



## TORPOR IN RELATION TO REPRODUCTION IN THE MULGARA, *DASYCERCUS CRISTICAUDA* (DASYURIDAE: MARSUPIALIA)

FRITZ GEISER<sup>1</sup> and PIP MASTERS<sup>2</sup>

<sup>1</sup>Department of Zoology, University of New England, Armidale, New South Wales 2351, Australia and

<sup>2</sup>CSIRO Division of Wildlife and Ecology, Alice Springs, Northern Territory 0871, Australia

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**Abstract**—1. We investigated the occurrence of spontaneous torpor (food and water *ad libitum*) of female (70 g) and male (100 g) Mulgaras, *Dasyercus cristicauda* (Marsupialia) during the reproductive season.

2. Torpor was observed frequently (76% of observations) in the females during pregnancy. Females never displayed torpor from 4–5 days before giving birth and throughout lactation.

3. Males regularly displayed torpor (47% of observations) throughout the period of investigation (June–November).

4. When animals displayed torpor it was always on a daily basis between early morning and mid-afternoon. Torpor bout duration during induced torpor (no food, no water) ranged between 3.3 and 12.3 h.

5. The metabolic rate of torpid *D. cristicauda* was reduced to <12% of that in normothermic, resting individuals at the same air temperature.

6. Body temperatures of normothermic resting animals was  $33.7 \pm 1.4^\circ\text{C}$ ; during torpor the body temperature was metabolically defended at about  $14^\circ\text{C}$ .

7. Our study provides further evidence that reproduction and torpor in mammals are not always exclusive and demonstrates that the pattern of torpor in *D. cristicauda* is similar to that of other dasyurid marsupials.

**Key Word Index:** Torpor; reproduction; body temperature; metabolic rate; marsupial; *Dasyercus cristicauda*

### INTRODUCTION

Reproduction and torpor in mammals are widely believed to be mutually exclusive. In many hibernating rodents the season of hibernation is followed by the season of reproduction, but there is no temporal overlap (Barnes *et al.*, 1986). In rodent species that display shallow daily torpor, like deer mice *Peromyscus maniculatus* and Djungarian hamsters *Phodopus sungorus*, the occurrence of torpor is not always strictly seasonal and can be manipulated by environmental factors; however, as for the hibernating species, torpor does not seem to occur in reproductive individuals (Blank and Desjardins, 1986; Goldman *et al.*, 1986; Steinlechner *et al.*, 1986).

While reproduction and torpor seem to be exclusive in many rodents, small bats regularly display torpor during pregnancy and lactation (Racey, 1973; Audet and Fenton, 1988; Kurta *et al.*, 1988). There is also evidence that some monotremes and marsupials may display torpor during the reproductive season. A pregnant echidna *Tachyglossus aculeatus*

(Monotremata) was observed in torpor in the laboratory 2 days before laying her apparently fully developed egg (Geiser and Seymour, 1989). Torpor was also observed in wild lactating feathertail gliders, *Acrobates pygmaeus* (Marsupialia) (Frey and Fleming 1984). Furthermore, a lactating fat-tailed dunnart, *Sminthopsis crassicaudata* (Marsupialia), was found torpid in the field and subsequently raised her young with success (Morton, 1978).

As these reports were based on only a few observations we decided to investigate the relationship between torpor and reproduction in marsupials in more detail. For this project, we studied in the laboratory the occurrence of torpor in female and male Mulgaras *Dasyercus cristicauda* (Dasyuridae: Marsupialia) throughout their reproductive season. *D. cristicauda* reproduces in the wild from June to December and has been observed mating in the laboratory from mid-May to mid-June (Woolley, 1983). The pattern of torpor was also investigated in some detail because very little is known about torpor in this species (Kennedy and McFarlane, 1971).

