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Do Patterns of Torpor Differ between Free-ranging and Captive Mammals and Birds?

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Abstract. Most studies on torpor in mammals and birds have been conducted in the laboratory. We compared whether patterns of torpor of several mammals and birds differ between the laboratory and field. Our comparison shows that in most species patterns of torpor in the laboratory differ substantially from those in the field. Some species, even if they use torpor extensively in the field, appear most reluctant to enter torpor in captivity. Moreover, torpor in the field is often more frequent, deeper, and longer than in captivity. Our comparison suggests that laboratory studies are likely to underestimate use and depth of torpor in the wild and thus may underestimate its impact on energy expenditure and survival.

Introduction

Data derived from laboratory studies on hibernation and daily torpor are often used to make predictions about energetics, survival, and fitness in the wild, although environmental conditions and the physical status of animals in the laboratory may differ substantially from those in the field. To our knowledge there has been no systematic comparison that explores the feasibility of such extrapolations. Here we compare torpor patterns (ie. seasonal torpor use, temporal organisation, depth, length) between captive and free-ranging heterothermic endotherms to see whether and in which groups or species they differ and discuss why this may be so.

Methods

The observations we used to compare torpor patterns in free-ranging and captive mammals and birds are summarised in Tables 1 & 2. In our comparison heterothermic mammals and birds were divided into hibernators (species that can enter prolonged torpor) and daily heterotherms (species that enter daily torpor

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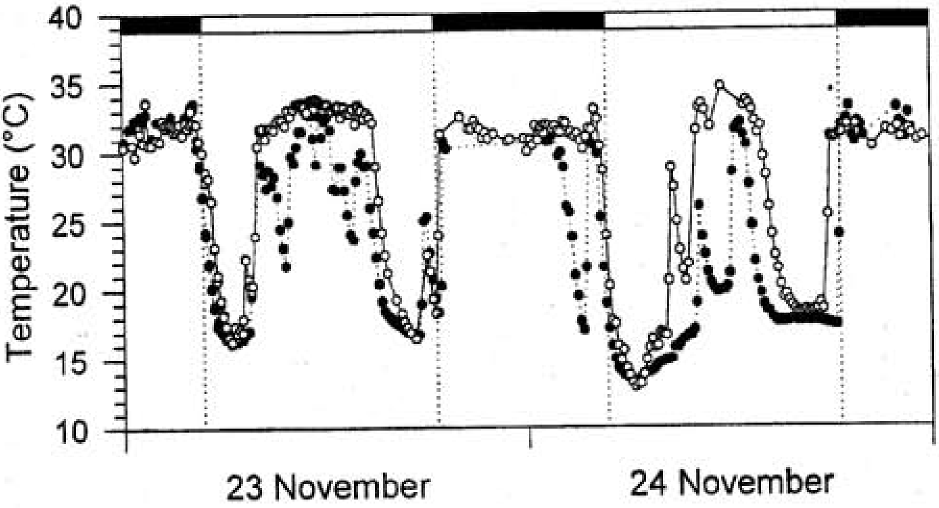

Fig. 1. Skin temperature fluctuations of two male bats (*Nyctophilus geoffroyi*, 7g) in the field over two days in summer (T_a 9-24 °C). Note the frequent arousals around midday and torpor re-entry in the afternoon.

exolusively)(Geiser and Ruf 1995) to see whether there are general differences between prolonged and daily torpor. It is possible that the two groups differ because hibernators usually fatten before the hibernation season, whereas daily heterotherms often lose mass, and body mass often varies between captive and free-ranging animals. Most data were taken from the literature, but unpublished observations on sugar gliders (*Petaurus breviceps*), owlet-nightjars (*Aegotheles cristatus*) and long-eared bats (*Nyctophilus geoffroyi*) are also used. Captive individuals measured here came from the same areas where data on the free-ranging individuals were collected. Sugar gliders were kept in outdoor aviaries under natural photoperiod and fluctuations of ambient temperature (T_a); body temperatures (T_b) were measured in the laboratory using temperature-telemetry (intraperitoneal transmitters; Geiser et al. 1996; Körtner and Geiser 2000a). The captive owlet-nightjar was also kept in an outdoor aviary where T_b (intraperitoneal transmitters) was measured in autumn/winter using temperature-telemetry (Körtner and Geiser 2000a). Free-ranging long-eared bats were fitted with external transmitters glued onto the interscapular skin for measurement of skin temperature in summer.

