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Daily torpor and hibernation in birds and mammals

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ABSTRACT

Many birds and mammals drastically reduce their energy expenditure during times of cold exposure, food shortage, or drought, by temporarily abandoning euthermia, i.e. the maintenance of high body temperatures. Traditionally, two different types of heterothermy, i.e. hypometabolic states associated with low body temperature (torpor), have been distinguished: daily torpor, which lasts less than 24 h and is accompanied by continued foraging, *versus* hibernation, with torpor bouts lasting consecutive days to several weeks in animals that usually do not forage but rely on energy stores, either food caches or body energy reserves. This classification of torpor types has been challenged, suggesting that these phenotypes may merely represent extremes in a continuum of traits. Here, we investigate whether variables of torpor in 214 species (43 birds and 171 mammals) form a continuum or a bimodal distribution. We use Gaussian-mixture cluster analysis as well as phylogenetically informed regressions to quantitatively assess the distinction between hibernation and daily torpor and to evaluate the impact of body mass and geographical distribution of species on torpor traits. Cluster analysis clearly confirmed the classical distinction between daily torpor and hibernation. Overall, heterothermic endotherms tend to be small; hibernators are significantly heavier than daily heterotherms and also are distributed at higher average latitudes (~35°) than daily heterotherms (~25°). Variables of torpor for an average 30 g heterotherm differed significantly between daily heterotherms and hibernators. Average maximum torpor bout duration was >30-fold longer, and mean torpor bout duration >25-fold longer in hibernators. Mean minimum body temperature differed by ~13°C, and the mean minimum torpor metabolic rate was ~35% of the basal metabolic rate (BMR) in daily heterotherms but only 6% of BMR in hibernators. Consequently, our analysis strongly supports the view that hibernators and daily heterotherms are functionally distinct groups that probably have been subject to disruptive selection. Arguably, the primary physiological difference between daily torpor and hibernation, which leads to a variety of derived further distinct characteristics, is the temporal control of entry into and arousal from torpor, which is governed by the circadian clock in daily heterotherms, but apparently not in hibernators.

Key words: daily torpor, hibernation, heterothermy, energy savings, hypothermia, hypometabolism, endotherms, thermoregulation, over-wintering.

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I. INTRODUCTION

Birds and mammals spend a large proportion of their energy expenditure on maintaining high euthermic body temperatures (T_b) (see section VIII (i.e. Appendix) for definitions of key terms). This optimises many physiological functions, such as mobility, digestion and brain function, but becomes costly during periods of cold exposure, which require substantial heat production that is impossible to sustain during food shortages. The only 'logical solution' (Schmidt-Nielsen, 1979) for animals that cannot escape harsh environmental conditions by migration is to suspend the maintenance of high T_b and employ a mode of living that saves energy. This is the strategy used by many birds and mammals that employ hypometabolism, i.e. periods of profoundly reduced metabolic rate (MR) and T_b, which typically occur on a seasonal basis (Lyman *et al.*, 1982). States of profound but controlled reductions of MR and T_b in endotherms are called torpor (cold-lethargy). Birds and mammals that use torpor are traditionally classified as either hibernators or species using daily torpor (i.e. daily heterotherms). The main distinguishing trait that is often invoked is that species regarded as hibernators are capable of consecutive multiday torpor bouts, lasting on average more than a week, whereas torpor in animals traditionally viewed as daily heterotherms usually lasts only between ∼3 and 12 h (Geiser & Ruf, 1995). Other traits that imply functional differences are the minimum MR during torpor (TMR_{min}), which in animals categorized as hibernators appears to be much lower, as well as the minimum T_b ($T_{b\,min}$) that is defended during torpor, which seems higher in species regarded as daily heterotherms, although the variation among species in $T_{b\,min}$ is large. It appears that body mass also differs between the two categories with species conventionally viewed as hibernators being significantly larger than species classified as daily heterotherms (Geiser & Ruf, 1995).

In recent years, the development of miniature temperature data loggers and transmitters has resulted in a large quantity of new data on torpor expression in free-living animals. Obviously, these species are subject to natural ambient conditions, especially to short-term fluctuations in ambient temperature (T_a) which may hamper the detection of the actual capabilities of species: (*i*) variables usually measured in the field, such as T_b and torpor bout duration (TBD), are strongly affected by T_a (e.g. Twente & Twente, 1965; Geiser & Kenagy, 1988; Bieber & Ruf, 2009; Stawski & Geiser, 2010). During torpor, T_b decreases with T_a over a wide range of T_a until $T_{b\,min}$ is reached (e.g. Buck & Barnes, 2000; Arnold *et al.*, 2011). (*ii*) Whereas species conventionally categorized as hibernators may remain torpid for more than a month at low T_a and thus T_b, the duration of torpor bouts shortens with increasing T_a. At high T_a between 20° and 30°C, where some of these species still express torpor, torpor bouts often last only for hours and superficially appear to be indistinguishable from the traditional category of daily torpor (e.g. Song, Körtner & Geiser, 1997; Bieber & Ruf, 2009). (*iii*) Many species are sensitive to fluctuating T_a as usually experienced in the wild and will not remain torpid if T_a is not stable (Henshaw, 1970). Thus, patterns of torpor observed in free-ranging animals are often not an indication of the animals' physiological capability, but rather reflect its response to current ambient conditions. Consequently, these data may not be suitable for meaningful interspecific comparisons of physiological capabilities. With regard to laboratory measurements, a commonly overlooked problem with quantitatively characterising torpor patterns is that species capable of very long torpor episodes often require a number of short torpor bouts before they express multiday bouts (Strumwasser, Schlechte & Streeter, 1967; Geiser, 2007). Laboratory measurements of torpor, especially when respirometry is involved, typically last for around 1 day or less and even species traditionally classified as hibernators under these conditions usually express torpor that lasts only for hours rather than days (Song *et al.*, 1997).