### MATERIAL AND METHODS

Six adult *Dasyercus cristicauda* (2 females; 4 males) were caught on 28 May 1990, 5 km west of the Ayers Rock Resort, Northern Territory. A collection permit for only 6 individuals was granted because the species is considered vulnerable to extinction. They were kept as a group in a large cage from 29 May to 23 June and were observed to mate for at least 7 h on 17 June and for several hours on 23 June 1990. From 24 June, the animals were held individually in cages and they were transported to the University of New England in Armidale. Animals were fed daily on a surplus of a mixture of dried and canned pet food; water was available *ad libitum*. From 26 June, they were maintained under a short photoperiod from 0700 to 1730 h, which is similar to the natural photoperiod they experience in their habitat at that time of the year. They were kept in a room with air temperatures ( $T_a$ ) fluctuating between 15 and 23°C and from 27 July in a temperature-controlled cabinet at  $T_a$  18.0 ± 0.5°C. Average daily temperatures at Ayers Rock in winter range from a minimum of 3.5°C to a maximum of 20.3°C (Climatic Averages, Australia). For measurements of body temperature ( $T_b$ ) and rate of oxygen consumption ( $\dot{V}_{O_2}$ ) they were exposed to different  $T_a$ s for 1-day periods. The females were kept in a temperature-controlled cabinet ( $T_a$  18°C) before they gave birth. After the births they were kept in an animal-holding room that was generally warmer than the temperature-controlled cabinets but were moved back into the temperature-controlled cabinet at  $T_a$  18°C on 6 September. The young developed apparently normally. One 67-day old pouch young weighed 6.9 g, which is similar to the rate of development described for other individuals of this species held in the laboratory (Michener, 1969). However, the young of both females were abandoned without apparent reason after 52 and 74 days of lactation. Loss of pouch young is a common problem with dasyurid marsupials in captivity. After completion of experiments, the six adult animals were transferred to the Territory Wildlife Park, Berry Springs, Northern Territory.

The occurrence of spontaneous torpor (food and water *ad libitum*) was monitored by observing the animals daily. The animals were considered torpid when they were slow and clumsy and when disturbed during this state, they shivered vigorously. To verify this visual observation of torpor,  $T_b$  was measured rectally; animals appearing torpid as described above always had a  $T_b$  of <30.0°C. The occurrence of torpor during the reproductive season was monitored daily between 0900–1300 h. The occurrence of torpor was also monitored as a function of time of day

(0700–1900 h) at  $T_a$  18°C; females were excluded from this data set after the young were born.

The metabolic rate (measured as rate of oxygen consumption  $\dot{V}_{O_2}$ ) was measured in males and in females before they gave birth over 1-day periods starting at about 1600 h. Food and water were not available during these measurements. Animals were placed in air tight 3-L respirometry vessels and the  $\dot{V}_{O_2}$  was continuously measured with an Applied Electrochemistry S 3A/II oxygen analyser connected to a Lloyd Graphics 2002 recorder. The flow rate (500–600 ml/min) of dry air through the respirometer vessel was measured with calibrated rotameters. Volumes were corrected to STP and the  $\dot{V}_{O_2}$  was calculated according to Withers (1977).  $\dot{V}_{O_2}$  for resting animals (RMR) and torpid animals were determined from the minima observed over 30-min periods. Animals were considered torpid when the  $\dot{V}_{O_2}$  fell below 75% of the resting metabolic rate (RMR) at the same  $T_a$  (Hudson and Scott, 1979).

When  $T_b$  was measured by 3-cm rectal insertion of a fine thermocouple probe, the animals were considered torpid if  $T_b$  was less than 30.0°C. During rewarming the thermocouple wire was taped to the tail and the  $T_b$  was measured at regular intervals. Temperatures ( $T_a$  in the respirometer vessel and  $T_b$ ) were measured with Omega HH-71T electronic thermometers. All thermocouples were calibrated to the nearest 0.1°C with a Dobros Precision mercury thermometer.

Numerical values in the text are expressed as means ± standard deviation (SD) unless otherwise stated.

### RESULTS

#### *Torpor and reproduction*

The reproductive status and the sex of the animals influenced the occurrence of spontaneous torpor. Both females frequently entered torpor during their time of pregnancy at  $T_a$ s between 15 and 23°C (76% of observations) (Fig. 1). The body mass of the females increased during this period from 66.0 ± 2.8 g on 26 June to 89.1 ± 5.4 g on 30 July, shortly before they gave birth. Torpor in the 2 pregnant females was first observed 2 days after mating and was last observed 4 and 5 days, respectively, before the pouch young were first observed. The period of gestation calculated from the date when females and males were separated to the date of birth was 43 and 48 days. As far as we could ascertain, both females remained normothermic during the entire period of lactation. However, torpor was again observed 5 and 14 days, respectively, after the pouch young had been

