

# Yearlong hibernation in a marsupial mammal

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Received: 5 March 2007 / Revised: 14 May 2007 / Accepted: 17 May 2007  
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**Abstract** Many mammals hibernate each year for about 6 months in autumn and winter and reproduce during spring and summer when they are generally not in torpor. I tested the hypothesis that the marsupial pygmy-possum (*Cercartetus nanus*), an opportunistic nonseasonal hibernator with a capacity for substantial fattening, would continue to hibernate well beyond winter. I also quantified how long they were able to hibernate without access to food before their body fat stores were depleted. Pygmy-possums exhibited a prolonged hibernation season lasting on average for 310 days. The longest hibernation season in one individual lasted for 367 days. For much of this time, despite periodic arousals after torpor bouts of ~12.5 days, energy expenditure was reduced to only ~2.5% of that predicted for active individuals. These observations represent the first report on body-fat-fuelled hibernation of up to an entire year and provide new evidence that prolonged hibernation is not restricted to placental mammals living in the cold.

**Keywords** Australian mammal · Energy expenditure · Fat storage · Prolonged hibernation · Unpredictable climate

## Introduction

Hibernation or prolonged torpor is characterized by pronounced reductions of body temperatures ( $T_b$ ) and energy expenditure (Wang 1978; Willis 1982a; French 1985; Geiser

et al. 1990; Buck and Barnes 2000). The hibernation season typically occurs during autumn and winter and is composed of a series of torpor bouts at low  $T_b$  (~5°C) lasting for several days or weeks that are interrupted by periodic, brief rewarming to high  $T_b$  (~37°C) lasting for several hours (French 1985; Geiser 2004). Although metabolic rates during torpor can be reduced to as little as ~1% of the basal metabolic rate in small species, energy expenditure during the entire hibernation season is usually ~10–20% of that in active individuals because of the energetically expensive periodic arousals that consume most of the energy during the hibernation season (Wang 1978; Thomas et al. 1990). Nevertheless, many hibernators can survive for months relying entirely on stored body fat (Willis 1982a; French 1985; Geiser et al. 1990; Nicol and Andersen 2007).

In high latitude northern hemisphere mammals, such as marmots and ground squirrels, hibernation is often strongly seasonal and largely restricted to the cold season when food availability and ambient temperatures ( $T_a$ ) are predictably low (Wang 1978; Geiser et al. 1990; Arnold 1993; Körtner and Geiser 2000). These species generally resist entering torpor during the spring/summer reproductive season (Buck and Barnes 2000; Körtner and Geiser 2000) and therefore the yearly cycle of many mammalian hibernators consists of about 6 months of hibernation followed by 6 months of reproduction, growth, and fattening for the next hibernation season (Willis 1982a; Körtner and Geiser 2000).

In contrast to this pattern, some other mammals, specifically bats and marsupials that occur in areas with unpredictable climates or depend on unpredictable food resources, are more opportunistic and may employ prolonged torpor at other times of the year when poor environmental conditions or low food availability require a reduction in energy expenditure (Turbill et al. 2003; Geiser 2004; Willis et al. 2006). For example, the insect,

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pollen- and nectar-eating Australian eastern pygmy-possum (*Cercartetus nanus*), an arboreal marsupial from woodlands and heath in southeastern Australia, can enter prolonged torpor at any time of the year (Geiser 1993; Song et al. 1997) and, importantly, has the ability to fatten enormously and rapidly when food is plentiful (Fig. 1). This marsupial appears to have evolved a strategy of extensive energy storage in the form of fat throughout the year whenever food is available combined with minimization of energy expenditure by employing torpor whenever food is limited. This may reflect the generally low energy availability and unpredictability of weather and flowering of trees on the Australian continent. The combination of opportunistic and aseasonal hibernation, and the ability by pygmy-possums to fatten extensively, make the species an ideal candidate for testing hypotheses about the duration of hibernation. Specifically, I investigated whether they could continue to display prolonged torpor for more than the widely observed 6 months, and, if so, for how long individuals could hibernate before body fat stores were depleted.

