferred from the T_a they had entered torpor to a different T_a at which rewarming was measured. ND: not determined. Food during the night prior to the measurement was either available (+) or not available (-).

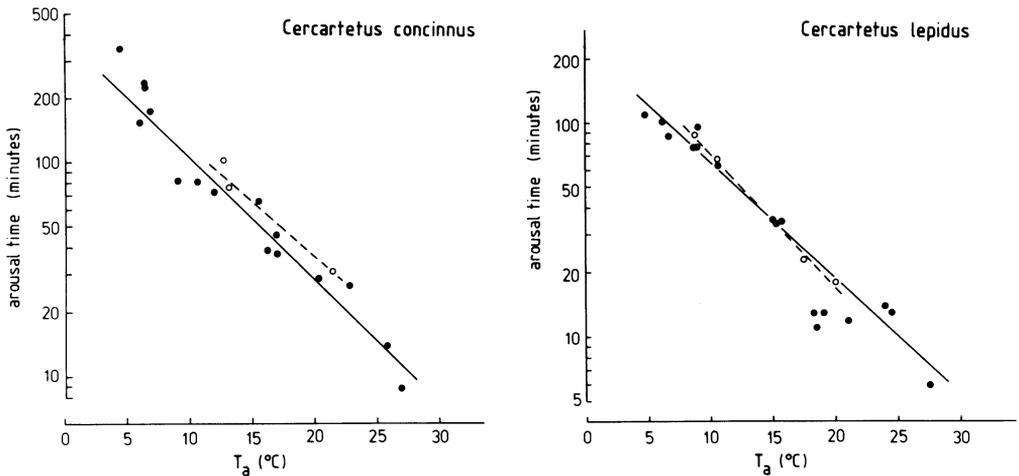


FIG. 5.—Semilogarithmic plot of the arousal times of *Cercartetus concinnus* and *C. lepidus* as a function of air temperature (T_a). The symbols indicate induced (●) and spontaneous (○) arousal. No significant differences between the two could be detected. The equations are: *C. concinnus*, induced: $\log y = 2.65 - 0.060x$, $r = -.97$, spontaneous: $\log y = 2.64 - 0.053x$, $r = -.98$; *C. lepidus*, induced: $\log y = 2.35 - 0.054x$, $r = -.99$, spontaneous: $\log y = 2.48 - 0.062x$, $r = -.998$.

lepidus entered torpor on a daily basis; and it appears that the torpor bouts increased with decreasing T_a , as in ground squirrels (French 1982). This suggests that prolonged torpor of pygmy possums in the wild occurs during cold weather. In dasyurid marsupials, prolonged torpor has not been observed even at low T_a (Wallis 1976; Geiser and Baudinette 1985).

Arousal in *C. concinnus* and *C. lepidus* was rapid, with the fastest arousal rates about 20% above the predicted arousal rates

for mammals and birds (Heinrich and Bartholomew 1971). This does not support the view that marsupials possess a lower thermogenic capacity than placentals (Fleming 1985a). The absence of a lag of the rectal temperature behind that of the anterior part of the body during arousal is most likely a reflection of the small body size of pygmy possums.

The tendency to enter torpor spontaneously was high in both burramyids investigated. Torpor could be induced in au-

TABLE 3
SUMMARY OF PHYSIOLOGICAL DATA OF AUSTRALIAN BURRAMYID MARSUPIALS

SPECIES	BODY MASS ^a (g)	T_b MIN (°C)	$\dot{V}O_2$ IN TORPOR		TORPOR DURATION (days)	T_b REST (°C)	BMR (liter O_2 /kg h)	SOURCES
			Min (liter O_2 /kg h)	Mean (liter O_2 /kg h)				
<i>Cercartetus nanus</i>	24 (35–90)	6	.05	.19	13	34.9 ^b	.86	1, 2
<i>C. concinnus</i>	13 (18.6)	4.7	.023	.046	11	34.4	1.20	3, *
<i>C. lepidus</i>	>8 (12.6)	5.9	.032	.052	6	33.7	1.49	*
<i>C. caudatus</i>	30	<1	4
<i>Burramys parvus</i>	42 (44.3)	6	.022	.063	7	36.1	.83	5
<i>Acrobates pygmaeus</i>	12 (14)	7	.07 ^c	...	2	34.9	1.08	6

SOURCES.—1, Bartholomew and Hudson 1962; 2, Dimpel and Calaby 1972; 3, Wakefield 1970; 4, Atherton and Haffenden 1982; 5, Fleming 1985b; 6, Fleming 1985a; *, present study.