Results

Hibernators: Patterns of torpor in the field and captivity in several hibernators differed, whereas in others only minor differences were observed (References in Table 1). In most hibernators, hibernation in the laboratory and field were qualitatively similar, but quantitative differences were apparent. In six of nine hibernators (Table 1) torpor bouts were much shorter in the laboratory than in the field. Moreover, the timing of arousals differed between captive and free-ranging

Table 1. Observations on patterns of torpor in free-ranging and captive hibernators (species that can enter prolonged torpor)

Birds	**Field**	**Captivity**	**References**
Phalaenoptilus nuttallii Poorwill (50g)	Prolonged hibernation, multiday torpor, T_b to 5 °C	Torpor bouts < 10 h, T_b to 5 °C	Bartholomew et al. 1957; Brigham 1992 French 1993 Brigham et al. 1999
Monotremes			
Tachyglossus aculeatus Echidna (5,000g)	Prolonged hibernation, multiday torpor, periodic arousal	Reluctant to hibernate. Occasional brief torpor bouts	Augee & Ealey 1968 Grigg et al. 1992
Marsupials			
Burramys parvus mountain pygmy-possum (50g)	Prolonged hibernation, multiday torpor, periodic arousal	Wild-caught: similar Hibernation to field. Laboratory-bred: No torpor at all	Geiser et al. 1990 Geiser & Broome 1991; Körtner & Geiser 1998a
Bats			
Myotis lucifugus little brown bat (5g)	Mean torpor bout duration 19.7 days	Mean torpor bout duration 12.7 days	Thomas 1993
Eptesicus fuscus big brown bat (22g)	Arousals and activity over a wide range of hours	Arousals coincide with beginning of activity phase	Twente & Twente 1987 Thomas 1993
Nyctophilus geoffroyi Long-eared bat (7g)	Prolonged torpor on cool summer days, frequent arousal near midday, active for most of night	Prolonged torpor rare, frequent arousal after lights off, torpid for most of night and day	Turbill et al. 1999 Geiser and Brigham 2000 present study
Rodents			
Spermophilus richardsonii ground squirrel (400g)	Prolonged hibernation, multiday torpor, periodic arousal	Hibernation less regular, torpor bouts shorter, less seasonal bout duration change	Wang 1978
Spermophilus columbianus ground squirrel (700g)	Maximum mean torpor bout duration 27.9 days	Maximum mean torpor bout duration 17.7 days	Twente et al. 1972 Young 1990
Marmota marmota alpine marmot (4,000g)	Prolonged hibernation, multiday torpor, synchronised periodic arousals, T_b to 2.5 °C	Prolonged hibernation, but asynchronous periodic arousals in groups, T_b to 5 °C	Arnold 1988, 1993, 1995 Ortmann 1997 Ruf and Arnold 2000

bats (*Eptesicus fuscus*) and in hibernating groups of alpine marmots (*Marmota marmota*) arousals in the laboratory were occasionally asynchronous among individuals whereas in the wild they were synchronised (Table 1). However, with the exception of *M. marmota*, no major differences were observed between the minimum T_b of torpid hibernators (Table 1).

Long-eared bats (*Nyctophilus geoffroyi*) entered multiday torpor in the field even in summer when T_a was low (8-18 °C), but in the laboratory usually

Table 2. Observations on patterns of torpor in free-ranging and captive daily heterotherms (species that display daily torpor exclusively)

Birds	Field	Captivity	References
Aegotheles cristatus owlet-nightjar (40g)	Frequent daily torpor for about 4-6 h, T_b to 22 °C	Occasional daily torpor for < 3 h, T_b to 26 °C	Brigham et al. 1999 present study
Podargus strigoides Tawny frogmouth (500g)	Frequent shallow torpor for up to 7 h, T_b to 29 °C	No torpor at all, minimum T_b > 37 °C	Körtner & Geiser 1998b Bech & Nicol 1999 Brigham et al. 1999
Oreotrochilus estella hummingbird (8g)	Minimum T_b 6.5 °C	Minimum T_b 20.3 °C	Carpenter 1974 Krüger et al. 1982
Marsupials			
Sminthopsis crassicaudata dunnart (17g)	Torpor (in 5 bouts observed) for several hours from about sunrise	Timing of torpor similar to limited field observations	Geiser and Baudinette 1987 Frey 1991
Petaurus breviceps sugar glider (120g)	Torpor on cold days for > 20 h, T_b to 10.5 °C	Shallow and brief torpor after starvation, T_b >18 °C	Körtner & Geiser 2000a Present study
Rodents			
Peromyscus leucopus white-footed mouse (20g)	Torpor entry (in 2 bouts observed) near sunrise, T_b to 18 °C	Temporal organisation and T_b similar to that in field	Vogt et al. 1983

rewarmed from torpor at the beginning of the dark phase even at low T_a. At higher T_a (9-24 °C), long-eared bats in the field often remained active for most of the night in summer (Fig. 1) whereas captive bats re-entered torpor after brief activity periods of about 2 hours. Long-eared bats in the field often rewarmed near midday (Fig. 1) when T_a increased, whereas bats kept in the laboratory at constant T_a always remained torpid. Moreover, long-eared bats in the field often re-entered torpor in the late afternoon (Fig. 1), which appears to be a common pattern in the field, but not in the laboratory.

