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ORIGINAL PAPER

Vertebrate diet decreases winter torpor use in a desert marsupial

Chris R. Pavey · Chris J. Burwell · Gerhard Körtner · Fritz Geiser

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Abstract One of the energetic benefits of daily torpor over prolonged hibernation is that it enables animals to regularly forage and, therefore, replenish food reserves between bouts of torpor. However, little is known about the diet of predators undergoing torpor or whether differences in prey composition among individuals influence torpor characteristics. Here, we test the hypothesis that prey composition affects winter torpor use and patterns of a population of carnivorous marsupial, the brush-tailed mulgara (*Dasycercus blythi*), in the Great Sandy Desert, Australia. Mulgaras in the study population captured a wide range of prey including vertebrates (mammals, reptiles, birds), seven insect orders, spiders and centipedes. The proportion of vertebrates in the diet was negatively correlated with both frequency of torpor use and maximum bout duration. This variation in torpor use with diet can be explained by the higher energetic content of vertebrates as well as their larger size. Even assuming uniform intake of prey biomass among individuals, those that subsisted on an invertebrate-dominated diet during winter apparently suffered energetic shortages as a result of the scarcity of invertebrate taxa with high energy content (such as insect larvae). Our study is the first to demonstrate a link between diet composition and daily torpor use in a free-ranging mammal.

Keywords Torpor · Diet · Energy content · Prey composition · Carnivorous marsupial

Introduction

Torpor is a controlled reduction of body temperature (T_b) and metabolic rate that functions to reduce energy expenditure during periods of food shortage or adverse environmental conditions (Brown and Bartholomew 1969; Boyer and Barnes 1999; Geiser 2004). Shallow daily torpor has the advantage over prolonged torpor (i.e. hibernation) in that daily arousals allow animals to feed and to continue important life history activities during the torpor season (Hiebert 1993). For example, small insectivorous/carnivorous marsupials (Dasyuridae) employ torpor frequently in winter (Körtner and Geiser 2009) but usually feed between bouts of torpor and even use daily torpor during the mating season and during development (Geiser and Masters 1994; Geiser et al. 2008).

The ecological and behavioural flexibility provided by the ability to undergo daily torpor is balanced by the need for insectivorous/carnivorous mammals to obtain sufficient energy from prey during bouts of foraging to replenish that lost by endogenous heat production and other physiological processes. Because daily torpor typically occurs during periods of food limitation, prey choice may be limited especially for insectivores given the reduction in invertebrate abundance during cooler weather. Currently, limited

C. R. Pavey (✉) · G. Körtner · F. Geiser
Centre for Behavioural and Physiological Ecology, Zoology,
University of New England,
Armidale 2351, Australia
e-mail: chris.pavey@nt.gov.au

C. R. Pavey · C. J. Burwell
Queensland Museum,
P.O. Box 3300, South Brisbane 4101, Australia

C. R. Pavey
Biodiversity Conservation, Northern Territory Government,
P.O. Box 1120, Alice Springs 0871, Australia

C. J. Burwell
Centre for Innovative Conservation Strategies and Griffith School
of Environment, Griffith University,
Nathan 4111, Australia

information is available on the dietary composition of free-ranging animals undergoing daily torpor. Further, it is not known whether variation in prey composition among individuals influences the expression and characteristics of daily torpor in the wild.

Here, we report the results of a study of the relationship between diet and torpor use in a marsupial, the brush-tailed mulgara, *Dasycercus blythi* (body mass 60–120 g; Dasyuridae), a nocturnal predator endemic to Australia that captures invertebrate and vertebrate prey (Chen et al. 1998; Masters 1998). *D. blythi* is threatened throughout its range and is listed as “Vulnerable” under national legislation in Australia. The species occupies sandy deserts and exhibits high site fidelity (Masters 1998, 2003). We assessed the diet of a population of mulgaras that we simultaneously radio-tagged to determine patterns of torpor use and examined the hypothesis that dietary variation among individuals resulted in variation in use of torpor.

Material and methods

The study site at Uluru-Kata Tjuta National Park (25° 20′ S, 131° 02′ E), Great Sandy Desert, Australia, consisted of a sand plain bordered by low dunes supporting *Triodia basedowii* dominated hummock grassland. Freshly deposited scats of *D. blythi* were collected during winter 2006 from animals in traps or from burrow entrances (if radio tracking established the identity of the burrow occupant). We collected scats (dimensions, 4–6 mm wide and 20–25 mm long) deposited by radio-tagged animals on multiple occasions until we had a sample of at least ten scats per animal. We radio-tagged nine animals and obtained a sample of ten or more scats from five of these (four males, one female). All animals entered torpor during the period of scat collection.