*Dasyercus cristicauda* females

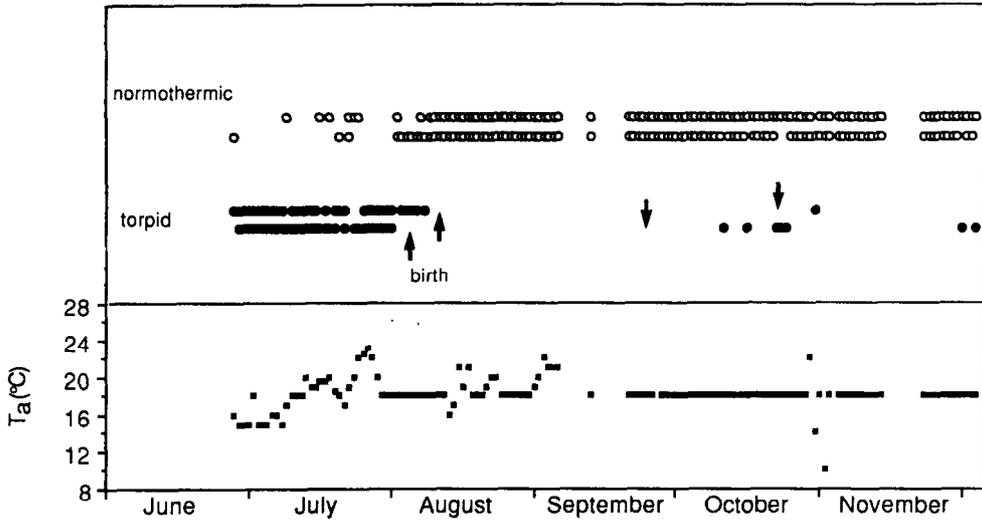


Fig. 1. The occurrence of normothermia (open symbols) and torpor (solid symbols) of 2 female *Dasyercus cristicauda* in relation to their reproductive status. Each point represents an individual observation. Births are indicated by upward arrows, loss of pouch young by downward arrows. The air temperatures ( $T_a$ ) are shown below.

lost. Females displayed torpor less frequently after lactation than during pregnancy (Fig. 1).

The males displayed spontaneous torpor throughout the period of investigation (47% of all observations) (Fig. 2). Torpor was first observed 4 days after matings. During the period of pregnancy of the females, the 4 males displayed torpor less frequently at  $T_a$  18°C (34% of observations) than the 2 females (53% of observations). Body mass of the males changed only little during this time from  $102.4 \pm 8.1$  g on 26 June to  $107.9 \pm 17.6$  on 30 July. No clear

seasonal change in the occurrence of torpor was observed in the males (Fig. 2).

*The pattern of torpor*

The frequency of spontaneous torpor (food and water *ad libitum*) in *Dasyercus cristicauda* was dependent on the time of day (Fig. 3). At  $T_a$  18°C, torpor in males and in females before they gave birth occurred in about 50% of observations between 0700 and 1300 h (Fig. 1). In the afternoon (1400–1600 h) the occurrence of torpor was reduced to < 30%. All

