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# Coping with chaos: unpredictable food supplies intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart (Sminthopsis crassicaudata)

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## Abstract

The severity, duration and amplitude of extreme weather events are forecast to intensify with current climate trends, over both long (e.g. seasonal) and short (e.g. daily) time-scales. As such, the predictability of food supplies for many small endotherms is likely to become increasingly important. Numerous small mammals and birds combat food shortages using torpor, a controlled reduction in metabolic rate and body temperature that helps lower their daily energy requirements. As such, torpor often has been cited as a key feature allowing some small endotherms to survive highly unpredictable climates, such as tropics or dry deserts, but mensurative demonstrations of this are lacking. We have shown here that when a small desert marsupial, the fat-tailed dunnart (Sminthopsis crassicaudata), is offered unpredictable levels of daily food, they increase frequency of daily torpor and length of bouts compared with animals offered ad libitum food, but this was not found for animals offered a 70% food-restricted diet. Our data suggest that simple food restriction may not be sufficient for evaluating the efficacy of torpor as a strategy for managing unpredictable climates.

## Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

## Publication Details

Coping with chaos: Unpredictable food supplies intensify torpor use in an arid-zone marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*).

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**Abstract**

The severity, duration and amplitude of extreme weather events are forecast to intensify with current climate trends, over both long (e.g. seasonal) and short (e.g. daily) time-scales. As such, the predictability of food supplies for many small endotherms is likely to become increasingly important. Numerous small mammals and birds combat food shortages using torpor, a controlled reduction in metabolic rate and body temperature that helps lower their daily energy requirements. As such, torpor often has been cited as a key feature allowing some small endotherms to survive highly unpredictable climates, such as tropics or dry deserts, but mensurative demonstrations of this are lacking. We have shown here that when a small desert marsupial, the fat-tailed dunnart (*Sminthopsis crassicaudata*) is offered unpredictable levels of daily food they increase frequency of daily torpor and length of bouts compared with animals offered *ad libitum* food, but this was not found for animals offered a 70% food-restricted diet. Our data suggest that simple food restriction may not be sufficient for evaluating the efficacy of torpor as a strategy for managing unpredictable climates.

**Key words**

Torpor, fat-tailed dunnart, unpredictability, energy restriction, food availability.

**Introduction**

Torpor is characterized by controlled reductions in metabolic rate and body temperature and reduces energy expenditure in times of food shortages (Geiser 2004, Pavey et al. 2009). Torpor is a physiological strategy used by many small endotherms to manage periods of energy deficit, or to combat thermally challenging environments (Geiser 2004). The ecological benefits of torpor often have been inferred from laboratory studies that rely on food restriction to trigger a torpor response (e.g. Godfrey 1968; Geiser and Baudinette 1987; Geiser 1994; Lovegrove and Raman 1998; Song et al. 1998; Giroud et al. 2009). The intensity of such induced torpors (i.e. bout frequency and length) may be used to predict how well a species could survive periods of energy deficit, but torpor has also been highlighted as a key feature allowing some animals to cope with unpredictable climate patterns, and hence unpredictable food availability (e.g Lovegrove and Raman 1998; Ehrhardt et al. 2005; Willis et al. 2006). Coping with unpredictable food supplies are expected to be especially important for small insectivorous endotherms; insectivorous prey can be highly influenced by weather (e.g. Frey 1991) and unpredictable weather patterns are predicted to increase with current climate trends (Baettig et al. 2007; Hughes 2003). Field studies would suggest that torpor use is influenced by the prey type (Pavey et al 2009), but experimental evidence for torpor use to manage unpredictable food sources is lacking. Therefore, we investigated the impact of unpredictable food supplies on torpor use by an Australian arid zone marsupial, the insectivorous fat-tailed dunnart (*Sminthopsis crassicaudata*; Dasyrideae family).