We placed each scat in a Petri dish and added four to five drops of 10% KOH directly to it, before teasing it apart with fine dissecting needles and covering it in 70% ethanol. We systematically searched each scat for identifiable material under a low-power (6.4 to 40 magnification) binocular microscope. Prey fragments were identified to the lowest taxonomic level possible. Material was identified by reference to collections in the Queensland Museum, Brisbane. Further, mammal hair was collected and sent for specialist identification (Barbara Triggs, Euroa, Victoria, Australia). This enabled identification of mammalian prey that was otherwise present only as bone fragments in the scats. The volume of each prey item in each pellet was calculated by spreading all the identifiable fragments in a Petri dish with graph paper underneath and estimating for each prey item the space (area) occupied by its fragments (including exoskeleton, hair, scales, feathers). Percentage volume was estimated to the nearest 5%. Taxa that contributed less than 2.5% were not included in percentage volume estimates. We then calculated the mean percentage volume of each prey item in the diet of each individual.

Torpor data were obtained from animals implanted intraperitoneally with sterilised temperature-sensitive radio transmitters (calibrated to the nearest 0.1°C; mass 2.4–3.9 g; <5% of body mass; Sirtrack, Havelock, New Zealand) under general oxygen/isoflurane anaesthesia. We held animals overnight following surgery and provided them with food *ad libitum* before releasing them the next evening at the capture site. All procedures were approved by the University of New England Animal Ethics Committee (AEC06/046), Armidale, Australia. Each morning, during the 3 h immediately post-sunrise, we radio-tracked each mulgara to its diurnal shelter using handheld receivers and antennae. A data logger unit was placed close by to record the interval between transmitter pulses every 10 min. Logged data were later downloaded to a PC and converted to T_b using the transmitter calibration (Körtner and Geiser 2000). Torpor was defined by a $T_b \leq 30°C$ (Körtner et al. 2008) and torpor bout duration as the time T_b remained below 30°C.

We used linear regression analyses to examine the relationship between dietary composition (percentage volume of vertebrate, invertebrate and plant material) and three torpor variables: frequency of torpor use (%), maximum bout duration (h) and minimum T_b (°C). Frequency of torpor use was defined as the percentage of days radio-tracked during which an animal entered torpor. We used this measure rather than the hours spent in torpor to represent torpor frequency because we considered it more representative of torpor use across the tracking period. Because scats were collected opportunistically during the duration of the study and consecutive collection dates varied among individuals, we did not use repeated-measures analyses. Torpor data used in the analyses were restricted to those collected during the period of scat collection for each individual. Ambient temperature (T_a) was not used in analyses because temperatures in burrows where torpor took place differed from surface T_a and the actual depths of torpid animals, and hence the burrow temperatures, were unknown (refer Körtner et al. 2008 for details).

Results

Mulgaras fed on a diverse range of prey including arthropods, vertebrates and plants (seeds and stem fragments; Table 1). Arthropod prey consisted of centipedes, spiders and seven insect orders (Coleoptera, Diptera, Heteroptera, Hymenoptera, Isoptera, Lepidoptera, Orthoptera). Major invertebrate prey, measured by percentage volume, were Orthoptera, Coleoptera and Formicidae (Table 1). Both

Table 1 Percentage volume of major prey categories in the diet of male and female mulgaras, *D. blythi*, at Uluru-Kata Tjuta National Park, Australia in winter 2006

Prey category	Male 1, 92.6g (10)	Male 2, 101.7g (10)	Male 3, 80.9g (12)	Male 4, 73.4g (10)	Female 1, 61.9g (10)
Vertebrate unidentified	1.6	1.6	20.1	29.1	1
Mammal	9.4	2.7	26.8	0.7	2.8
Reptile	7.1	18.1	18	25.5	8.5
Bird	21.2	0.1	8.3	0	0
Vertebrate sub-total	39.3	22.5	73.2	55.3	12.3
Insect larvae	0.5	0	0	0	0.5
Coleoptera (beetle)	7.8	8	4.2	1.7	2.0
Heteroptera (bug)	6.0	8.0	3.8	0	0
Orthoptera (grasshopper)	43.0	57.0	15.4	11.5	32.7
Formicidae (ant)	0.5	0	4.9	7.5	7.6
Insect other	1.3	0	0.4	1.7	2.0
Araneae (spider)	0.7	2.7	0.1	0.6	0.6
Chilopoda (centipede)	0	0.1	0.1	0	31.0
Invertebrate sub-total	52.6	75.4	27.3	43.8	86.5
Plant	8.6	2.5	0.9	1.6	2.6

Body mass is given for each animal followed by number of scats examined in parentheses. All invertebrates captured, unless otherwise mentioned, were adults

flying and non-flying forms of insects were captured. Flightless forms included moth and beetle larvae and worker ants and termites.

