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REPRODUCTIVE STATUS AND TORPOR OF THE MARSUPIAL *SMINTHOPSIS CRASSICAUDATA*: EFFECT OF PHOTOPERIOD

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Abstract—1. We investigated the effects of photoperiod on the reproductive state and the occurrence and pattern of torpor in male *Sminthopsis crassicaudata*.

2. Testes regressed when animals were exposed to a short photoperiod (L:D 8:16) and recrudesced under a long photoperiod (L:D 16:8).

3. Animals entered torpor under both photoperiods and no significant differences were observed in the frequency or physiological variables of torpor of *S. crassicaudata* between the short and long photoperiods.

4. The differences in the response to photoperiod in thermal physiology and reproduction suggest that, unlike in many rodent species, torpor and reproduction in *S. crassicaudata* are controlled by separate environmental cues and mechanisms. Copyright © 1996 Elsevier Science Ltd.

Key Word Index: Torpor; reproduction; photoperiod; marsupial; *Sminthopsis crassicaudata*; testes; metabolic rate

INTRODUCTION

In small mammals both thermoregulation at low temperatures and reproduction require a substantial increase in energy metabolism and thus food intake. Since many small mammals are thermally stressed in winter and may have to resort to torpor to reduce energy expenditure, most species reproduce in spring or summer when the cost of thermoregulation is relatively low, and food is generally more abundant than in winter. In many small mammals, therefore, torpor and reproduction appear to be mutually exclusive.

The regular seasonal occurrence of reproduction and torpor, combined with the fact that the physiological changes are established prior to the initiation of these events, has resulted in many investigations into the factors that govern these processes. It is well established that external factors such as temperature and nutrient supply, as well as internal circannual rhythms, are involved in the appropriate timing of seasonal physiological changes. However, the most common environmental stimulus, triggering the onset of both reproduction and torpor, appears to be photoperiod (Pengelley and Fisher, 1963; Grocock and Clarke, 1974; Smith *et al.*, 1978; Johnston and Zucker, 1980; Goldman *et al.*, 1986; McAllan and Dickman, 1986; Steinlechner *et al.*, 1986; Kirsch *et al.*, 1991). While ambient temperature (T_a) and food supply generally show pronounced fluctuations, the extent of these cycles may vary from year to year. Photoperiod, however, maintains a constant annual cycle and can, therefore, be used as a precise and reliable cue.

Although the effects of photoperiod on reproduction and torpor have been studied in numerous eutherian mammals, with the majority of these studies involving rodents, little is known about its effect on marsupials. Therefore, we investigated the effects of photoperiod on torpor and reproductive state in the small (16 g), nocturnal dasyurid marsupial, *Sminthopsis crassicaudata*, which inhabits the mesic to arid regions of southern and central mainland Australia (Morton, 1978a). This species has a well-defined reproductive season, from mid–late July to late February (Morton, 1978c), that, at least in females, appears to be controlled by photoperiod (Godfrey, 1969; Smith *et al.*, 1978). It is also known that *S. crassicaudata* enters daily torpor, both in the wild (Morton, 1978b, d; Frey, 1991) and, when subjected to cold T_as and/or food restriction, in the

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laboratory (Godfrey, 1968; Geiser and Baudinette, 1987; Holloway and Geiser, 1995). This species shows a seasonal change in the occurrence of torpor and, what is most interesting, torpor is most pronounced in winter when the reproduction season commences. We, therefore, tested the hypothesis that interrelations between torpor and reproduction in marsupials differ from those in rodents. We investigated whether torpor patterns and occurrence are affected by photoperiod, and how these are related to the reproductive status of male *S. crassicaudata*.

MATERIALS AND METHODS

Fourteen adult male *S. crassicaudata* were obtained from a laboratory colony maintained by the Genetics Department of the University of Adelaide and transported to the University of New England (UNE), Armidale, NSW. Upon arrival at UNE in April 1992, the animals were divided into two groups of matched body mass, and kept in environmental chambers at a T_a of $18 \pm 1°C$. The animals were housed individually in cages, and were fed *ad libitum* a mixture of dried and commercial pet food and water. Vitamin (Pentavite) and calcium supplements were given twice a week and several *Tenebrio* larvae were provided weekly.