**Methods**

Nineteen sexually mature male fat-tailed dunnarts were sourced from a breeding colony maintained at the University of Sydney. Animals were housed individually in plastic containers (20x33x25cm), and maintained at ambient temperature ($T_a$) of $19° \pm 0.5°C$ under 12L:12D light regimen, which reflected of the photoperiod conditions experienced by the colony at that time of year. Cages were lined with wood shavings, contained a toy for behavioural enrichment and a custom made nest-box. Animals were fed a blended mix of canned cat food (Whiskas®; protein 7.5%, fat 5.5%) and moistened cat biscuits (Whiskas®; protein 29%, fat 10.5%) supplemented with calcium and vitamins. Food was

replenished each evening between 1500-1700 hours. Water was available *ad libitum* throughout the study. For eight days before experimental treatment daily *ad libitum* food intake was recorded and used to derive there experimental diet levels: 1) Control food level = 150% of *ad libitum*; 2) Restricted intake (70% of *ad libitum*); and 3) Unpredictable food level, consisting of four possible and randomly allocated feeding levels of 0%, 30%, 70%, and 120% of *ad libitum* offered daily. The same randomized food regimen was offered to all animals in the unpredictable-diet treatment, and was controlled so that no animals experienced two consecutive days of 0% food. Over the course of the study, the total possible amount of consumable food made available to those animals in the unpredictable group was the same as that available to those receiving a food-restricted treatment. Thus, we tested a response to food unpredictability rather than simply to different levels of feed restriction. Animals were randomly allocated to a diet treatment and, once body masses and tail widths for each animal had stabilized, a 19-day experimental period commenced. Daily food consumption was measured and animals were weighed and tail widths measured on days 5, 10 and 15 and 19 of the trial.

Torpor bouts were measured using custom made nest boxes that recorded the presence of an animal within the nest, and also the skin temperature of the animal using a thermally-sensitive data logger (iButton; DS1921 Thermocron, Dallas Semiconductor, Dallas, USA; calibrated to $\pm 0.5°C$) based on the method described by (Willis et al 2005). A nest box consisted of cardboard cylinder (4cm diameter, 7cm length) that was left open at one end to allow access. The other end of the tube was covered with gauze to provide some insulation. On the floor of each tube small metallic discs were glued from the entrance to the rear, leaving sufficient space for an iButton. Each iButton was covered with 2-ply gauze fabric. The metallic discs were sufficient to deter animals from nesting along the tube entrance and always used the gauze-covered iButton at the rear for nesting. Temperature data were logged every three minutes, indicating the presence/absence of animals in the nest and showing torpor bouts (see Willis et al. 2005). Room ambient temperatures ($T_a$) were logged using iButtons adjacent to each cage, and because torpid animals always maintain their deep body/skin temperatures slightly above $T_a$ (Willis et al. 2005; Dausmann 2005), torpor use and length were observed. Further, all animals were

recorded continuously using a digital video system with infrared lighting to validate nest use. One animal in the unpredictable treatment would not use a nest and their torpor patterns were identified using video footage validated against distinct behavioral features indicative of torpor (adoption of spherical, "tucked-in" posture, reduced breathing rates, and uncoordinated movements prior to re-warming; Geiser 1986).

**Results**

Mean ($\pm$ standard error of the mean; SEM) body mass of all dunnarts at the start of the study was $13.5 \pm 0.3$ g (range 11.2 - 15.5 g), and was not significantly different between treatment groups (control n = 7, restricted n = 6, unpredictable n = 6; $F_{2,18} = 0.43$, $P = 0.7$). Similarly, there was no difference in tail width between treatments; the average across all treatments being $5.8 \pm 0.2$ mm ($F_{2,18} = 0.12$, $P = 0.9$). Differences were apparent in body mass between treatments at the end of the study (ANOVA, $F_{2,18} = 11.2$, $P=0.001$), where animals from the control treatment were significantly heavier ($14.7 \pm 0.4$ g) than those from the restricted ($12.2 \pm 0.4$ g; Tukey q = 5.8 $P = 0.002$) or unpredictable ($12.3 \pm 0.2$; Tukey q = 5.6, $P = 0.003$) treatments, but no significant difference was between the restricted and unpredictable groups (Tukey q = 0.25, $P = 0.99$). At the end of the study, there was no significant difference between treatments regarding tail width (ANOVA, $F_{2,18} = 3.1$, $P = 0.07$); the values being $4.8 \pm 0.2$, $4.4 \pm 0.4$ and $3.8 \pm 0.3$ mm for animals in the control, restricted and unpredictable treatments, respectively. However, it is noteworthy that animals from the unpredictable group tended to have narrower tails than those from the control (Tukey q = 3.5, $P = 0.06$).