Vertebrate prey consisted of mammals (carnivorous marsupials, Dasyuridae; rodents, Muridae), reptiles (dragons, Agamidae; skinks, Scincidae; monitors, Varanidae) and unidentified birds. Mammals and reptiles were consumed by all individuals and birds by three of the radio-tagged mulgara (Table 1).

Dietary composition (percentage volume) varied among individuals (Table 1). Torpor frequency and maximum bout duration showed a strong negative relationship with the incorporation of vertebrates in the diet (Fig. 1; torpor frequency [%]=109.19−1.24 vertebrate [%], $F_{1,\ 3}$=19.76, R^2=0.87, p=0.02; Fig. 2; maximum bout duration [h]= 16.63−0.25 vertebrate [%], $F_{1,\ 3}$=13.15, R^2=0.81, p=0.04). However, the relationship between minimum T_b and incorporation of vertebrates was not significant (Fig. 3; $F_{1,\ 3}$= 4.64, R^2=0.61, p=0.12). Mulgara body mass (61.9–101.7 g) and incorporation of vertebrates in the diet were not correlated ($F_{1,\ 3}$=0.002, R^2=0.0006, p=0.96). Consumption of plants by volume was <10% in all individuals (Table 1), and incorporation of plants in the diet was not correlated with torpor frequency (R^2=0.25, p=0.39), maximum bout duration (R^2=0.0003, p=0.98) or minimum T_b (R^2=0.01, p=0.88).

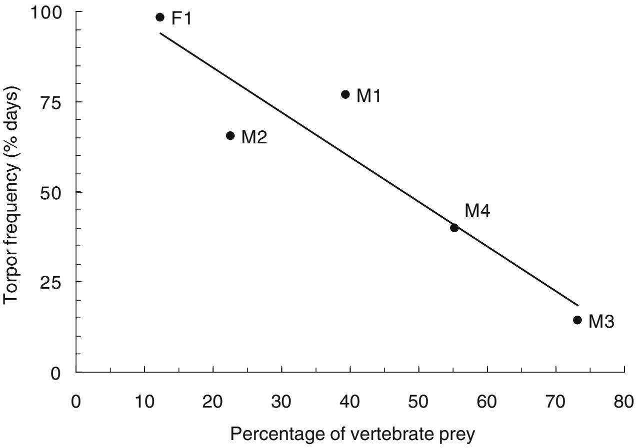

Fig. 1 Relation between frequency of torpor use and consumption of vertebrates (torpor frequency [%]=109.19−1.24 vertebrate [%], R^2= 0.87, p=0.02). Abbreviations: *M*, male; *F*, female

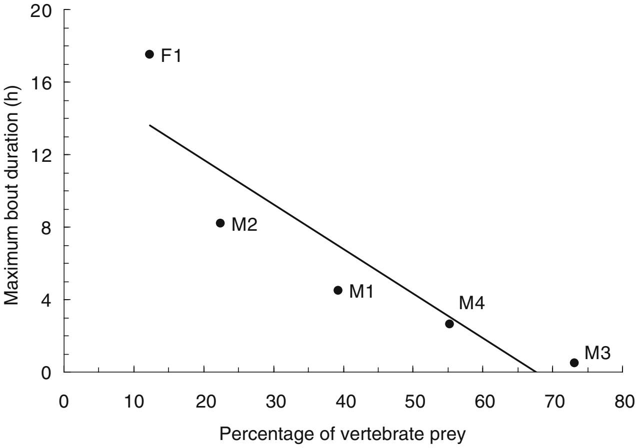

Fig. 2 Relation between maximum torpor bout duration (h) and consumption of vertebrates (maximum bout duration [h]=16.63−0.25 vertebrate [%], R^2=0.81, p=0.04). Abbreviations: *M*, male; *F*, female

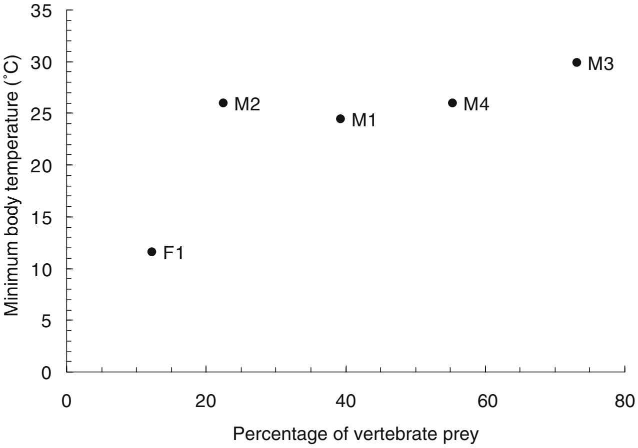

Fig. 3 Relation between minimum T_b (°C) during torpor and consumption of vertebrates (minimum T_b (°C)=14.58+0.22 vertebrate [%], R^2=0.61, p=0.12). Abbreviations: *M*, male; *F*, female