The lighting conditions within the Adelaide colony, which were designed to optimise the breeding potential of the animals (Smith *et al.*, 1978), consisted of 16 h daylight and 8 h darkness (L:D 16:8) for 6 months, followed by a period of 3 weeks of L:D 8:16 and then a return to the L:D 16:8 photoperiod (Bennett *et al.*, 1982). After their arrival at UNE all animals were initially subjected to a photoperiod of L:D 12:12 (lights on 0600 h) for a period of 8 weeks before the photoperiod was changed. One group (N = 7) was then exposed to a photoperiod of L:D 16:8 (lights on 0400 h) and the other (N = 7) to L:D 8:16 (lights on 0800 h). After 8 weeks under long or short photoperiods, the photoregimes of the two groups were exchanged. Light in each chamber was provided by two 8 W fluorescent tubes which emitted a light intensity of approximately 100 lx (Gossen Panlux electronic light meter) throughout each chamber.

Subsequent to 7 weeks' acclimation at L:D 12:12, the length and breadth of testes were measured with vernier callipers (mean of three independent measurements) on a weekly basis. Body mass was measured at the same time and a 'testes index', which is length × breadth/body mass (Heath and Lynch, 1983), was calculated.

Metabolic rates (MR), measured as rate of oxygen consumption ($\dot{V}O_2$), were determined over a 23 h period (± 30 min), commencing in the late afternoon, at T_a $12 \pm 1°C$ using an open-flow system. Food and water were not available to the animals for the duration of these measurements. Animals were placed within a 0.5 l respirometry vessel and $\dot{V}O_2$ was continuously monitored, after the removal of water from the air stream, with an Applied Electrochemistry S-3A oxygen analyser connected to a Lloyd Instruments Graphic 2002 recorder. The flow rate was 350–450 ml min^{-1} and was measured with calibrated rotameters. With this chamber size and these flow rates, 99% equilibrium was obtained between 5 and 6.5 min. T_a was measured by a calibrated thermocouple placed within the respirometry vessel. Photoperiods during measurements always matched those of the environmental chambers.

The MR of normothermic resting animals (RMR) was determined during the photophase when a variation of less than 5% over 15 min occurred after an inactive period of at least 30 min; the MR of active animals (AMR) was derived from the maximum rate observed during the scotophase taken over a 30 min interval; the arousal peak was derived from the maximum rate, measured over at least 5 min, after a torpor bout; and the minimum MR of torpid animals (TMR) was determined when $\dot{V}O_2$ was constant over at least 30 min (see Fig. 1). Animals were considered torpid when MR fell below 75% of the RMR at the same T_a (Hudson and Scott, 1979). Duration of entry (75% RMR to steady state TMR), torpor bout (75% RMR to 75% RMR) and arousal (steady state TMR to 75% RMR) were derived from the measurements of $\dot{V}O_2$. For measurements of ADMR, $\dot{V}O_2$ was integrated over the entire 23 h period using intervals of 10 min for calculations of the means.

All gas volumes were corrected to STP and rates of oxygen consumption were calculated using equation 3a of Withers (1977). For mass-specific $\dot{V}O_2$ calculations, the animals were weighed before and after the experiments and body mass interpolated assuming a constant rate of loss.

Mean values in the text and figures are shown $\pm$ standard error (SE). Paired observations underwent an F_{max} test to see if the variances were significantly different prior to being compared by a Student's *t*-test for equal or unequal variances (Zar, 1984). Multiple observations were compared using a one-way analysis of variance (ANOVA) and the Tukey test (Zar, 1984), or Chi-square analysis. Straight lines were fitted using regression analysis (Minitab). Differences were assumed to be significant at the 5% level ($P < 0.05$). In the text and figures, N = number of individuals and n = number of observations.