Despite these shortcomings, data from the field under varying thermal conditions and short-term measurements in the laboratory have been used to question whether 'hibernators' and 'daily heterotherms' are two distinct functional groups or simply a single group of heterotherms characterized by a continuum of variables (Wilz & Heldmaier, 2000; Lovegrove, Raman & Perrin, 2001; Canale, Levesque & Lovegrove, 2012; Boyles *et al.*, 2013). For instance, using indices of heterothermy in a recent comprehensive study, Boyles *et al.* (2013) found that, with the exception of permanent homoeotherms, T_b variation was otherwise largely continuously distributed, and concluded that the traditional classification of mammals as hibernators *versus* daily heterotherms is 'clouded or possibly misleading'

(p. 1029). Here, we re-address this controversy by analysing physiological variables characterising torpor in both birds and mammals. In contrast to Boyles *et al.* (2013), however, we focused on extremes of characteristics such as $T_{b\,min}$ or maximum TBD (TBD_{max}) in order to assess species-specific physiological capabilities, rather than short-term responses to environmental conditions. Compared with previous studies on these variables (e.g. Geiser & Ruf, 1995) we investigated a much larger dataset now available for 214 heterothermic bird and mammal species.

We hypothesized that variables characterizing each species' capacity for torpor would support the classical distinction between daily torpor and hibernation. Specifically we hypothesized: (*i*) that frequency distributions of TBD_{max} [and possibly also mean TBD (TBD_{mean})], TMR_{min}, the relative reduction of TMR below basal metabolic rate (BMR) (TMR_{rel},) and $T_{b\,min}$ would all show clearly bimodal patterns. (*ii*) That statistical cluster analysis based on the above variables would support the existence of two distinct subgroups among heterotherms and show a high degree of coherence with the traditional classification. (*iii*) That phylogenetically informed regression analysis within hibernators and daily heterotherms, if maintaining these categories was justified by results of the above analyses, would support earlier findings (e.g. Geiser & Ruf, 1995; Geiser, 2004) suggesting that: (*a*) mean body mass of hibernators is higher than in daily heterotherms; (*b*) TBD_{max} (and probably also TBD_{mean}) is different between the two subgroups; (*c*) both TMR and $T_{b\,min}$ show allometric relationships to body mass with distinctly different intercepts and/or slopes in the two categories. (*iv*) That similar to results for general heterothermy indices (Boyles *et al.*, 2013), the maximum depth or duration of torpor may increase with latitude of the species' geographical range.

II. METHODS

Data were collected using primary literature on 43 birds and 171 mammals. As a 'working hypothesis' all species were initially classified according to TBD_{max} as reported by the respective authors or determined by us (see below; TBD_{max} <24 h, or $TBD_{max}>24$ h; Table 1) and preliminarily labelled 'daily heterotherms' (42 birds, 78 mammals) or 'hibernators' (1 bird, 93 mammals). The only exception to this rule was classifying *Sminthopsis macroura* as a daily heterotherm, despite a reported TBD_{max} of 25.9 h, which was observed only once (see Section IV.2). Our initial classification was identical to that of the original authors of the studies evaluated, except for *Elephantulus myurus,* as it showed a TBD_{max} of 39 h, but has been classified as a daily heterotherm previously (see sources in Table 1). If data for a species were available in more than one publication, the season in which torpor was most pronounced, or the reference with the most extensive data set was used. For TBD the maximum values and mean values as reported were used. However, TBD_{mean} was often not reported. In these cases we either calculated TBD_{mean} from raw data obtained during 'mid-hibernation' presented in figures, or, if only a range of torpor bout durations was provided, we estimated the mean from the average minimum and maximum given. TBD_{max} was difficult to define in a few species (e.g. *Cheirogaleus medius*) that maintained T_b slightly above fluctuating T_a for up to several weeks with no indications of active warm-ups (e.g. Dausmann *et al.*, 2004). In these species we used two alternative methods to determine TBD_{max}: (1) we used the maximum time of passively fluctuating T_b observed, and (2) we used TBD_{max} from conventional torpor bout patterns (with clear arousals) determined in the same species at lower and more constant mean T_a. Because using type 1 or type 2 TBD_{max} did not affect any of the conclusions, we maintained only type 2 $TBD_{max,}$ because using maximum observation periods (as in type 1) seemed somewhat arbitrary. TBD_{max} was also difficult to assign in three carnivores (*Ursus americanus*, *Ursus arctos* and *Meles meles*), which – based on records of T_b, MR and behaviour – were initially classified as 'hibernators' as they are capable of consecutive multiday torpor episodes (e.g. Tøien *et al.*, 2011). Whereas these species show multiday T_b cycles, the peaks in these cycles are not considered homologous to arousal episodes in small hibernators (Tøien *et al.*, 2011). Therefore, we assigned no values for TBD in these three species. For TMR_{min} only values that were below the BMR of a species were included in our analyses. TMR_{min} that were not steady state, according to visual inspection of graphs, usually because animals were not measured for long enough (or if torpor was induced for brief periods at inappropriate times of day), were excluded. If only T_b measurements were available, we considered animals with a T_b reduction of $>5^{\circ}$C below euthermic resting values to be torpid.

The duration of euthermic intervals between torpor episodes (interbout euthermia, IBE) was taken from the literature for species traditionally classified as hibernators, but limited data on IBE were available for species traditionally considered daily heterotherms. To obtain at least a rough estimate of IBE for this subgroup, we computed IBE as 24 h − TBD.

Both euthermic and torpor MR were analysed as mass-specific MR. We are aware that this is a potential source of error and that computing allometric relationships based on absolute MR would be preferable (e.g. Packard & Boardman, 1988; Hayes, 2001). However, the vast majority of MRs in the literature we cite were given as mass-specific MR and – also in the majority of cases – body masses were provided for the species or experimental animals in general, but not the actual individuals in which MR was measured (typically, only mean body masses were given). Thus, estimating total MRs from these different sources (i.e. multiplying mass-specific MR from one sample of individuals by mean body mass from another set) would lead to the same potential error pointed out by Packard & Boardman (1988): assuming a linear isometric relationship when this assumption may not be valid. Balancing the possible error in using mass-specific MR *versus* omitting most MR data altogether, we decided