^a Body masses were taken from Strahan (1983); *C. lepidus* from Coventry and Dixon (1984). Body masses in parentheses show the values for the animals used in the $\dot{V}O_2$ and T_b measurements. T_b min and $\dot{V}O_2$ min represent the minima recorded for each species. The torpor duration is the maximum recorded for each species. The other values represent means.

^b "Active" animals.

^c Calculated from percent of $\dot{V}O_2$ at rest.

tumn, spring, and summer by exposing animals to low T_a in a similar manner as in the rodent *Sicista betulina* (Johansen and Krog 1959). Prolonged and deep torpor in pygmy possums could be induced within 1 day of cold exposure when food was withdrawn, and there was no evidence that cold acclimation was necessary for the process. However, it is likely that cold acclimatization would lower the minimum T_b as in dasyurid marsupials (Geiser et al. 1986). The ability to enter torpor at any time of the year suggests that *Cercartetus* spp. do not possess a strong endogenous seasonal cycle of torpor and activity. Torpor in these marsupials appears to be an opportunistic response to unpredictable conditions rather

than to seasonal temperature stress and food shortages.

The physiological variables associated with torpor in burramyids are strikingly similar between the various species (table 3). This is in contrast to cricetid and sciurid rodents, which show a large range of thermoregulatory modes and contain species that are strict homeotherms, species that enter shallow, daily torpor, and "deep" hibernators (Lyman 1982). Among those placental species that enter prolonged torpor, there are great differences in the minimum T_b , metabolic rate, duration of torpor, and rate of rewarming; and the pattern of torpor in burramyid marsupials is within this range of variations.