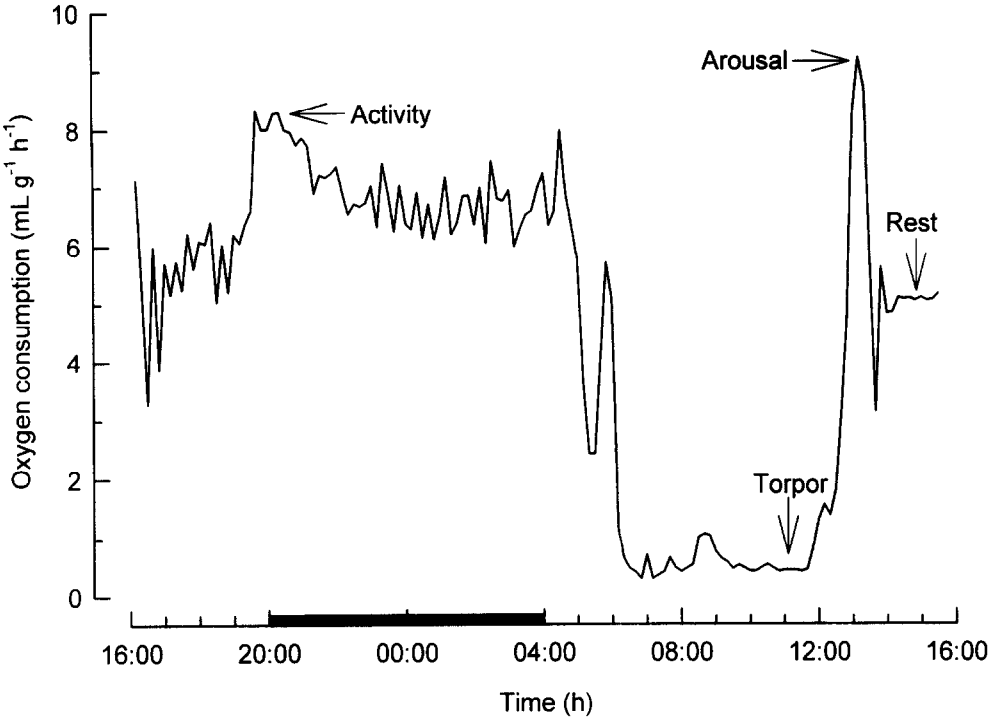

Fig. 1. A typical set of records of metabolic rate measurements. Different physiological states are indicated by arrows. Metabolic rates for activity were derived from the maximum nocturnal rate over a 30 min interval, those during torpor from a constant minimum rate over at least 30 min, those during arousal from the maximum rate of at least 5 min after a torpor bout, and during rest from diurnal measurements which were fairly constant over at least 15 min. Horizontal bar indicates period of darkness.

RESULTS

Testes size was affected by photoperiod (Figs 2 and 3). When subjected to L:D 16:8 the testes enlarged, reached a maximum size within 3–4 weeks and subsequently remained at that level (Fig. 2). Regression of the testes occurred in those animals under L:D 8:16, and this was also completed within approximately 4 weeks. After 7 weeks' acclimation to

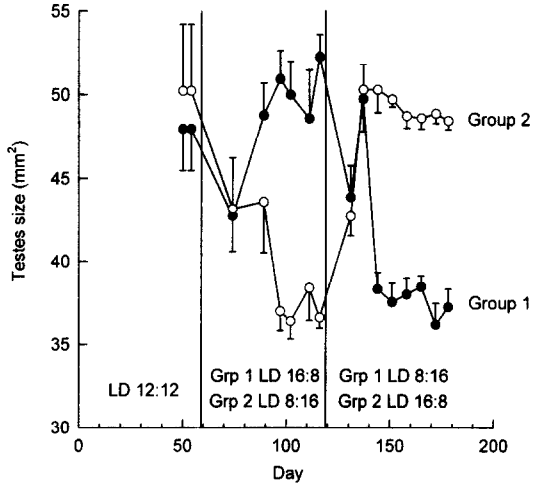

Fig. 2. Effects of photoperiod on mean testes size (± SE) in *S. crassicaudata* as a function of time. Measurements commenced following 7 weeks' exposure to L:D 12:12. The vertical lines indicate the time when photoperiods were exchanged.