Table 1. Torpor characteristics in birds and mammals

Taxon	T	BM	$T_{b\,min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
AVES										
Coraciiformes										
Dacelo novaeguineae	DT	0.35	28.6	—	—	11.1	9.3	—	−25	Cooper *et al.* (2008)
Todus mexicanus	DT	0.0062	22.4	2	62	—	—	—	18	Merola-Zwartjes & Ligon (2000)
Coliiformes										
Colius castanotus	DT	0.058	18	0.49	21	11	—	—	−10	Prinzinger *et al.* (1981) and Hoffmann & Prinzinger (1984)
Colius colius	DT	0.035	26	—	—	—	—	—	−27	McKechnie & Lovegrove (2001*b*)
Colius striatus	DT	0.051	18.2	0.11	13	10	—	—	−4	Hoffmann & Prinzinger (1984) and McKechnie & Lovegrove (2001*a*)
Urocolius indicus	DT	0.053	—	0.68	28	10	—	—	−23	Hoffmann & Prinzinger (1984)
Urocolius macrourus	DT	0.049	22	0.65	24	11	—	—	3	Hoffmann & Prinzinger (1984) and Schaub, Prinzinger & Schleucher (1999)
Apodiformes										
Aeronautes saxatalis	DT	0.0305	20	—	—	10	—	—	23	Bartholomew, Howell & Cade (1957)
Apus apus	DT	0.042	28	0.4	—	5	—	—	50	Koskimies (1948)
Hirundapus caudacutus	DT	0.085	28	—	—	10	—	—	−25	Pettigrew & Wilson (1985)
Trochiliformes										
Amazilia versicolor	DT	0.0039	21.8	—	—	10.4	6.3	—	−8	Bech *et al.* (1997)
Archilochus alexandri	DT	0.0032	13.5	0.2	5.7	—	—	—	35	Lasiewski (1963, 1964)
Calypte anna	DT	0.0034	16	0.17	4.4	—	—	—	39	Lasiewski (1963)
Calypte costae	DT	0.0032	9	0.38	12.7	—	—	—	37	Lasiewski (1963, 1964)
Chrysuronia oenone	DT	0.005	18	2.05	—	—	—	—	−4	Krüger, Prinzinger & Schuchmann (1982)
Clytolaema rubricauda	DT	0.0077	18	0.5	16	—	—	—	−22	Bech *et al.* (2006)
Eugenes fulgens	DT	0.008	10	0.5	—	—	—	—	27	Wolf & Hainsworth (1972)
Eulampis jugularis	DT	0.008	18	1	33	—	—	—	15	Hainsworth & Wolf (1970)
Eupetomena macroura	DT	0.0085	22	—	—	9	5.8	—	−15	Bech *et al.* (1997)
Lampornis clemenciae	DT	0.008	19.6	0.45	17	—	—	—	25	Krüger *et al.* (1982)
Melanotrochilus fuscus	DT	0.0069	22	—	—	11.2	9.6	—	−26	Bech *et al.* (1997)
Oreotrochilus estella	DT	0.0085	6.5	0.75	—	—	10	—	−17	Carpenter (1974) and Krüger *et al.* (1982)
Orthorhynchus cristatus	DT	0.0029	20.8	1.25	20	—	—	—	16	Krüger *et al.* (1982)
Panterpe insignis	DT	0.005	10	0.5	—	—	—	—	9	Wolf & Hainsworth (1972)
Selasphorus platycercus	DT	0.0035	6.5	0.54	—	—	—	—	37	Calder & Booser (1973) and Bucher & Chappell (1992)
Selasphorus rufus	DT	0.0033	13	0.43	12.8	10	5	—	48	Lasiewski (1963) and Hiebert (1990, 1993)
Selasphorus sasin	DT	0.003	23	1.24	32.6	—	—	—	38	Lasiewski (1963)
Strigiformes										
Otus senegalensis	DT	0.061	29	—	—	5	2.8	—	−2	Smit & McKechnie (2010)
Caprimulgiformes										
Aegotheles cristatus	DT	0.05	22.4	—	—	10.7	3	—	−25	Brigham *et al.* (2000) and Doucette *et al.* (2012)

Table 1. Continued

Taxon	T	BM	$T_{b\ min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
Caprimulgus europaeus	DT	0.07	14	—	—	16	3	—	−7	Peiponen (1965) and Schlegel (1969)
Caprimulgus guttatus (argus)	DT	0.075	29.6	0.4	48	—	—	—	−28	Dawson & Fisher (1969)
Caprimulgus tristigma	DT	0.073	10.5	—	—	15	6.4	—	−11	Smit *et al.* (2011) and McKechnie & Mzilikazi (2011)
Caprimulgus vociferus	DT	0.055	18.5	—	—	—	—	—	34	Lane, Brigham & Swanson (2004)
Chordeiles acutipennis	DT	0.05	15.7	—	—	—	—	—	33	Marshall (1955)
Chordeiles minor	DT	0.073	18	—	—	—	—	—	43	Lasiewski & Dawson (1964)
Phalaenoptilus nuttallii	HIB	0.035	3	0.05	6	120	—	—	35	Withers (1977), Brigham (1992) and Woods & Brigham (2004)
Podargus strigoides	DT	0.5	29.1	—	—	11	7	—	−25	Körtner *et al.* (2000) and Körtner, Brigham & Geiser (2001)
Columbiformes										
Drepanoptila holosericea	DT	0.2	24.8	0.27	38	10	7	—	21	Schleucher (2001)
Scardafella inca	DT	0.044	29	1	66	10	—	—	23	MacMillen & Trost (1967)
Passeriformes										
Artamus cyanopterus	DT	0.035	29	—	—	12	—	—	−30	Maddocks & Geiser (2007)
Delichon urbicum	DT	0.022	26	0.75	59	12	—	—	50	Prinzinger & Siedle (1986, 1988)
Nectarinia famosa	DT	0.017	25.4	—	—	10	—	—	−12	Downs & Brown (2002)
Manacus vitellinus	DT	0.0155	26.8	1.8	66	3.5	—	—	5	Bartholomew, Vleck & Bucher (1983)
MAMMALIA										
Monotremata										
Tachyglossus aculeatus	HIB	2.8	4	0.03	20	648	271	25	−22.26	Augee & Ealey (1968), Grigg *et al.* (1989) and Nicol & Andersen (2002)
Placentalia										
Rodentia										
Acomys russatus	DT	0.064	25	0.25	38	10	7.5	—	22.84	Ehrhardt, Heldmaier & Exner (2005) and Levy, Dayan & Kronfeld-Schor (2011)
Aethomys namaquenesis	DT	0.046	18.9	—	—	—	—	—	−23.16	Withers, Louw & Henschel (1980)
Allactaga euphratica	HIB	0.09	—	—	—	336	96	—	33	Çolak & Yiğit (1998)
Allactaga williamsi	HIB	0.15	—	—	—	144	96	—	39	Çolak & Yiğit (1998)
Apodemus peninsulae	DT	0.026	20	—	—	6.5	2.1	—	48.26	Masaki *et al.* (2005)
Baiomys taylori	DT	0.0064	22	0.5	26	20	10	—	26.19	Hudson (1965)
Calomys musculinus	DT	0.017	—	0.52	32	16	13	—	−31.61	Bozinovic & Rosenmann (1988)
Calomys venustus	DT	0.05	16.4	0.96	67	8	7	—	−37	Caviedes-Vidal *et al.* (1990)
Cricetus cricetus	HIB	0.4	3.6	0.032	4	160	87	—	51.6	Eisentraut (1933), Kayser (1964), Waßmer & Wollnik (1997), Siutz *et al.* (2012) and C. Siutz (personal communication)
Cynomys leucurus	HIB	1.5	8	—	—	199	121	—	41.59	Bakko & Nahornia (1986)
Cynomys ludovicianus	HIB	1	15	—	—	214	141	—	39.25	Lehmer *et al.* (2001)
Cynomys parvidens	HIB	0.8	6	—	—	418	252	—	38.49	Lehmer & Biggins (2005)