Discussion

Our study is the first to examine the prey composition during the torpor season of individuals of a population of marsupial carnivore. Because we collected dietary and torpor data from the same individuals, we were able to assess the relationship between prey composition and the use of torpor. In contrast to previous research on this species, where scats have been collected across multiple years and seasons (Chen et al. 1998; Masters 1998), the current study was carried out during a 10-week period over winter of 1 year.

Our results show that the incorporation of vertebrate prey in the diet of free-ranging mulgaras decreased with increasing frequency of torpor use and maximum torpor bout duration. The relationship between diet and minimum T_b was not significant; however, the only mulgara with <20% vertebrates in the diet (F1) had a minimum T_b over 10°C lower than other individuals. This result suggests the presence of a threshold level of vertebrates in the diet below which T_b falls considerably.

The finding of an effect of diet composition on torpor expression provides a plausible explanation for observations of inter-individual variation in use of torpor in wild populations experiencing similar environmental conditions (Brigham et al. 2000; Christian and Geiser 2007). Mulgaras in the study population likely entered torpor during winter as a means to reduce energy expenditure (Geiser and Masters 1994; Körtner et al. 2008). If we assume that energy is limited in our study system, our finding that animals with a higher proportion of vertebrates in the diet entered torpor less frequently and for shorter periods provides evidence of the importance of vertebrate prey in maintaining energy balances during winter. This is likely a consequence of the higher, on average, energy content of vertebrates, measured as kilojoule per gram dry mass, compared to invertebrates, as well as their larger size. Although energy content varies across taxa, the energy content of vertebrate prey is typically 1–2 kJ/g higher than that of invertebrates (Knox et al. 2001; Grayson et al. 2005; Willmer et al. 2005). Therefore, even if the biomass of prey consumed is constant across individuals, those with an invertebrate-dominated diet will have a lower energy intake than those with a vertebrate-dominated diet.

The energy content of invertebrates varies both among taxa and, within a species, with life stage and reproductive form (Bell 1990). Larval stages generally and reproductive forms of social insects including termites and wasps have the highest energy content because of a higher fat content than other life stages (Bell 1990). Therefore, mulgara should select invertebrates high in energy content when these are available. However, in comparison to year-round sampling at the same site when 45% (males) and 35% (females) of invertebrates reported in mulgara scats were taxa with high energy content such as larvae of moths and beetles (Masters 1998), during our winter-only study, these taxa very rarely appeared. This rarity of insect larvae in the diet in winter is likely the result of a decrease in availability (or complete absence) of these life stages. Both overall activity and reproduction of desert invertebrates decline with decreasing temperatures in winter (e.g., Holm and Edney 1973).

Most of the invertebrate taxa frequently captured by mulgaras in our samples (adult Orthoptera, adult Coleoptera and worker ants; Table 1) have energy contents that are at the lower end of the recorded range for invertebrates (Kunz 1988; Bell 1990). Therefore, it is likely that mulgaras subsisting on an invertebrate-dominated diet during winter in the Great Sandy Desert required frequent and long daily torpor to reduce energy expenditure to combat a negative energy balance.

An alternative explanation of our data is that the variation in use of torpor could be related to specific food compounds in the diet (Geiser and Kenagy 1987; Florant 1998; Frank 1994; Fietz et al. 2003). It is known that polyunsaturated fatty acids (PUFAs), especially those of the n-6 and n-3 series, influence torpor variables (Ruf and Arnold 2008). Specifically, increased PUFA content in the diet increases the proportion of individuals entering torpor, increases torpor bout duration and decreases T_b and mass loss during torpor (summarised in Munro and Thomas 2004). Under this scenario, the patterns we observed could occur if vertebrate prey has lower PUFA levels than invertebrates irrespective of the energy content of the prey. However, PUFA content of vertebrates overlaps with that of invertebrates and in both also reflects that of their diet (Geiser 1990; Schalk and Brigham 1995; Falkenstein et al. 2001). Thus, while dietary fats may have a possible effect on torpor use in mulgaras, it is well established that energy availability strongly affects daily torpor use, which suggests that in our study system, torpor expression was predominantly governed by energetic constraints.

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