## Material and Methods

Eastern pygmy-possums ( $n=5$ ), originating from a population at ~1,000 m on the cool-temperate New England Tablelands of New South Wales (habitat details in Bladon et al. 2002), were maintained at  $T_a=20^\circ\text{C}$  under natural photoperiod. Animals were offered a surplus of food, which consisted of a mixture of high-protein baby cereal, honey, and water with added multivitamins/minerals; nuts and apples were also provided. In late austral autumn (21 May 2002) when body mass was high ( $53.8\pm3.6$  g SD, 2.6 times the lean adult mass), individually caged animals were transferred to a temperature-controlled cabinet at  $T_a=7.3\pm0.3^\circ\text{C}$  SD. This  $T_a$  is near the mean daily  $T_a$  of the New England Tablelands in winter and also approximates the  $T_a$  where the  $T_b$  and metabolic rate are near the minimum for the species and torpor bouts are long, and consequently energy expenditure is minimal (Geiser 1993; Song et al. 1997). The photoperiod of dim light (10 W incandescent bulb) was L10/D14, which approximates the shortest yearly photoperiod within the species' range in southeastern Australia. Water was freely available and food was withheld. Arousals were quantified by passive infrared detectors (Jaycar Electronics LA-5017; Körtner and Geiser 1995) that determined when each animal rewarmed periodically. These infrared detectors monitored the temperature profile of the cage and animal surface over an angle of  $90^\circ$  from the top of each cage; activity events and thus arousals were summed over 30-min intervals and stored on a data logger (Electronic Services Unit, University of New England). Arousals were confirmed by checking daily whether fine

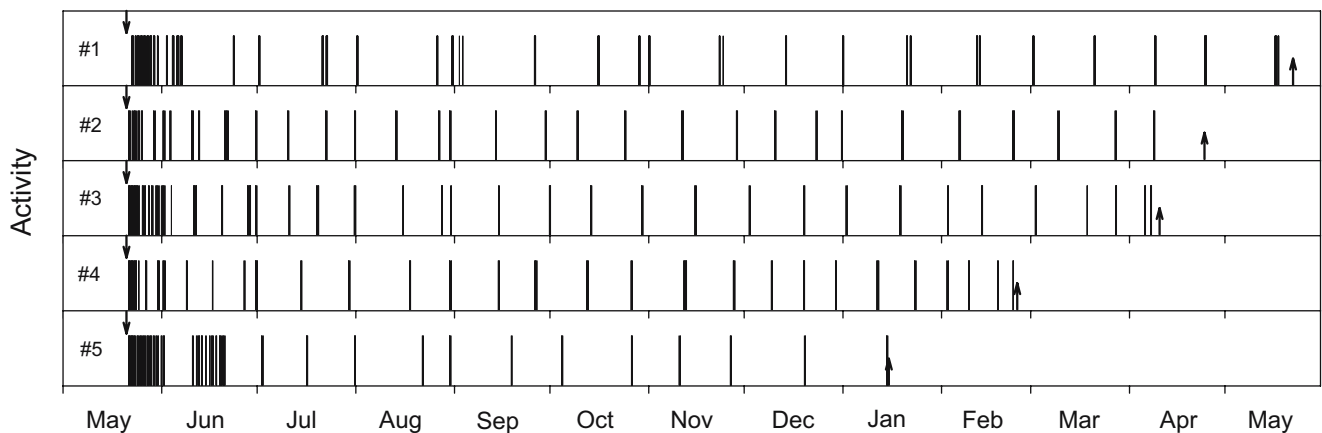


**Fig. 1** Lean-active (top), and fat-hibernating (bottom) pygmy-possums (*C. nanus*)

sawdust that had been placed on animals when they first entered torpor had been removed (Geiser and Kenagy 1988). Animals were weighed once a month and were removed from the experiment, maintained at  $T_a=20^\circ\text{C}$ , and offered food when their body mass reached  $20.9\pm0.5$  g SD, the lean mass of adults. Loss in body mass after the initial hibernation phase when gut content was voided was assumed to be entirely the result of fat metabolism (Willis 1982b; Florant 1998; Boyer and Barnes 1999; Carey et al. 2003) because animals had access to water and likely maintained body water content of fat-free tissues at a steady percentage (Fisher and Manery 1967; Thomas and Geiser 1997). All animals survived the hibernation season, with the exception of one individual that died several days after the reintroduction of food. Numerical values are expressed as individual means  $\pm$  SD.

## Results

All pygmy-possums hibernated within 1 day of exposure to  $T_a=7.3^\circ\text{C}$ . Initially, as in other hibernators, animals rewarmed frequently and torpor bouts were brief (<1 to 4 days, Fig. 2); during this time the loss of body mass was rapid ( $0.40\pm0.08$  g/day) because it involved both loss of gut content and fat mass and frequent arousals. After ~6 weeks of hibernation, torpor bouts had lengthened to  $12.7\pm1.8$  days (1 July to end of hibernation). Body mass loss over this time period was reduced to  $0.061\pm0.017$  g/day, which is equivalent to 2.4 kJ/day, assuming 100% fat metabolism (39.3 kJ/g fat; Schmidt-Nielsen 1997), and represents only ~2.5% of the predicted normothermic field