Table 1. Continued

Taxon	T	BM	$T_{b\ min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
Eliomys quercinus	HIB	0.07	1	0.034	3	480	336	12	42.91	Kayser (1964) and Pajunen (1984)
Fukomys damarensis	DT	0.145	28.5	—	—	—	—	—	−18.37	Streicher (2010)
Gerbillus pusillus	DT	0.0126	16.7	0.38	43	20	9	—	0.57	Buffenstein (1985)
Glirulus japonicus	HIB	0.025	—	—	—	380	254	—	34.25	Otsu & Kimura (1993)
Glis glis	HIB	0.2	1	0.026	3	977	222	6.7	45.93	Wyss (1932), Kayser (1939, 1961), Pengelley & Fisher (1961), Bieber & Ruf (2009) and C. Bieber & T. Ruf (unpublished data)
Graphiurus murinus	HIB	0.028	1.5	—	—	192	33	—	−10.12	Mzilikazi *et al.* (2012)
Graphiurus ocularis	HIB	0.068	—	—	—	312	176	16	−30.24	Perrin & Ridgard (1999)
Ictidomys tridecemlineatus	HIB	0.14	1.5	—	—	456	336	14.4	41.11	Kisser & Goodwin (2012)
Jaculus orientalis	HIB	0.17	10	—	—	158	77	24	29.53	El Ouezzani *et al.* (2011)
Marmota broweri	HIB	3.094	—	—	—	480	334	18.4	68.5	Lee, Barnes, & Buck (2009)
Marmota flaviventris	HIB	2.5	7.5	0.022	9	360	206	15	42.67	Florant & Heller (1977), Florant, Hill & Ogilvie (2000) and French (1985)
Marmota marmota	HIB	3.1	2.4	0.013	4	353	280	27.8	46.15	Arnold (1993), Ortmann & Heldmaier (2000), Ruf & Arnold (2000), Arnold *et al.* (2011) and T. Ruf & W. Arnold (unpublished data)
Marmota monax	HIB	3.4	5	0.014	5	185	364	28.3	48.68	Lyman (1958), Armitage, Woods & Salsbury (2000) and Zervanos *et al.* (2010)
Mesocricetus auratus	HIB	0.09	4	0.07	6	264	90	—	36.76	Lyman (1948) and Pohl (1961)
Mesocricetus brandti	HIB	0.15	—	—	—	144	108	—	38.08	Goldman (1989)
Microdipodops pallidus	HIB	0.012	6	0.1	4.8	84	48	8.2	38.57	Brown & Bartholomew (1969) and Bartholomew & MacMillen (1961)
Mus musculus	DT	0.037	16	0.7	47	11	5.9	—	50	Hudson & Scott (1979)
Muscardinus avellanarius	HIB	0.0235	0	0.04	2	624	218	6	47.96	Kayser (1939, 1964), Eisentraut (1956) and Prezlaff & Dausmann (2012)
Perognathus californicus	DT	0.021	15	0.15	15	15.4	11.1	—	31.11	Tucker (1962, 1965)
Perognathus fasciatus	DT	0.04	11	0.15	12	17	9.7	—	44.7	Wang & Hudson (1970)
Perognathus longimembris	HIB	0.008	4	—	—	112	—	—	35.77	Bartholomew & Cade (1957) and French (1977)
Perognathus parvus	HIB	0.024	2	0.05	3	192	120	—	43.39	MacMillen (1983)
Peromyscus boylii	DT	0.033	18	—	—	8.8	4.3	—	32.94	Morhardt (1970)
Peromyscus crinitus	DT	0.02	17	—	—	9.5	4.6	—	36.88	Morhardt (1970)
Peromyscus eremicus	DT	0.017	16	0.3	19	11.2	6.3	—	29	Macmillen (1965) and Morhardt (1970)
Peromyscus gossypinus	DT	0.022	14	—	—	—	4.9	—	31.36	Tannenbaum & Pivorun (1984)
Peromyscus leucopus	DT	0.02	16.8	0.47	28	13	4.6	—	33.49	Hill (1975), Deavers & Hudson (1981) and Tannenbaum & Pivorun (1988)