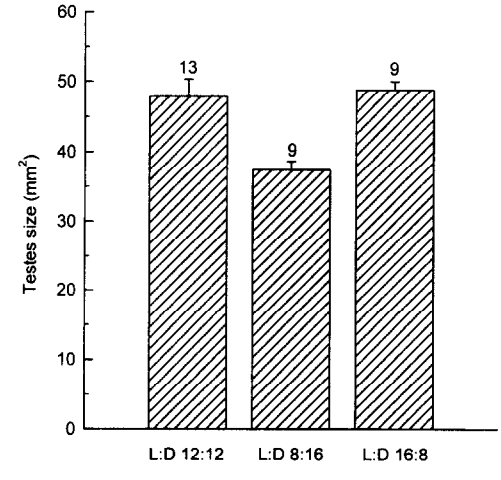

Fig. 3. Effects of photoperiod on the mean size of testes in *S. crassicaudata* after 7 weeks' acclimation to the three photoperiods. Number of individuals is shown above the columns. Testes size of those animals held under L:D 8:16 were significantly smaller than those held under both L:D 16:8 and L:D 12:12 ($P < 0.001$, ANOVA; $P < 0.01$, Tukey test).

Table 1. Summary of data on torpor occurrence and body mass in *S. crassicaudata* when exposed to different photoperiods

Photoperiod	*N*	*n*	Number torpid	Number normothermic	% Torpid	Mass (g)
L:D 12:12	13	41	28	13	68.3	16.5 ± 0.5
L:D 8:16	10	46	14	32	30.4	18.1 ± 0.8
L:D 16:8	11	48	21	27	43.8	17.1 ± 0.7
					$P < 0.01$ Chi-square	$P > 0.2$ ANOVA

Body mass (mean ± SE) was measured prior to a night without food to try and induce torpor. *N* = number of animals; *n* = number of observations

each photoperiod, testes size differed significantly between L:D 8:16 (37.40 ± 1.22 mm^2; N = 9), and both L:D 16:8 (48.74 ± 1.21 mm^2; N = 9) and L:D 12:12 (47.85 ± 2.42 mm^2; N = 13) (Fig. 3; $P < 0.001$, ANOVA; $P < 0.01$, Tukey test). This alteration in testes size combined with the tendency for body masses to change under different photoperiods also resulted in a significant difference in the mean testes index between L:D 8:16 (2.09 ± 0.10 mm^2 g^{-1}), and both L:D 16:8 (2.88 ± 0.12 mm^2 g^{-1}), and L:D 12:12 (2.92 ± 0.15 mm^2 g^{-1}) ($P < 0.001$, ANOVA; $P < 0.01$, Tukey test). The testes index of animals at L:D 8:16 was 38 and 40% less than those at L:D 16:8 and L:D 12:12, respectively. Testes size and mean testes index of animals at L:D 16:8 and L:D 12:12 did not differ significantly ($P > 0.05$, Tukey test).

Photoperiod also appeared to influence the number of animals entering torpor (Table 1; $P < 0.01$, Chi-square). However, this result was primarily due to the higher proclivity of the relatively light animals under L:D 12:12 to enter torpor (Fig. 4) as there was no significant difference in torpor occurrence between animals at L:D 8:16 and L:D 16:8 (Table 1; $P > 0.05$, Chi-square). When all animals were compared, those that entered torpor had a significantly lower body mass than those that remained normothermic (Fig. 5; $P < 0.001$, *t*-test) and body mass and torpor occurrence were negatively correlated (Fig. 4;