Differences were apparent between treatments for gross food intakes (g wet-matter; adjusted for evaporative losses over 24 h) over the entire trial (ANOVA, $F_{2,18} = 450$, P < 0.001). Mean ($\pm$SEM) gross intake by control animals ($201.6 \pm 2.8$ g) was significantly higher than for animals in either the restricted ($135.9 \pm 0.03$ g; Tukey q = 35, $P < 0.001$) and unpredictable ($130.3 \pm 0.06$ g; Tukey q = 38, $P < 0.001$) treatments. Importantly, total food consumed over the entire study by animals in the restricted and unpredictable treatments were not significantly different (Tukey q = 2.5, $P = 0.21$). Further, there was no significant difference in average daily rate of food intake between animals from the

restricted (7.6 ± 0.001 g wet-matter d$^{-1}$) and unpredictable (7.2 ± 0.003 g wet-matter d$^{-1}$) respectively (Tukey q = 2.8, $P$ = 0.15), both of these values being significantly less than that from the control group (11.3 ± 0.17 g g wet-matter d$^{-1}$; Tukey $P$ < 0.001 in both cases)

Not all animals used their nest everyday. As such frequency of torpor use was measured as a proportion of nest-days where animals expressed torpor. Importantly, there was no significant difference between treatments for nest use (i.e. number days a nest was used as a proportion of total days of the trial), which ranged from 44% to 100% across all groups (arcsine transformed ANOVA, F = 0.23, $P$ = 0.60). Frequency of torpor use (as a proportion of days when nests were used; % nest-days) was significantly different between groups (arcsine transformed ANOVA, $F_{2,18}$ = 4.3, $P$ = 0.03), increasing as a graded response by animals from the control, through the restricted and unpredictable treatments (Fig. 1).

Of note, one control animal did not use torpor during the entire study and was excluded from analysis of torpor bout lengths. But when torpor was detected, differences in bout length were found between treatments (log transformed ANOVA $F_{2,17}$ = 6.1, $P$ = 0.01; Fig. 2). Specifically, average bout lengths by animals in the unpredictable treatment were 1.6 times that displayed by control animals (Tukey q = 4.8, $P$ = 0.01), and tended to be longer those from the restricted group (Tukey q = 3.3 $P$ = 0.12).

**Discussion**

Recent field studies have indicated that laboratory manipulations relying on food restriction or thermal challenges to induce torpor may not adequately reflect a species' capabilities (Körtner and Geiser 2000; Christian and Gesier 2007), particularly for dealing the vagaries of weather that drive food availability. The wide distribution of the fat-tailed dunnart in Australia suggests they are well adapted to the challenges of resource scarcity (Morton 1982; Frey 1991). We have shown here that fat-tailed dunnarts can use torpor to manage both restricted and unpredictable food supplies, but they showed a greater increase in intensity of torpor use (Fig. 1) and bout length (Fig. 2) with variable

food supplies compared with those offered food *ad libitum*. Therefore, while many dasyurids are known to use torpor as a response to short-term food shortages, including the fat-tailed dunnart, simple feed restriction may not sufficiently define their ecological limits, or their abilities to combat climate changes.

Other species are apparently capable of using torpor to manage unpredictable supplies of food (Brown and Bartholomew 1969) or water (Ibuka and Fukumara 1997). But what is important in our study is that we have controlled food intakes in a manner that induced torpor responses to a pattern of unpredictability, rather than simply providing a different level of energy restriction. Our data are suggestive that torpor in fat-tailed dunnarts is largely a response to immediate food intakes, probably mediated by body condition, but involving food-factors and hormonal triggers associated with feeding (Ruf et al. 1991; Westman and Gesier 2004; Giroud et al. 2009).

Our results highlight the importance of incorporating environmental patterns that realistically reflect free-ranging situations in order to fully appreciate species' physiological capabilities. Nonetheless, further work is needed to thoroughly describe the energetics of managing unpredictable food supplies in fat-tailed dunnarts and other species. These studies should focus on oxygen consumption during torpor, resting and active periods, and interactions with declining environmental temperatures and shifting photoperiods, which can also induce torpor (Geiser 1994).