Table 1. Continued

Taxon	T	BM	$T_{b\,min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
Peromyscus maniculatus	DT	0.018	13.4	0.55	28	10.8	7.3	—	40.92	McNab & Morrison (1963), Morhardt (1970) and Geiser (1991)
Petromyscus collinus	DT	0.019	18	—	—	—	—	—	−24.17	Withers *et al.* (1980)
Phodopus sungorus	DT	0.025	12.3	0.88	46	13.8	6.3	—	50.89	Ruf *et al.* (1993) and T. Ruf (unpublished data)
Phyllotis darwini	DT	0.036	17.5	0.19	15	12	—	—	−30.74	Bozinovic & Marquet (1991)
Reithrodontomys megalotis	DT	0.008	13	0.3	12	10	4	—	33.28	Thompson (1985)
Saccostomus campestris	DT	0.071	25	0.35	56	2.7	6.8	—	−19.68	Mzilikazi & Lovegrove (2002)
Spermophilus armatus	HIB	0.5	—	—	—	576	302	9.5	42.02	Cranford (1986)
Spermophilus beecheyi	HIB	0.6	6.1	—	—	72	48	—	38.32	Strumwasser (1960) and Pengelley & Kelley (1966)
Spermophilus beldingi	HIB	0.4	—	—	—	400	—	9	41.29	French (1985)
Spermophilus citellus	HIB	0.25	−0.7	—	—	415	192	14	45.52	Németh, Nyitrai & Altbäcker (2009)
Spermophilus columbianus	HIB	0.5	0	—	—	424	600	12	49.15	Young (1990)
Spermophilus dauricus	HIB	0.35	−2.4	—	—	377	260	12.75	43.33	Yang *et al.* (2011)
Spermophilus elegans	HIB	0.3	—	—	—	450	338	24	43.96	Harlow & Menkens (1986)
Spermophilus lateralis	HIB	0.2	−1	0.028	4	504	408	13.5	44.51	Hammel *et al.* (1968) and Healy *et al.* (2012)
Spermophilus mexicanus	HIB	0.2	7	0.06	7	60	36	—	26.39	Neumann & Cade (1965)
Spermophilus parryii	HIB	0.65	−2.9	0.012	2	550	420	14.8	63.39	Hock (1960), Barnes (1989), Barnes & Ritter (1993), Buck & Barnes (2000) and Karpovich *et al.* (2009)
Spermophilus richardsonii	HIB	0.4	2	0.02	4	456	—	10.3	49.39	Hudson & Deavers (1973) and Wang (1978)
Spermophilus saturatus	HIB	0.23	0.3	0.017	4	360	254	—	47.94	Geiser, Hiebert & Kenagy (1990)
Spermophilus tereticaudus	HIB	0.125	—	0.048	7	120	—	—	32.04	Pengelley & Kelley (1966) and Bickler (1984)
Spermophilus variegatus	HIB	0.7	8	—	—	172	110	—	29.99	Pengelley (1964) and Pengelley & Kelley (1966)
Spermophilus xanthoprymnus	HIB	0.3	4	—	—	468	199	—	38.76	Kart Gür, Refinetti & Gür (2009)
Steatomys pratensis	DT	0.028	16.4	0.3	22	16.9	21.5	—	−20	Ellison (1995)
Tamias amoenus	HIB	0.054	−0.2	0.026	2	312	211	—	45.07	Kenagy & Vleck (1982) and Geiser *et al.* (1990)
Tamias striatus	HIB	0.087	4.9	0.06	6	150	120	18	40.78	Wang & Hudson (1971), Pivorun (1976) and Levesque & Tattersall (2010)
Zapus hudsonius	HIB	0.0226	—	0.043	3	451	—	—	48.34	Muchlinski & Rybak (1978)
Zapus princeps	HIB	0.0336	5.5	0.024	2	650	480	5	47.4	Cranford (1983) and French (1985)
Primates										
Cheirogaleus crossleyi	HIB	0.5	9	—	—	168	111	10.2	−18.72	Blanco & Rahalinarivo (2010)
Cheirogaleus medius	HIB	0.25	9.3	0.044	8.3	1680	160	6	−19.03	Dausmann, Ganzhorn & Heldmaier (2000) and Dausmann *et al.* (2004, 2005, 2009)

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Table 1. Continued

Taxon	T	BM	$T_{b\,min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
Galago moholi	DT	0.18	21.8	0.09	10	6.5	5	—	−13.46	Nowack, Mzilikazi & Dausmann (2010)
Microcebus griseorufus	HIB	0.05	6.5	—	—	1848	43.1	—	−22.94	Dausmann *et al.* (2012) and Kobbe, Ganzhorn & Dausmann (2011)
Microcebus murinus	DT	0.06	7.8	0.16	19	17.6	9.3	—	−18.95	Perret (1998) and Schmid (2000)
Microcebus myoxinus	DT	0.033	6.8	0.09	4.5	19.2	4.6	—	−20.08	Schmid, Ruf & Heldmaier (2000)
Microcebus ravelobensis	DT	0.063	25	—	—	7	5	—	−19.32	Lovegrove *et al.* (2013)
Carnivora										
Meles meles	HIB	13	28	—	—	—	—	—	51	Fowler & Racey (1988)
Mephitis mephitis	DT	2.88	26	—	—	20	7.8	—	43.15	Hwang, Larivière & Messier (2007)
Proteles cristata	DT	9	31	—	—	—	—	—	−5.74	Anderson (2004)
Taxidea taxus	DT	9	28	0.13	43	22	14	—	38.45	Harlow (1981)
Ursus americanus	HIB	80	29.4	0.042	19	—	—	—	47.57	Watts *et al.* (1981) and Tøien *et al.* (2011)
Ursus arctos	HIB	100	32.5	—	—	—	—	—	50.76	Hissa (1997)
Chiroptera										
Barbastella barbastellus	HIB	0.007	—	0.04	2	—	—	—	44.28	Pohl (1961)
Carollia perspicillata	DT	0.018	22	1	53	—	—	—	−4.14	Audet & Thomas (1997)
Chalinolobus gouldii	HIB	0.018	5	0.05	3	—	—	—	−27.37	Hosken & Withers (1997)
Corynorhinus rafinesquii	HIB	0.01	13.9	—	—	—	58	—	32.8	Johnson (2012)
Eptesicus fuscus	HIB	0.0147	1	0.03	3	600	488	2	31.15	Kulzer (1965), French (1985) and Willis *et al.* (2005*a*)
Glossophaga soricina	DT	0.01	21	0.23	9	17.5	11.4	—	−2.61	Kelm & von Helversen (2007)
Hipposideros terasensis	HIB	0.057	13.8	0.046	7	456	185	1.8	17.13	Liu & Karasov (2011, 2012)
Lasiurus borealis	HIB	0.011	3	0.035	2	260	190	2.83	36.39	Dunbar & Tomasi (2006)
Lasiurus cinereus	HIB	0.033	2	—	—	135	105	—	12.6	Cryan & Wolf (2003) and Willis, Brigham & Geiser (2006)
Macroglossus minimus	DT	0.016	21.6	0.52	40	9.5	6.7	—	−1.28	Bartels, Law & Geiser (1998)
Megaloglossus woermanni	DT	0.012	26.2	0.8	50	—	—	—	−1.12	Kulzer & Storf (1980)
Miniopterus schreibersii	HIB	0.015	5	—	—	288	—	—	5.87	Hall (1982) and Brown & Bernard (1994)
Mops condylurus	HIB	0.029	13	—	—	—	—	—	−5.77	Vivier & van der Merwe (2011)
Myotis adversus	HIB	0.0078	9	—	—	192	—	—	4.84	Kulzer *et al.* (1970)
Myotis lucifugus	HIB	0.0052	1.3	0.022	1	1152	314	2.4	43	Hock (1951) and Jonasson & Willis (2012)
Myotis myotis	HIB	0.025	2	0.04	3	2352	989	—	47.44	Pohl (1961), Harmata (1987) and Koteja, Jurczyszyn & Wołoszyn (2001)
Myotis nattereri	HIB	0.009	7	—	—	490	160	—	46.05	Hope & Jones (2012)
Myotis velifer	HIB	0.012	0.6	0.04	3	—	—	—	27.11	Tinkle & Patterson (1965) and Riedesel & Williams (1976)
Nyctalus noctula	HIB	0.029	3	0.036	2	—	192	—	39.16	Ransome (1990) and Arlettaz *et al.* (2000)