*Dasyercus cristicauda* males

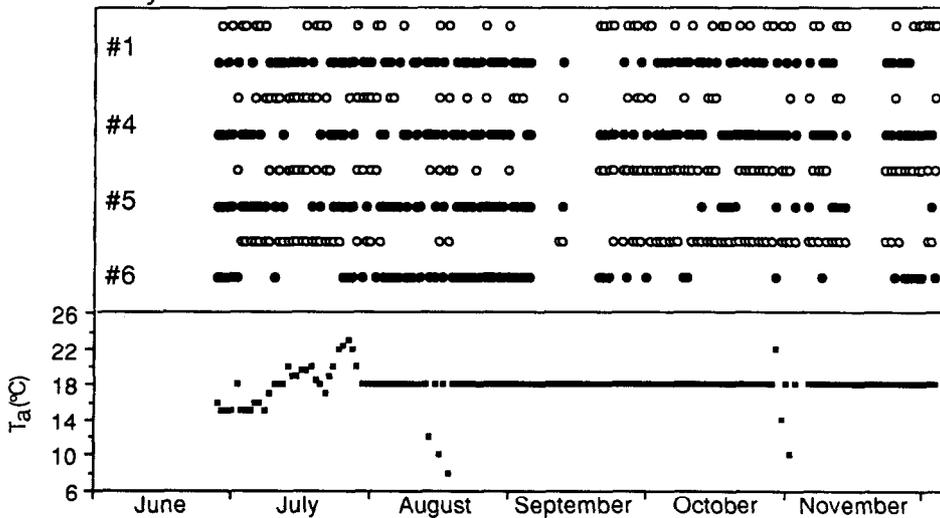


Fig. 2. The occurrence of normothermia (open symbols) and torpor (solid symbols) of 4 male *Dasyercus cristicauda*. Each point represents an individual observation. The air temperatures ( $T_a$ ) are shown below.

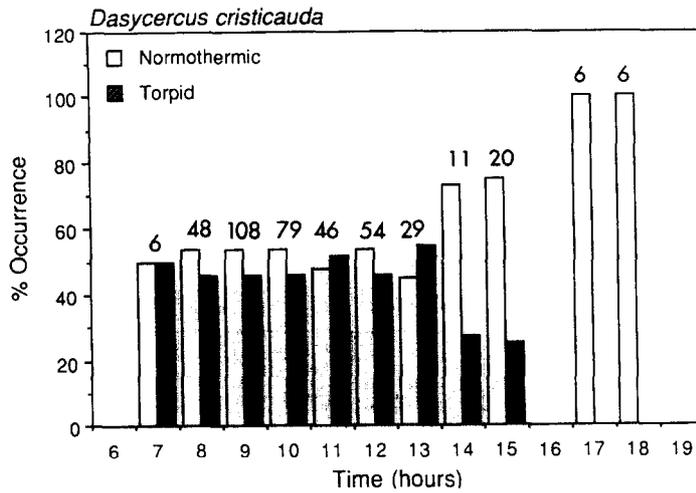


Fig. 3. Percent of torpid and normothermic *Dasyercus cristicauda* at different times of day. Lactating females were excluded from the calculations and the numbers of observations are shown above the columns.  $T_a$  was  $18.0 \pm 1.0^\circ\text{C}$ .

individuals were normothermic after lights off between 1730 and 1900 h.

Body temperature of normothermic, resting *D. cristicauda* was stable at  $33.7 \pm 1.4^\circ\text{C}$  between  $T_a$  5 and  $25^\circ\text{C}$  (Fig. 4). During torpor,  $T_b$  ranged from values that were only  $0.8^\circ\text{C}$  above  $T_a$  to values that were  $14.9^\circ\text{C}$  above  $T_a$ . The smallest  $T_b - T_a$  were observed between  $T_a$  10 and  $T_a$   $20^\circ\text{C}$ ; below  $T_a$   $10^\circ\text{C}$ ,  $T_b - T_a$  increased. The lowest values of  $T_b$  ( $13.2$  and  $14.0^\circ\text{C}$ ) were observed at  $T_a$  10 and  $9.5^\circ\text{C}$ . The increase in  $T_b - T_a$  below  $T_a$   $10^\circ\text{C}$  indicates that  $T_b$  was metabolically defended in that temperature range. Most torpid *D. cristicauda* had  $T_b$ s between  $18$ – $22^\circ\text{C}$

(60%); lower (16%) and higher (24%)  $T_b$ s were less common.

The metabolic rate of *D. cristicauda* showed strong daily fluctuations and differed substantially between the torpid and normothermic state (Fig. 5). The mean  $\dot{V}_{O_2}$  in normothermic, resting animals increased with decreasing  $T_a$  from  $1.04 \pm 0.06$  ml/g h ( $T_a$   $20^\circ\text{C}$ ) to  $2.44 \pm 0.51$  ml/g h ( $T_a$   $9.5^\circ\text{C}$ ) (Fig. 6). The  $\dot{V}_{O_2}$  during torpor fell to  $<12\%$  of normothermic, resting animals. The  $\dot{V}_{O_2}$  of torpid animals was similar at  $T_a$   $20^\circ\text{C}$  ( $0.12 \pm 0.06$  ml/g h) and  $T_a$   $15^\circ\text{C}$  ( $0.15 \pm 0.09$  ml/g h) and showed a slight increase to  $0.25 \pm 0.17$  ml/g h at  $T_a$   $9.5^\circ\text{C}$  (Fig. 6). The duration of torpor derived from measurements of  $\dot{V}_{O_2}$  ranged between 3.3 and 12.3 h.