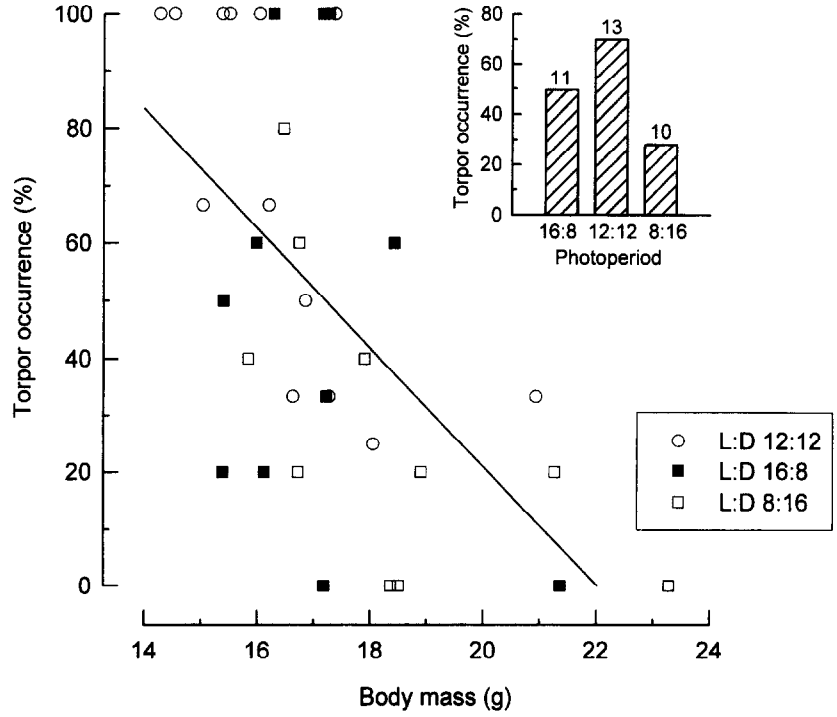

Fig. 4. Relationship between body mass and occurrence of induced torpor (main graph). Occurrence of induced torpor at the three photoperiods is shown as a bar graph (inset). Number of individuals is shown above the columns. Animals held under L:D 12:12 entered torpor more frequently than those held under L:D 16:8 or L:D 8:16 ($P < 0.01$, Chi-square). Since torpor occurrence was negatively related to body mass ($y = 229 \times 10.4x$; $P < 0.001$, $r^2 = 0.32$), this result was due to the lower body mass of animals at L:D 12:12.

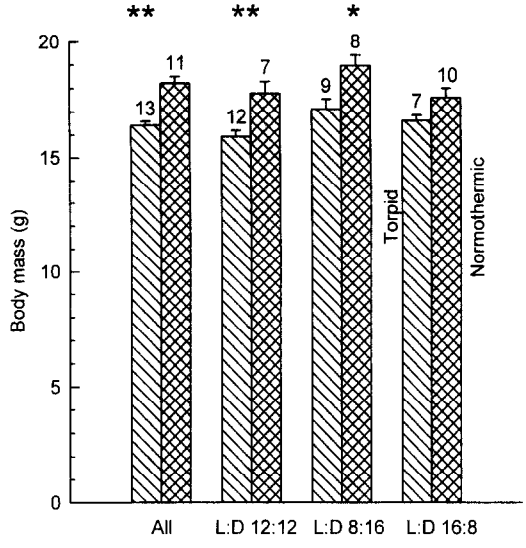

Fig. 5. Relationship between the mean body mass, measured prior to entry into the metabolic chamber, of *S. crassicaudata* entering torpor ("torpid") or remaining normothermic. Number of individuals is shown above the columns. Significant differences were observed when all animals were compared (**, $P < 0.001$, t-test), at L:D 12:12 (**, $P < 0.001$, t-test) and L:D 8:16 (*, $P < 0.02$, t-test).