Table 1. Continued

Taxon	T	BM	$T_{b\ min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
Nycteris thebaica	DT	0.011	27	—	—	—	—	—	1.28	Cory Toussaint & McKechnie (2012)
Nyctimene albiventer	DT	0.028	25.5	0.67	47	—	—	—	−4.02	Bartholomew, Dawson & Lasiewski (1970)
Nyctophilus bifax	HIB	0.01	7.3	0.046	3	129	27	3	−16.48	Stawski, Turbill & Geiser (2009) and Stawski & Geiser (2010, 2011)
Nyctophilus geoffroyi	HIB	0.007	1.4	0.037	3	362	106	3	−27.37	Geiser & Brigham (2000) and Turbill & Geiser (2008)
Nyctophilus gouldi	HIB	0.01	2.3	0.052	4	259	106	3	−33.54	Geiser & Brigham (2000) and Turbill & Geiser (2008)
Pipistrellus pipistrellus	HIB	0.0074	3	0.024	1	—	—	—	43.44	Kayser (1964) and Kulzer (1965)
Pipistrellus subflavus	HIB	0.005	—	—	—	1800	607	1.5	31.01	Brack & Twente (1985) and French (1985)
Plecotus auritus	HIB	0.01	−2	—	—	—	—	—	44.65	Eisentraut (1956)
Rhinolophus ferrumequinum	HIB	0.023	9	—	—	432	104	4.3	38.48	Kulzer (1965) and Park, Jones & Ransome (2000)
Rhinolophus hipposideros	HIB	0.006	—	—	—	2064	427	—	31.68	Harmata (1987)
Rhinopoma microphyllum	HIB	0.01	23	—	—	—	—	—	18.84	Kulzer (1965) and Levin *et al.* (2010)
Scotophilus dinganii	DT	0.029	18.5	—	—	19	15	—	−8.02	Jacobs *et al.* (2007)
Scotophilus mhlanganii	DT	0.028	17.2	—	—	18.5	17.2	—	−6	Jacobs *et al.* (2007)
Sturnira lilium	DT	0.016	22	0.5	25	—	—	—	−2.47	Audet & Thomas (1997)
Syconycteris australis	DT	0.018	17.2	0.47	36	8.2	7.3	—	−16.55	Coburn & Geiser (1998)
Tadarida aegyptiaca	HIB	0.017	6	—	—	228	—	—	1.12	Cory Toussaint, McKechnie & van der Merwe (2010)
Tadarida brasiliensis	HIB	0.01	9	0.06	3	—	—	—	1.23	Herreid (1963) and Herreid & Schmidt-Nielsen (1966)
Tadarida teniotis	HIB	0.035	6.7	0.04	4	192	528	4.5	35.4	Arlettaz *et al.* (2000) and Marom *et al.* (2006)
Vespadelus vulturnus	HIB	0.004	5	0.014	1.3	—	—	—	−34.21	Willis, Turbill & Geiser (2005*b*)
Eulipotyphla										
Atelerix algirus	HIB	0.63	9.7	—	—	168	84	16	33.74	Mouhoub-Sayah *et al.* (2008)
Atelerix frontalis	HIB	0.4	1	—	—	116	22	12	−23.03	Hallam & Mzilikazi (2011)
Crocidura flavescens	DT	0.032	19	—	—	—	—	—	−30.94	Baxter (1996)
Crocidura leucodon	DT	0.012	18.6	—	—	—	—	—	42.54	Nagel (1985)
Crocidura russula	DT	0.01	17.9	0.9	38	3	—	—	40.48	Nagel (1977, 1985)
Crocidura suaveolens	DT	0.008	21.6	—	—	—	—	—	45	Nagel (1985)
Erinaceus europaeus	HIB	0.7	5.4	0.01	2.5	288	213	22.1	53.78	Kristoffersson & Soivio (1964) and Thäti (1978)
Notiosorex crawfordi	DT	0.004	27.4	1.42	43	—	—	—	31	Lindstedt (1980)
Sorex sinuosus	DT	0.0078	—	1.3	28	1	—	—	31.46	Newman & Rudd (1978)
Suncus etruscus	DT	0.002	12	0.6	10	7.6	2	—	28.2	Vogel (1974) and Frey (1979, 1980)
Xenarthra										
Zaedyus pichiy	HIB	1.1	12.5	—	—	112	75	—	−40.89	Superina & Boily (2007)
Afrosoricida										
Amblysomus hottentotus	HIB	0.075	8.6	—	—	96	78	—	−29.74	Scantlebury *et al.* (2008)