Rewarming from torpor was measured at  $T_a$   $23^\circ\text{C}$  in a male (body mass 93 g) that had entered torpor at  $T_a$   $18^\circ\text{C}$ . The animal rewarmed slowly at low  $T_b$  ( $T_b$   $23.5$  to  $26.1^\circ\text{C}$  over 10 min;  $0.26^\circ\text{C}/\text{min}$ ), reached a maximum of  $0.67^\circ\text{C}/\text{min}$  over 10 min between  $T_b$   $28.1$  and  $T_b$   $34.8^\circ\text{C}$ . The overall rewarming from  $T_b$   $23.5$  to  $36.0^\circ\text{C}$  took 27 min at a rate of  $0.46^\circ\text{C}/\text{min}$ .

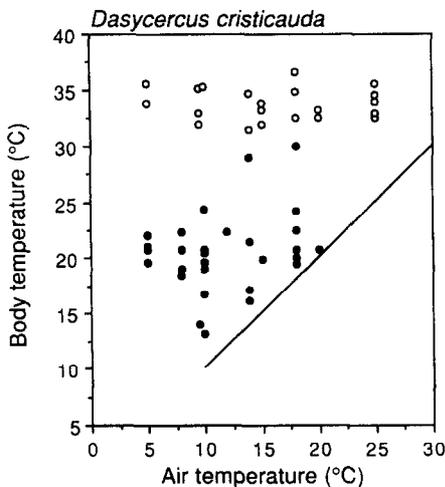


Fig. 4. Body temperatures ( $T_b$ ) of normothermic (open symbols) and torpid (solid symbols) *Dasyercus cristicauda*. Each point represents a single measurement. The solid line represents  $T_b = T_a$ .

DISCUSSION

Torpor and reproduction

Our study shows that torpor in *Dasyercus cristicauda* may occur in reproductive individuals. Females displayed torpor throughout most of pregnancy and males throughout the reproductive season.

Torpor in parts of the reproductive season has been observed in all three mammalian subclasses. It occurs in pregnant monotremes (Geiser and Seymour, 1989) in pregnant and lactating marsupials (Morton, 1978; Frey and Fleming 1984; Geiser, 1988; present study)

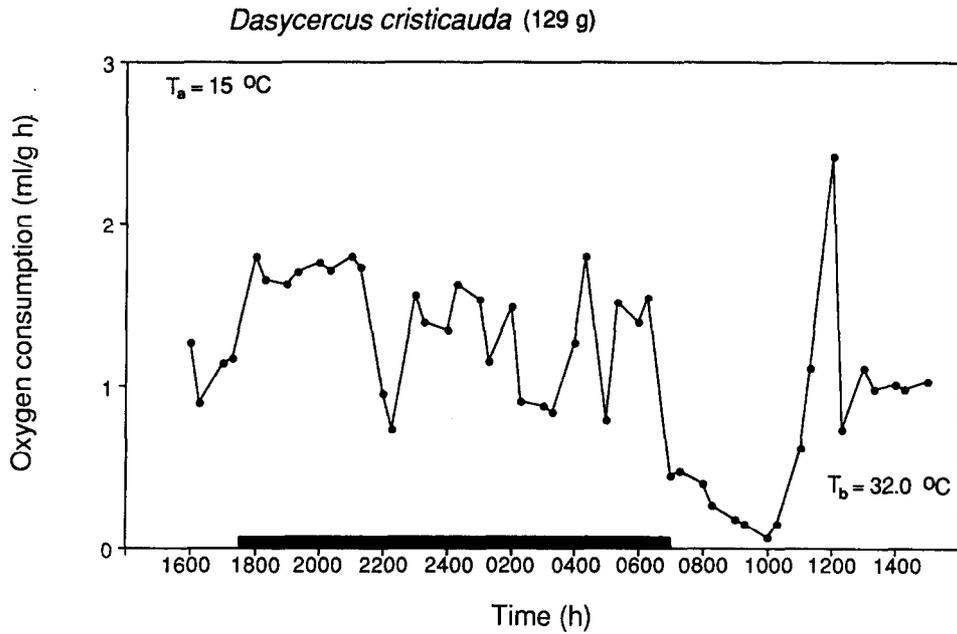


Fig. 5. The daily fluctuation of oxygen consumption of a male *Dasyercus cristicauda*. Arousal from torpor, indicated by the steep increase in oxygen consumption, was spontaneous. The body mass at the start of the experiment was 129 g. The body temperature was measured after the animals had aroused from torpor and was resting. The black bar indicates the period of darkness.