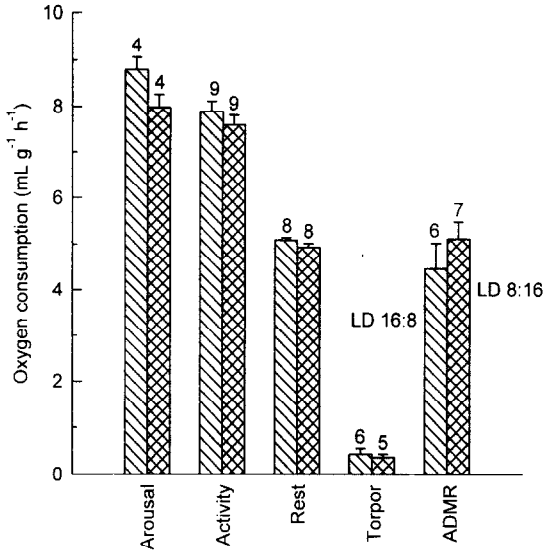

Fig. 6. Effect of photoperiods L:D 16:8 and L:D 8:16 on metabolic rates, measured as rate of oxygen consumption, in *S. crassicaudata* at T_a 12°C. Number of individuals is shown above the columns; ADMR = average daily metabolic rate. Photoperiod has no significant effect on any of the five metabolic states ($P > 0.05$, t-test).

$P < 0.001$, $r^2 = 0.31$). When body masses of individuals remaining normothermic at each photoperiod were compared with those entering torpor, the latter were significantly lighter at both L:D 12:12 (Fig. 5; $P < 0.001$, t-test) and L:D 8:16 (Fig. 5; $P < 0.02$, t-test) but not under L:D 16:8 (Fig. 5; $P > 0.05$, t-test).

While testes size was affected by photoperiod, there were no significant differences between MRs in any of the metabolic states at long and short photoperiods ($P > 0.05$, t-test) (Fig. 6). TMR, 0.43 ± 0.12 ml g^{-1} h^{-1} (N = 6) at L:D 16:8 and 0.36 ± 0.07 ml g^{-1} h^{-1} (N = 5) at L:D 8:16, was significantly lower ($P < 0.001$, t-test) than RMR, 5.08 ± 0.06 ml g^{-1} h^{-1} (N = 8) and 4.93 ± 0.08 ml g^{-1} h^{-1} (N = 8) at L:D 16:8 and L:D 8:16, respectively, representing a 92–93% energy saving at each photoperiod. Torpor durations were highly variable (6.79 ± 2.32 h (N = 6) at L:D 16:8 and 3.55 ± 1.24 h (N = 5) at L:D 8:16), and were also not affected by photoperiod (Fig. 7). The times for torpor entry and arousal were very similar at the two photoperiods (Fig. 7).

DISCUSSION

The present study shows that torpor occurrence and patterns in *S. crassicaudata* were not significantly affected by photoperiod. In contrast, testes size was affected by photoperiod. These observations suggest that the two physiological traits, although both are known to be seasonal, are controlled by separate cues and mechanisms.

When held in outside pens *S. crassicaudata* displayed a number of seasonal changes in the pattern of thermoregulation and torpor (Geiser and Baudinette, 1987). The species showed a greater tendency to enter torpor and had lower TMR, body

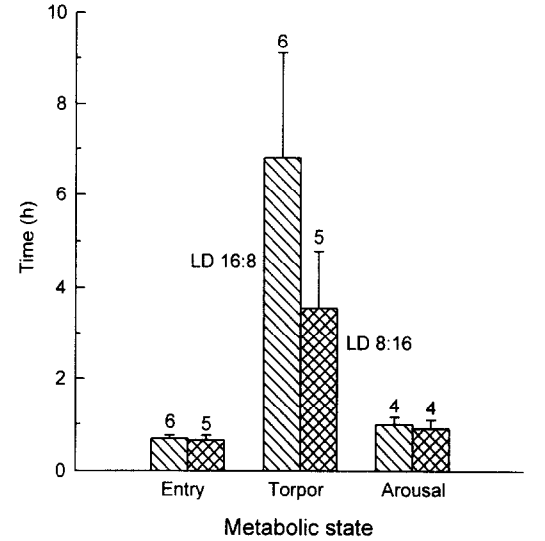

Fig. 7. Effect of photoperiods L:D 16:8 and L:D 8:16 on duration of torpor entry, torpor bout and arousal in *S. crassicaudata* at T_a 12°C. Number of individuals is shown above the columns. Durations of the three metabolic states were not affected by photoperiod ($P > 0.05$, t-test).