In three hibernators, both qualitative and quantitative differences between field and laboratory studies were observed. Poorwills and echidnas entered prolonged torpor only in the field and captive echidnas were reluctant to enter torpor at all.

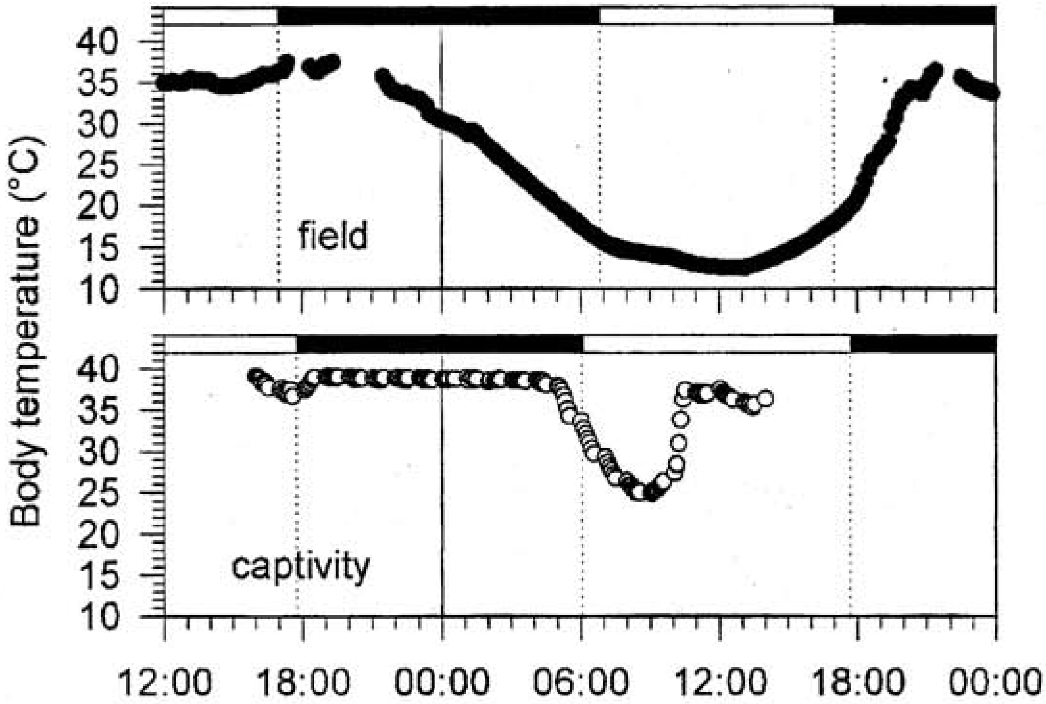

Fig. 2. Body temperature fluctuations of a free-ranging and a captive sugar glider in autumn/winter. The torpor bout for the captive glider was one of the longest observed and was measured at T_a 14 °C; the T_a for the free-ranging glider was 1.3 to 19.0 °C.

Wild-caught mountain pygmy-possums held at similar T_a as experienced by the wild populations, showed similar torpor patterns to those in the wild. In contrast, captive-bred mountain pygmy-possums, which were kept under identical conditions as the hibernating wild-caught individuals, did not show a seasonal change in body mass, were lighter than free-ranging individuals, and never entered torpor.

Daily heterotherms: Although published information about daily torpor in the field is extremely scant, the available literature and our unpublished data suggest that torpor bouts in the field are longer (usually about twice as long) and, in contrast to most hibernators, also substantially deeper than in the laboratory (References in Table 2). Pronounced differences in the minimum T_b of more than 5 °C have been observed for the tawny frogmouth (*Podargus strigoides*), a hummingbird (*Oreotrochilus estella*), and the sugar glider (*Petaurus breviceps*) (Table 2). Frogmouths regularly entered torpor in the wild, but never did so in captivity. Sugar gliders, which were about 30% heavier in the laboratory than in the field, were reluctant to enter torpor in captivity, did so only after starvation, and torpor was brief and shallow. In the field, torpor in sugar gliders was frequent, lasted for over 20 hours and T_b was much lower than in the laboratory (Fig. 2). Captive owlet-nightjars also entered torpor less frequently and torpor was more shallow and shorter than in the field (Fig. 3). Two species (*Sminthopsis crassicaudata* and *Peromyscus leucopus*) appear to show a similar pattern of