Table 1. Continued

Taxon	T	BM	$T_{b\ min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
Echinops telfairi	HIB	0.085	11	0.026	2	264	162	—	−22.58	Dryden, Gębczyński & Douglas (1974) and Scholl (1974)
Geogale aurita	DT	0.006	16	0.15	13	—	—	—	−22.55	Stephenson & Racey (1993*a*)
Microgale dobsoni	DT	0.045	20	0.22	24	—	—	—	−18.56	Stephenson & Racey (1993*b*)
Setifer setosus	HIB	0.32	13	0.014	4	3600	—	—	−18.96	Kayser (1964), Hildwein (1970) and Lovegrove *et al.* (2013)
Tenrec ecaudatus	HIB	0.65	15	0.027	9	6480	—	—	−18.96	F. Lachiver cited in Kayser (1961), Kayser (1964), Hildwein (1970) and Lobban & Lovegrove (2012)
Macroscelidea										
Elephantulus edwardii	HIB	0.045	9.3	—	—	44	17.3	—	−31.59	Geiser & Mzilikazi (2011)
Elephantulus myurus	HIB	0.057	5.5	0.078	7	39	8.8	—	−23.07	Lovegrove *et al.* (2001), Mzilikazi & Lovegrove (2004) and McKechnie & Mzilikazi (2011)
Elephantulus rozeti	DT	0.045	5.1	0.023	2	20.1	13.6	—	32.6	Lovegrove *et al.* (2001)
Elephantulus rupestris	DT	0.06	12	—	—	12	5	—	−25.59	Oelkrug *et al.* (2012)
Macroscelides proboscideus	DT	0.046	9.4	—	—	18	10.7	—	−26.24	Lovegrove, Lawes & Roxburgh (1999)
Marsupialia										
Diprodontia										
Acrobates pygmaeus	HIB	0.011	1.6	0.056	5	192	85	—	−24.91	Fleming (1985) and Geiser & Ferguson (2001)
Burramys parvus	HIB	0.063	1.8	0.025	2	480	342	—	−36.29	Geiser & Broome (1991)
Cercartetus concinnus	HIB	0.018	4.7	0.046	4	264	102	—	−33.82	Geiser (1987)
Cercartetus lepidus	HIB	0.012	5.9	0.052	3	144	—	—	−38.97	Geiser (1987)
Cercartetus nanus	HIB	0.02	1.3	0.018	2.7	840	101	—	−35.06	Geiser (1993), Song *et al.* (1997) and Turner *et al.* (2012)
Petaurus breviceps	DT	0.13	10.4	0.07	9.5	23	13	—	−20.7	Fleming (1980) and Körtner & Geiser (2000*b*)
Tarsipes rostratus	DT	0.01	5.4	0.15	5	14.4	10.5	—	−31.3	Collins, Wooller & Richardson (1987) and Withers, Richardson & Wooller (1990)
Microbiotheria										
Dromiciops gliroides	HIB	0.0402	7.1	0.03	3.8	144	120	—	−39.86	Grant & Temple-Smith (1987); Bozinovic, Ruiz & Rosenmann (2004) and Franco *et al.* (2012)
Dasyuromorphia										
Antechinomys laniger	DT	0.027	11	0.14	13	16	11.5	—	−27.09	Geiser (1986)
Antechinus flavipes	DT	0.026	24.5	0.48	46	5.5	2	—	−26.92	Geiser (1988)
Antechinus stuartii	DT	0.026	19.9	0.66	62	9	4	—	−26.74	Geiser (1988)
Dasycercus cristicauda/blythi	DT	0.1	10.8	0.12	23	20.8	5.8	—	−25.02	MacMillen & Nelson (1969), Geiser & Masters (1994) and Körtner, Pavey & Geiser (2008)
Dasykaluta rosamondae	DT	0.027	21	—	—	16.4	12.3	—	−22.58	Körtner, Rojas & Geiser (2010)

Table 1. Continued

Taxon	T	BM	$T_{b\,min}$	TMR_{min}	TMR_{rel}	TBD_{max}	TBD_{mean}	IBE	LAT	References
Dasyuroides byrnei	DT	0.12	20.4	0.4	54	7.5	2.7	—	−26.08	Geiser & Baudinette (1987)
Dasyurus geoffroii	DT	1	23.1	—	—	—	—	—	−33.17	Arnold (1976)
Dasyurus hallucatus	DT	0.516	28.4	—	—	—	—	—	−18	Cooper & Withers (2010)
Dasyurus viverrinus	DT	1	25	—	—	—	—	—	−41.61	Moyle in Reardon (1999)
Myrmecobius fasciatus	DT	0.5	19.1	—	—	15.3	9.7	—	−33.82	Cooper & Withers (2004)
Ningaui yvonnae	DT	0.011	15.3	0.3	23	12.3	7.5	—	−31.98	Geiser & Baudinette (1988)
Planigale gilesi	DT	0.008	14.3	0.36	25	15.3	8.8	—	−29.48	Geiser & Baudinette (1988)
Planigale ingrami	DT	0.0076	—	0.48	30	4	—	—	−18.58	Dawson & Wolfers (1978)
Planigale maculata	DT	0.013	19.6	0.4	40	1.8	—	—	−21.9	Morton & Lee (1978)
Planigale tenuirostris	DT	0.007	—	0.48	30	4	—	—	−28.53	Dawson & Wolfers (1978)
Pseudantechinus macdonnellensis	DT	0.031	15.9	—	—	14.3	5.8	—	−22.83	Geiser & Pavey (2007)
Sminthopsis crassicaudata	DT	0.017	10.8	0.27	22	19.5	15	—	−28.79	Geiser & Baudinette (1987) and Warnecke, Turner & Geiser (2008)
Sminthopsis douglasi	DT	0.06	16.9	0.43	40	8.8	3.2	—	−20.1	Muller (1996)
Sminthopsis macroura	DT	0.024	11.3	0.3	29	25.9	11	—	−24.29	Geiser & Baudinette (1987) and Körtner & Geiser (2009)
Sminthopsis murina	DT	0.019	15	0.25	22	8	—	—	−27.47	Geiser *et al.* (1984)
Sminthopsis ooldea	DT	0.0111	—	0.77	48	—	—	—	−24.7	Tomlinson, Withers & Maloney (2012)
Didelpimorphia										
Gracilinanus agilis	DT	0.0291	20	0.3	30	—	—	—	−18.71	Cooper, Withers & Cruz-Neto (2009)
Marmosa microtarsus	DT	0.013	16	0.25	18	9	—	—	15.53	Morrison & McNab (1962)
Thylamys elegans	DT	0.032	14	0.4	47	20	14	—	−30	Opazo, Nespolo & Bozinovic (1999) and Silva-Duran & Bozinovic (1999)

T, type: daily torpor (DT) or hibernation (HIB); BM, body mass (kg); $T_{b\,min}$, minimum body temperature in torpor (°C); TMR_{min}, minimum torpor metabolic rate (ml O_2 g^{-1} h^{-1}); TMR_{rel}, relative metabolic rate in torpor (TMR_{min} expressed as a percentage of basal metabolic rate); TBD_{max}, maximum torpor bout duration (h); TBD_{mean}, mean torpor bout duration (h); IBE, duration of interbout euthermia (h); LAT, latitude of mid species range (>0: °N, <0: °S).