**Fig. 2** The hibernation season of five individuals of the eastern pygmy-possum. Vertical bars represent activity periods during arousals (measured by passive infrared detectors); periods between

bars represent torpor bouts. Arrow down shows the commencement of exposure to  $T_a=7.3^\circ\text{C}$  and food withdrawal, arrow up shows when food was offered and the end of hibernation measurements

metabolic rate (97 kJ/day for a 37-g marsupial, the mean mass of *C. nanus*; Degen and Kam 1995). In comparison to the minimum metabolic rate of torpid pygmy-possums (0.37 kJ/day; Song et al. 1997), arousals increased energy expenditure by 6.5-fold. In other words, arousals accounted for ~85% of the energy consumed during hibernation. The mass loss over the entire hibernation period (Fig. 2) was  $33.1 \pm 3.5$  g ( $0.107 \pm 0.009$  g/day). This is equivalent to 4.2 kJ/day and, although it is only ~4% of the predicted field metabolic rate (Degen and Kam 1995), it represents an overestimate because it includes the initial loss of gut content and likely protein (Willis 1982b).

The mean hibernation season lasted for  $310 \pm 50$  days. The longest hibernation season of an individual pygmy-possum lasted for 367 days (Fig. 2). A large proportion (52 and 63%) of the variation in the duration of the hibernation season among individuals was explained by the total body mass loss [hibernation season ( $d$ ) =  $710.87 - 3,744.6$  g/day mass loss;  $R^2=0.52$ ;  $p=0.168$ ] and initial body mass [hibernation season ( $d$ ) =  $285.6 + 11.08$  g initial mass;  $R^2=0.63$ ;  $p=0.168$ ], but neither regression was significant because of the small sample size ( $n=5$ ).

## Discussion

The study shows that mammalian hibernation can be extremely prolonged, even when an animal relies entirely on stored fat for energy metabolism. To my knowledge, this is the first observation of yearlong hibernation fuelled by body fat. Previous work on jumping mice (*Zapus princeps*, body mass 43 g), a rodent that also can continue to hibernate in spring and summer, reported hibernation periods lasting up to ~320 days (French 1985). This duration of hibernation was exceeded by three of the five pygmy-possums and was ~47 days shorter than the maxi-

mum hibernation period reported here. It is interesting to note that torpor bouts in *Z. princeps* in spring/summer were about half those in midwinter, whereas in *C. nanus*, torpor bout length remained long and rather constant after the maximum bout duration had been reached after ~6 weeks of hibernation, which likely explains why the latter were able to hibernate for a longer period.

The energy expenditure of *C. nanus* during the hibernation season was only ~4% of the field metabolic rate, which is extremely low. Previous estimates of the reduction of energy expenditure in ground squirrels and bats during the hibernation season in comparison to active individuals derived from respirometry measurements were two- to threefold that observed in the present study (Wang 1978; Thomas et al. 1990). This emphasizes that pygmy-possums are exceptionally frugal with energy use when hibernating. Whereas one gram of fat is sufficient to support the energy requirements of an active pygmy-possum for only 0.4 day, during the hibernation season the same amount of fat is sufficient to fuel metabolism for 16.4 days (a 41-fold increase in time). However, energy requirements during hibernation could be reduced to even lower levels were it not for periodic arousals. In the absence of arousals, pygmy-possums could hibernate for 106 days on a single gram of fat. Although the reasons for periodic arousal during hibernation are still not fully understood (Willis 1982a; Geiser and Kenagy 1988; Geiser et al. 1990; Thomas and Geiser 1997; Körtner and Geiser 1998; Milesi et al. 2001; Arendt et al. 2003), the enormous energetic investment suggests they must offer some ecological or physiological fitness benefits.

In the past, hibernation has been regarded as an adaptation primarily of placental mammals living in cold northern climates and was considered to be entirely absent in marsupials (Strahan 1983). Clearly, the view that hibernation is a cold climate adaptation is not supported

by a study on prolonged hibernation in a tropical primate in Madagascar (Dausmann et al. 2005) and the present study on a mammal that is found from subtropical to cool-temperate regions of eastern Australia. The view that marsupials cannot hibernate stems from the misconception that mammalian hibernation is continuous throughout winter, which obviously is not the case as all known hibernators rewarm periodically from torpor throughout the hibernation season (Willis 1982a). Nevertheless, it is truly astonishing that a marsupial from the comparatively warm Australia evolved the ability to hibernate opportunistically for up to 1 year, clearly longer than required in the field. This apparent overcompensation suggests that a large safety margin has been favored by natural selection in response to the unpredictability of rainfall and food availability of the continent.

**Acknowledgements** I would like to thank Nereda Christian, Rebecca Drury, and Wendy Westman for technical assistance as well as Bronwyn McAllan, Gerhard Körtner, and Chris Pavey for constructive comments on the manuscript. The Australian Research Council supported this work. Permits were provided by the New South Wales National Parks and Wildlife Service and the University of New England Animal Ethics Committee.

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