temperature (T_b) and RMR in winter when compared to the values in summer. However, Geiser and Baudinette (1987) did not further scrutinise whether photoperiod or temperature or both were responsible for this seasonal change. Our study suggests that photoperiod, which in many species is the instigating factor in the timing of both torpor and reproduction (Heldmaier and Steinlechner, 1981; Goldman *et al.*, 1986; Steinlechner *et al.*, 1986), does not induce these seasonal changes in torpor patterns and that some other factor(s) must be involved.

In the study of Geiser and Baudinette (1987) the animals were exposed to changes in both photoperiod and T_a. It would therefore appear that an important stimulus for the seasonal change in thermoregulation and torpor patterns in this species is T_a. However, it is also likely that food restriction acts as a major stimulus, as Morton (1978d) only observed torpid *S. crassicaudata* in the field at relatively moderate T_as of 9–17°C, despite night-time T_as often falling below 5°C, and concluded that the use of torpor in this species is a response to short-term food shortages. That food availability is an important factor is confirmed by laboratory studies where torpor can be induced through food deprivation (Godfrey, 1968; Frey, 1991; present study) and spontaneous torpor (food available) occurs only occasionally (Geiser and Baudinette, 1987). Therefore, it appears that in *S. crassicaudata* a combination of both low T_a and food shortage acts as a stimulus for the use of torpor.

Sminthopsis crassicaudata is a nocturnal species. Since the period of activity is prolonged under a short photoperiod, and consequently long nights, one might expect an increase of ADMR as torpor frequency and TMR were not affected by photoperiod. However, ADMR was similar at both short and long photoperiods. Therefore, it appears that *S. crassicaudata* can balance its ADMR by reducing the intensity of its activity during short photoperiods (Holloway and Geiser, 1996) rather than having to change their pattern of torpor.

The direct response of the adult male testes to the changes in photoperiod in the current study indicates that the seasonal timing of this species' reproductive cycle is controlled by photoperiod. This is supported by the observations that females can be stimulated into oestrus with increased daylength (Godfrey, 1969; Smith *et al.*, 1978) and males sire more litters if they are subjected to a period of short days when 3–4 months old (Bennett *et al.*, 1990). Further, absolute length of photoperiod or possibly an increasing photoperiod, rather than the rate of change of photoperiod, as has been found in the related *Antechinus stuartii* (McAllan and Dickman, 1986), appears to control reproduction in *S. crassicaudata*. In the wild, pregnancies have been observed as early as the last week of July (short photoperiod), although the majority occur during August and September (approximately L:D 12:12) (Morton, 1978c). Therefore, with a gestation period of 13–16 days (Smith *et al.*, 1978), times of conception must occur from early July onwards. Consequently, males probably respond to a critical photoperiod length, or increase in photoperiod, soon after the winter solstice. The onset of oestrus in female *S. crassicaudata* within the laboratory also coincides with the winter solstice (Godfrey, 1969), which supports our interpretation.

In many rodent species it appears that torpor and reproduction are mutually exclusive (Heldmaier and Steinlechner, 1981; Goldman *et al.*, 1986; Steinlechner *et al.*, 1986). In these species it has been observed that high concentrations of steroid hormones, such as testosterone, inhibit the incidence of torpor (Goldman *et al.*, 1986). Consequently, it has been proposed that the pineal gland, stimulated by short photoperiods, initiates production of antigonadotrophic hormones that cause atrophy of the reproductive organs and consequently allow the species to enter torpor (Hoffmann, 1973; Reiter, 1975, 1981). While the effects of the concentration of sex hormones on torpor have not been investigated in marsupials, the mutual exclusiveness of torpor and reproduction that is seen in many rodent species is not apparent in *S. crassicaudata*, with torpor occurring in both reproductive and non-reproductive individuals (Morton, 1978d; present study). In addition, a number of other species, from all three mammalian subclasses, have now been observed to display torpor during their reproductive season. These include a monotreme, *Tachyglossus aculeatus* (Geiser and Seymour, 1989); two marsupials, *Dasycercus cristicauda* (Geiser and Masters, 1994), and *Acrobates pygmaeus* (Frey and Fleming, 1984); and within the placental mammals, the tenrec, *Geogale aurita* (Stephenson, 1994) and several bat species (Racey, 1973; Audet and Fenton, 1988).