and in pregnant and lactating placentals (bats) (Racey, 1973; Racey and Speakman, 1987; Audet and Fenton 1988). Furthermore, torpor has been observed in incubating hummingbirds (Calder and Booser 1973). The occurrence of torpor during reproduction in such diverse groups suggests that it is a convergent adaptation for reduction of

energy expenditure during the period of reproduction.

But why is it then, that torpor has not been observed in reproductive rodents (Goldman *et al.*, 1986; Steinlechner *et al.*, 1986; Darrow *et al.*, 1988)? Monotremes and marsupials generally have short gestation periods (Tyndale-Biscoe, 1973; Russell, 1982) and the weight of the single egg in *Tachyglossus aculeatus* (Monotremata) and that of single neonates or neonate litters of marsupials is less than 0.3% of the mothers' weights (Tyndale-Biscoe, 1973; Russell, 1982; Geiser and Seymour, 1989). The reproductive costs during gestation in both groups therefore should be relatively low as has been verified for some marsupials (Thompson and Nicoll, 1986; Nicoll and Thompson, 1987). Similarly, energetic costs during lactation in marsupials also tend to be relatively low (Green, 1984; Thompson and Nicoll, 1986; Nicoll and Thompson, 1987), because many show relatively slow growth and development after birth. By contrast, small rodents have a relatively short gestation period, relatively heavy neonate litters (10–65% of maternal weight) (Eisenberg, 1981) and a relatively fast development after birth and both gestation and lactation are energetically expensive (Nicoll and Thompson, 1987). At first glance, bats seem to be similar to rodents in having relatively large, but often single, neonates (13–40% of maternal weight; Ransome, 1990). However, growth in fetal and young bats, as in marsupials and monotremes, is slow and

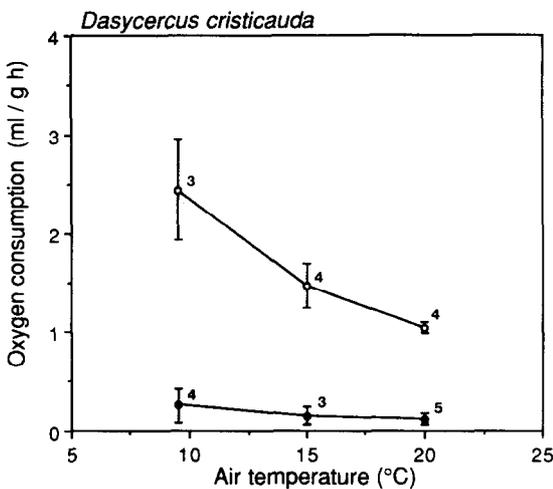


Fig. 6. The metabolic rate (measured as rate of oxygen consumption  $\dot{V}O_2$ ) of normothermic, resting (open symbols) and torpid (solid symbols) *Dasyercus cristicauda*. Values represent means  $\pm$  SD for number of individuals shown. Body masses of the individuals at the beginning of the measurements were  $103.6 \pm 19.7$  ( $T_a$  20°C),  $108.9 \pm 20.8$  ( $T_a$  15°C) and  $105.5 \pm 16.3$  ( $T_a$  9.5°C).

energy expenditure at least during gestation is much lower than in small rodents (Racey and Speakman, 1987; Nicoll and Thompson, 1987). It therefore appears that mammals that spread the reproductive effort and the associated metabolic costs over a long time, may display torpor during the period of reproduction. This may further slow the rate of development of young, but may not adversely affect the chance of survival of offspring because a small delay in growth within the long period of development may not have a strong negative impact. In contrast, mammals with a short reproductive period and rapid energetically demanding development appear to be locked into rigid homeothermy during reproduction that ensures fast production of offspring during times of plenty, but does not allow for safety mechanisms, such a torpor, when supply of food is low.