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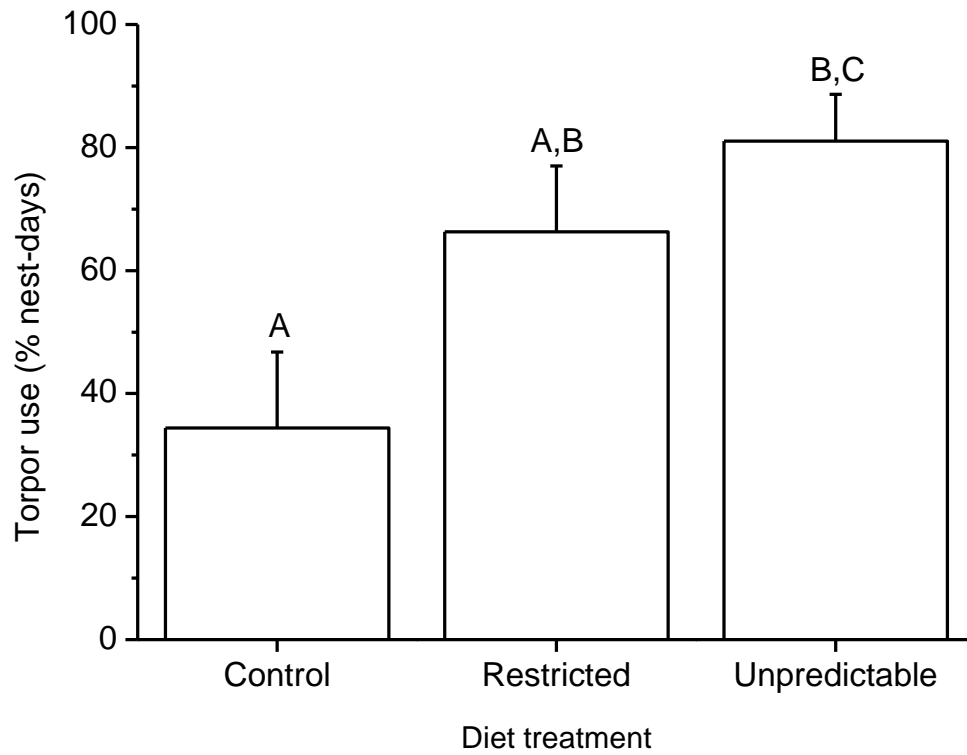
Fig. 1. Frequency of torpor use (% nest-days) for fat-tailed dunnarts on Control, Restricted and Unpredictable diet-treatments. Column letters denote significant differences among treatments ($P < 0.05$).
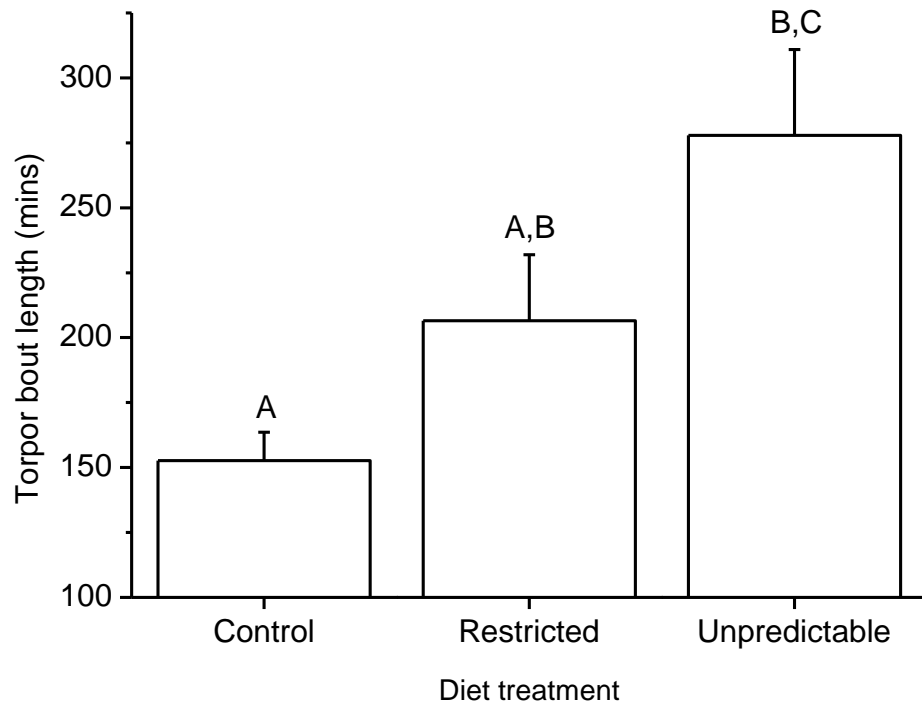
Fig. 2. Mean (± SEM) duration of torpor bouts (minutes) for fat-tailed dunnarts on
Control, Restricted and Unpredictable diet-treatments. Column letters denote significant
differences among treatments ($P < 0.05$).