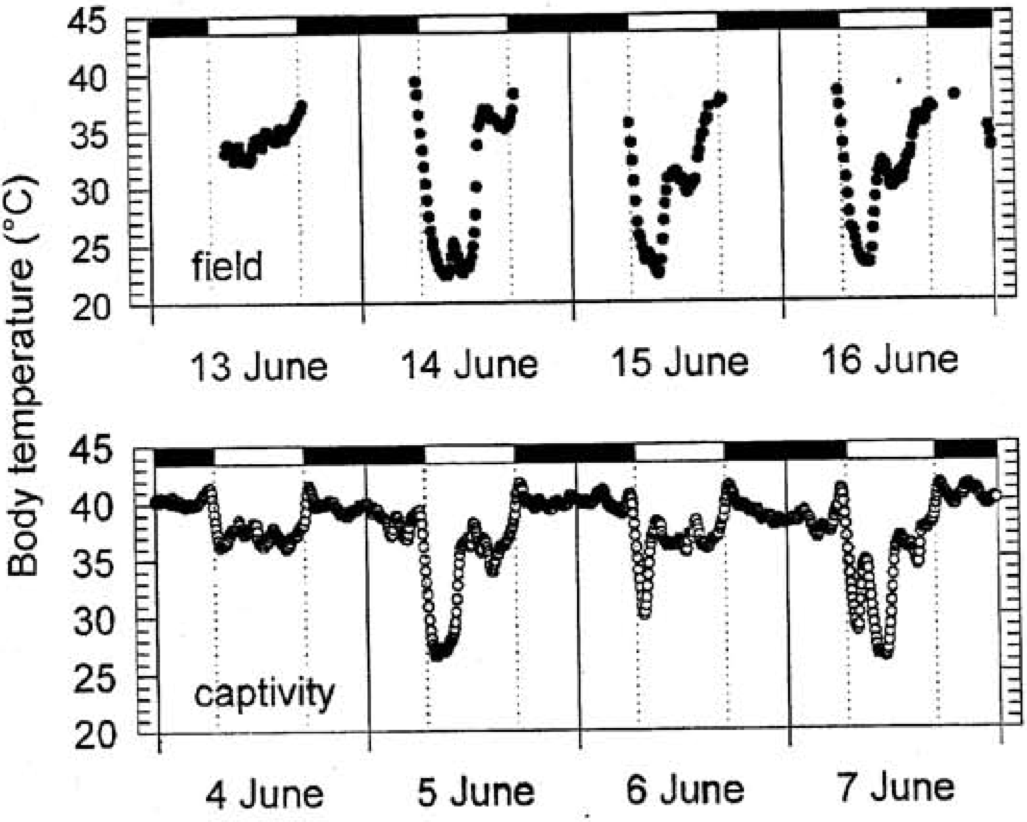

Fig. 3. Body temperature fluctuations of a free-ranging and a captive owlet-nightjar (outdoor aviary) in winter. Note the deeper and longer torpor bout in the free-ranging in comparison to in the captive individual.

torpor in the wild and in captivity although the data for free-ranging individuals are extremely few (Table 2).

Discussion

Our comparison shows that patterns of torpor differ between most free-ranging and captive mammals and birds. However, such differences are not uniform among species. Hibernators with strong circannual cycles, such as marmots and ground squirrels, exhibit hibernation that is qualitatively similar, however, differences particularly with respect to timing of torpor and bout duration appear common. Obviously, this has implications for laboratory studies on the temporal organisation of torpor (Körtner and Geiser 2000b). Hibernators with less pronounced circannual cycles appear to be more strongly affected by captivity with some species, such as echidnas and captive-bred mountain pygmy-possums, displaying only short torpor bouts or no hibernation at all. In bats, mainly the temporal organisation of activity and torpor appear to be altered by captivity. However, most of those hibernators that do enter torpor in captivity show minimum T_b that are similar to those in the field suggesting that the thermoregulatory threshold for T_b of torpid hibernators is not strongly affected by captivity.

In most daily heterotherms, the temporal organisation, duration and depth of torpor appear to be affected by captivity. But again, effects of captivity differ among species (see Table 2). Since daily heterotherms often enter torpor only at low body mass, whereas hibernators often only enter torpor when fat, the usually larger mass in captive individuals is likely to have a greater impact on daily torpor than on hibernation. The effect on the minimum T_b on daily torpor in captivity is likely caused by the persistent awareness of torpid daily heterotherms some of which, in contrast to hibernators in deep torpor, are capable of locomotion and feeding even when torpid.

Our comparison suggests that captive studies may underestimate the use, depth, and length of torpor by animals. This implies that further studies on torpor in the wild will reveal a more widespread and intensive use of torpor than previously thought. Thus, only further field studies can clarify how important torpor is for survival and fitness in the wild.

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