Geiser and Masters (1994) have suggested that these differences in the reproductive patterns between the two groups may be due to two factors: (i) length of development and parental care, with those species observed to go into torpor while reproductively active all having a relatively long gestation/lactation period compared with rodents, and (ii) food source, with rodents tending to be herbivore/granivores while the groups which display torpor during the reproductive season are all insectivorous/nectivorous — food sources which may be prone to large fluctuations in abundance.

Male hibernating ground squirrels arouse several weeks before their female counterparts and Barnes

(1996) proposed that this is so that spermatogenesis can proceed. In addition, if the animal returns to hibernation before the testes have fully matured, gonadal regression occurs (Barnes *et al.*, 1986). This is in contrast to *S. crassicaudata* which appear able to maintain fully developed testes despite periodically entering torpor. One reason for the difference may be due to the body temperature of the animals during torpor. Ground squirrels drop their T_bs during hibernation to as low as 0 to −3°C (Barnes, 1989; Geiser *et al.*, 1990), which is considerably lower than the minimum T_b of approximately 15°C of *S. crassicaudata* during daily torpor (Holloway and Geiser, 1995). Since testicular development does not appear to proceed at low T_bs (Barnes, 1987), spermatogenesis may only be slowed in *S. crassicaudata* but may completely cease at the near freezing T_bs of ground squirrels. Another factor that could affect sperm production is the duration of the torpor bouts. In *S. crassicaudata* torpor bouts last only a few hours, while in ground squirrels the torpor bouts, and consequently the low tissue temperatures, last for several days.

Only male *S. crassicaudata* were used in this study because energy allocations for reproduction are much less for male (spermatogenesis) than for female (gestation and lactation) mammals. This is unlike the situation which occurs in many bird species where the responsibilities, and thus energy costs, for incubation and brooding are shared, thus precluding both males and females from entering torpor during the reproductive season (Csada and Brigham, 1994). In reproductively active mammals the use of torpor appears to differ between the sexes (Grinevitch *et al.*, 1995). It is, therefore, possible that some of the short-term benefits gained from the use of torpor in reproductively active female mammals are outweighed by the long-term costs of a prolonged gestation and a slowed neonatal growth (Racey, 1973; Audet and Fenton, 1988; Grinevitch *et al.*, 1995). For males though, while torpor may slow spermatogenesis (Kurta and Kunz, 1988), it seems that the energetic benefits outweigh any costs and, consequently, males may frequently use torpor during the reproductive season (Grinevitch *et al.*, 1995; present study). It should be noted, however, that while torpor occurrence in reproductive females may not be as prevalent as in reproductive males (Grinevitch *et al.*, 1995), it has been recorded in a number of species (Frey and Fleming, 1984; Geiser and Seymour, 1989; Geiser and Masters, 1994), including one report of a torpid female *S. crassicaudata* with six young (Morton, 1978d).

Since reproduction is generally timed to coincide with the period when offspring survival is most favoured, most species time the births of their litters so that weaning will occur in spring and summer, the seasons when food is usually most prolific. Many rodents are able to maintain strict homeothermy throughout their short reproductive season because they are able to begin their breeding season at a time when it is warm and food is plentiful. For small marsupials, on the other hand, with their long periods of developmental and parental care, pregnancy and lactation often begin in winter, at a time when T_as and food availability are low. Consequently, animals using this strategy may need to reduce their T_b and metabolism, by entering torpor, to ensure they survive the reproductive season.

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