While reproductive strategies may provide a possible explanation for the differences between thermoregulatory patterns during reproduction in different mammalian groups, other influences have to be considered. It is evident that all species in which torpor has been observed during the reproductive period are insectivorous. Abundance of most insects strongly fluctuates with season. During the mating season of *D. cristicauda* in winter, insect supply is low. Nevertheless, if the young are to be weaned in spring or summer when insects are most abundant, adults have to begin reproduction in winter because of the 5 month period of gestation and lactation (Woolley, 1983). In contrast, Australian rodents from arid areas quickly reproduce when food is abundant, regardless of season (Morton, 1982; Breed, 1990) and therefore torpor may not be required for maintenance of energetic balance. Occurrence of torpor during reproduction therefore may be linked to the food consumed by the mammals. Species that have access to relatively predictable food supplies during the period of reproduction may be able to adopt strict homeothermy during reproduction, whereas species with relatively unpredictable food supplies may be better off utilising torpor for only a small extension of the reproductive period.

Extension of gestation by periods of torpor has been observed in bats, with the birthdate being negatively related to the temperature experienced by the animals (Racey, 1973). A similar relationship between  $T_a$ , torpor occurrence and length of gestation may occur in *Dasyercus cristicauda*. The gestation period of 43 and 48 days observed in the present study at about  $T_a$  18°C is considerably longer than of animals maintained at  $T_a$  21°C (35–44 days in 6 litters; Woolley, 1971). An even shorter gestation period of 30 days was observed in this species (Fleay, 1961). The  $T_a$  under which the animals were main-

tained in Fleay's (1961) study was not reported, but the animals had access to sunlight and were frequently observed basking in the sun. Thus, it is possible that individuals in the present study which were maintained at lower environmental temperatures than those in the other studies, may have prolonged their period of gestation by their frequent display of torpor.

It is interesting that the females increased their body mass during pregnancy when they displayed torpor most frequently. As pointed out above this is not due to the weight of the young. It appears that the females build up fat during pregnancy for the time of lactation. The strong proclivity towards torpor with free access to food at relatively high  $T_a$ s in comparison to those experienced by wild populations in winter suggests that torpor may be used by pregnant females in the wild. It is possible that they try to build up fat stores for the more energetically demanding period of lactation (Thompson and Nicoll, 1986) by becoming torpid and saving energy during their daily period of inactivity.

Torpor in the females occurred throughout pregnancy, but animals remained normothermic from 4–5 days before birth and throughout lactation. It is possible that after implantation of the young, females remained normothermic. Implantation occurs very late during the embryonic development of *Sminthopsis macroura* (Selwood and Woolley, 1991) and it is likely that *D. cristicauda* shows a similar pattern of development (Selwood, personal communication).

#### *The pattern of torpor*

Torpor in *D. cristicauda* occurred strictly on a daily basis and torpor bouts lasted from early morning for 3.3–12.3 h. This is a similar pattern to that displayed by other dasyurids (Wallis, 1979; Geiser 1986). Our results are in contrast to the impression given by Kennedy and MacFarlane (1971) that, during withdrawal of food from *D. cristicauda* for 7 days, torpor lasted for 7 days with a progressive fall of  $T_b$ . Observations reported here provide further evidence that dasyurid marsupials display daily torpor differing from the marsupial pygmy possums (Burramyidae), which display deep and prolonged torpor (Geiser, 1986). In other mammals, such a clear distinction in torpor patterns between families does not appear to exist. For example, individual rodent families may contain species that show daily torpor whereas others display prolonged torpor (Goldman *et al.*, 1986).

The metabolic rate of torpid *D. cristicauda* was similar to that of other dasyurids (Wallis, 1979; Geiser, 1986). However, values measured here for torpid *D. cristicauda* were less than half of animals

starved for 7 days at  $T_a$  20°C (Kennedy and MacFarlane, 1971).

The minimum  $T_b$  of about 14°C in *D. cristicauda* measured in the present study is similar to that of small (<30 g) dasyurid marsupials (Wallis 1979; Geiser, 1986), but somewhat lower than that in other species of similar size (Geiser and Baudinette, 1987). Therefore the general pattern of daily torpor in *D. cristicauda* appears to be like that of other dasyurids and there is no evidence that they display deep and prolonged torpor.

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