LITERATURE CITED

- ARCHER, M. 1984. The Australian marsupial radiation. Pages 633–808 in M. ARCHER and G. CLAYTON, eds. Vertebrate zoogeography and evolution in Australasia. Hesperian Press, Western Australia.
- ATHERTON, R., and A. T. HAFFENDEN. 1982. Observations on the reproduction and growth of the long-tailed pygmy possum, *Cercartetus caudatus* (Marsupialia: Burramyidae), in captivity. *Aust. Mammal.* 5:253–259.
- BARTHOLOMEW, G. A., and J. W. HUDSON. 1962. Hibernation, estivation, temperature regulation, evaporative water loss, and heart rate of pigmy possums *Cercaertus nanus*. *Physiol. Zool.* 35:94–107.
- COVENTRY, A. J., and J. M. DIXON. 1984. Small native mammals from the Chinaman Well area, north-western Victoria. *Aust. Mammal.* 7:111–115.
- DAWSON, T. J., and A. J. HULBERT. 1970. Standard metabolism, body temperature and surface area of Australian marsupials. *Am. J. Physiol.* 218:1233–1238.
- DIMPEL, H., and J. H. CALABY. 1972. Further observations on the mountain pygmy possum, *Burramys parvus*. *Victorian Nat.* 89:101–106.
- FLEMING, M. R. 1985a. The thermal physiology of the feathertail glider, *Acrobates pygmaeus* (Marsupialia: Burramyidae). *Aust. J. Zool.* 33:667–681.
- . 1985b. The thermal physiology of the mountain pygmy-possum *Burramys parvus* (Marsupialia: Burramyidae). *Aust. Mammal.* 8:79–90.
- FRENCH, A. R. 1982. Effects of temperature on the duration of arousal episodes during hibernation. *J. Appl. Physiol.* 52:216–220.
- . 1985. Allometries of the duration of torpid and euthermic intervals during mammalian hibernation: a test of the theory of metabolic control of the timing of changes in body temperature. *J. Comp. Physiol.* B156:13–19.
- GEISER, F. 1985a. Physiological and biochemical aspects of torpor in Australian marsupials. Ph.D. diss. Flinders University, Adelaide.
- . 1985b. Hibernation in pygmy possums (Marsupialia: Burramyidae). *Comp. Biochem. Physiol.* 81A:459–463.
- . 1986. Thermoregulation and torpor in the kultarr, *Antechinomys laniger* (Marsupialia: Dasyuridae). *J. Comp. Physiol.* B156:751–757.
- GEISER, F., and R. V. BAUDINETTE. 1985. The influence of temperature and photophase on torpor in *Sminthopsis macroura* (Dasyuridae: Marsupialia). *J. Comp. Physiol.* B156:129–134.
- GEISER, F., R. V. BAUDINETTE, and E. J. MCMURCHIE. 1986. Seasonal changes in the critical arousal temperature of the marsupial *Sminthopsis crassicaudata* correlate with the thermal transition in mitochondrial respiration. *Experientia*, 42:543–547.
- GREEN, R. H. 1983. Little pygmy-possum, *Cercartetus lepidus*. Pages 164–165 in R. STRAHAN, ed. Complete book of Australian mammals. Angus & Robertson, Sydney.
- HEINRICH, B., and G. A. BARTHOLOMEW. 1971. An analysis of pre-flight warm-up in the sphinx moth, *Manduca sexta*. *J. Exp. Biol.* 55:223–239.
- HICKMAN, V. V., and J. L. HICKMAN. 1960. Notes on the habits of the Tasmanian dormouse phalangers *Cercaertus nanus* (Desmarest) and *Eudromicia lepida* (Thomas). *Proc. Zool. Soc. Lond.* 135:365–375.
- JOHANSEN, K., and J. KROG. 1959. Diurnal body temperature variations and hibernation in the birchmouse, *Sicista betulina*. *Am. J. Physiol.* 196:1200–1204.
- KAYSER, C. 1961. The physiology of natural hibernation. Pergamon, Oxford.
- KENAGY, G. J. 1981. Effects of the day length, temperature, and endogenous control on annual rhythms of reproduction and hibernation in chipmunks (*Eutamias* spp.). *J. Comp. Physiol.* A141:369–378.
- LYMAN, C. P. 1982. Who is who among the hibernators. Pages 12–36 in C. P. LYMAN, J. S. WILLIS, A. MALAN, and L. C. H. WANG. Hibernation and torpor in mammals and birds. Academic Press, New York.
- MANSENGH, I. M. 1984. Ecological studies and conservation of *Burramys parvus*. Pages 545–552 in A. P. SMITH and I. D. HUME, eds. Possums and gliders. Australian Mammal Society, Sydney.

- MORRISON, P. R., and B. K. MCNAB. 1962. Daily torpor in a Brazilian murine opossum (*Marmosa*). *Comp. Biochem. Physiol.* **6**:57-68.
- PENGELLEY, E. T. 1964. Responses of a new hibernator (*Citellus variegatus*) to controlled environments. *Nature* **203**:892.
- PENGELLEY, E. T., and K. C. FISHER. 1961. Rhythmic arousal from hibernation in the golden-mantled ground squirrel *Citellus lateralis tescorum*. *Can. J. Zool.* **39**:105-120.
- POHL, H. 1961. Temperaturregulation und Tagesperiodik des Stoffwechsels bei Winterschläfern. *Z. vergleichende Physiol.* **45**:109-153.
- SMITH, M. J. 1983. Western pygmy-possum, *Cercartetus concinnus*. Pages 162-163 in R. STRAHAN, ed. Complete book of Australian mammals. Angus & Robertson, Sydney.
- STRAHAN, R. 1983. Pygmy possums and feathertail glider. Page 158 in R. STRAHAN, ed. Complete book of Australian mammals. Angus & Robertson, Sydney.
- STRUMWASSER, F. 1960. Some physiological principles governing hibernation in *Citellus beecheyi*. *Bull. Mus. Comp. Zool.* **124**:282-318.
- WAKEFIELD, N. A. 1970. Notes on Australian pygmy possums (*Cercartetus*, Phalangeridae, Marsupialia). *Victorian Nat.* **87**:11-18.
- WALLIS, R. L. 1976. Torpor in the dasyurid marsupial *Antechinus stuartii*. *Comp. Biochem. Physiol.* **53A**:319-322.
- WANG, L. C. H., and J. W. HUDSON. 1971. Temperature regulation in normothermic and hibernating eastern chipmunk, *Tamias striatus*. *Comp. Biochem. Physiol.* **38A**:59-90.