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to analyse MR as given, especially as there is no apparent source of bias that could lead to larger errors in any subgroup of species investigated.

To test if either single variables (e.g. TMR_{min}) or combinations of torpor characteristics suggested the existence of a grouping structure within heterotherms we used cluster analysis based on Gaussian mixture models as implemented in the R-package 'mclust' (Fraley & Raftery, 2002). This procedure determines the number of clusters (one, two or more) of normally distributed variables that minimize the variance in the dataset based on the Bayesian Information Criterion (BIC), which adds a penalty term on the number of parameters to the log-likelihood of each model. To obtain approximately equal variances between potential groups, all variables (except $T_{b\,min}$) were log-transformed. We did not attempt to include IBE duration into these cluster analyses, as this variable may be affected by prior torpor episodes, but is not a characteristic of torpor episodes as such. As a measure of the strength of clustering, we used χ^2 and *P*-values from likelihood-ratio tests comparing the best model for each variable with the null model (i.e. a model assuming no subgroups). To minimize multiplicity of *P*-values, we limited testing of combinations of variables to those unrelated to TBD (i.e. TMR_{min}, TMR_{rel} and $T_{b\,min}$). We did not discriminate between birds and mammals in these cluster analyses. For models resulting in more than one cluster, each data point can be assigned to one of the groups determined. We compared these independent, model-generated classifications to our initial categories that were based on TBD_{max} being greater or less than 24 h.

To investigate the relationship of variables characterizing torpor (e.g. TBD_{max} or $T_{b\,min}$) to body mass or latitude of the species' geographical range we fitted phylogenetically informed generalized least-squares (PGLS) models. Models were computed using function 'gls' from package 'nlme' (Pinheiro *et al.*, 2013) in R 3.0.2 (R Development Core Team, 2013). In these models, phylogenetic correlation between taxonomically related species is used for sample-weighting, as data points obtained from closely related species cannot be considered entirely independent.

The bird phylogeny used was based on Sibley & Ahlquist (1990). Two families (the Artamidae and the Pipridae) were added to this tree using information on their phylogenetic position given by Norman *et al.* (2009) and Ericson *et al.* (2006) (Fig. 1). As no sufficient information on branch lengths was available for birds, all initial branch lengths in this tree were set to 1. We are aware that more recent, albeit controversial, phylogenies of birds are available (e.g. Hackett *et al.*, 2008). However, we decided to use the phylogeny proposed by Sibley & Ahlquist (1990), mainly to allow for comparisons with McKechnie & Lovegrove (2002) who used the same phylogeny. For mammals we used an updated version (Fritz, Bininda-Emonds & Purvis, 2009) of the mammalian supertree (Bininda-Edmonds *et al.*, 2007). For each data set analysed, tips for unavailable data were trimmed from this tree. The mammalian tree (which includes different branch lengths) for all species investigated here is shown in Fig. 2.

To compute phylogenetically informed regressions we used the evolutionary models and branch-length transformation algorithms implemented in the R-library 'ape' (Paradis, Claude & Strimmer, 2004). These included the Ornstein-Uhlenbeck model, the Brownian model, the ACDC model, Grafen's method and Pagel's algorithm. Initial trials showed that for all response variables investigated, using Pagel's method (Pagel, 1999; Freckelton, Harvey & Pagel, 2002) led to much lower estimates of model Akaike's information criterion (AIC) than any other algorithm. Hence, all PGLS models were computed using Pagel's method. Pagels' λ is expected to vary between 0 and 1 and can be determined by maximum-likelihood fits. A λ of 0 indicates the absence of a phylogenetic signal, i.e. the trait under consideration is not more similar among closely related species. If λ equals 1 the trait distribution matches a Brownian model of evolution (i.e. 'random walk' evolution). To determine 95% confidence limits for λ we used function 'pgls' from the R-package 'caper' (Orme *et al.*, 2013), which also provides their probabilities of differing from 0 and 1 (which we give as $P_{lower>0}$ and $P_{upper<1}$, respectively). Parameter estimates (i.e. intercepts and slopes) were obtained from function 'gls', because this function allows the use of restricted maximum likelihood (REML), which returns unbiased estimates, and in this regard is preferable to full maximum likelihood (ML) as used by function 'pgls' (e.g. Ives, Midford & Garland, 2007). Since the subset of species differed completely between the classical categories (i.e. avian and mammalian daily heterotherms and mammalian hibernators) separate statistical models were computed for each subgroup (note that there was only a single bird species preliminarily classified as a hibernator). This separation of subgroups was justified by the results from cluster analysis, which confirmed the initial categories based on TBD_{max}.

The primary predictor variable to explain variation in torpor characteristics was body mass (*cf.* Geiser & Ruf, 1995). Initially, we also included the absolute values of the latitude of the centre of species ranges as a predictor variable for all response variables. Species range latitudes (as a proxy for environmental harshness) were obtained from the PanTHERIA database (Jones *et al.*, 2009) for 159 mammal species. For 12 additional mammals the latitude was estimated from visually locating the approximate centre of the species range in maps provided by the International Union for Conservation of Nature (www.iucn.org) and determining its latitude. This procedure was also used for all bird species. For migratory species with two ranges, we used the geographic range in which torpid animals had been observed. The latitude of the species range was indeed the best predictor of avian torpor bout duration (see Section III.2). In all other cases, including latitude complicated the models without substantially decreasing the residual variance, as indicated by unchanged or strongly increased AIC values. This was probably caused at least partly by multicollinearity, i.e. a correlation between body mass and latitude among hibernators (see Section III.2). Therefore, latitude was omitted from these models. In models with TMR as the response variable and body

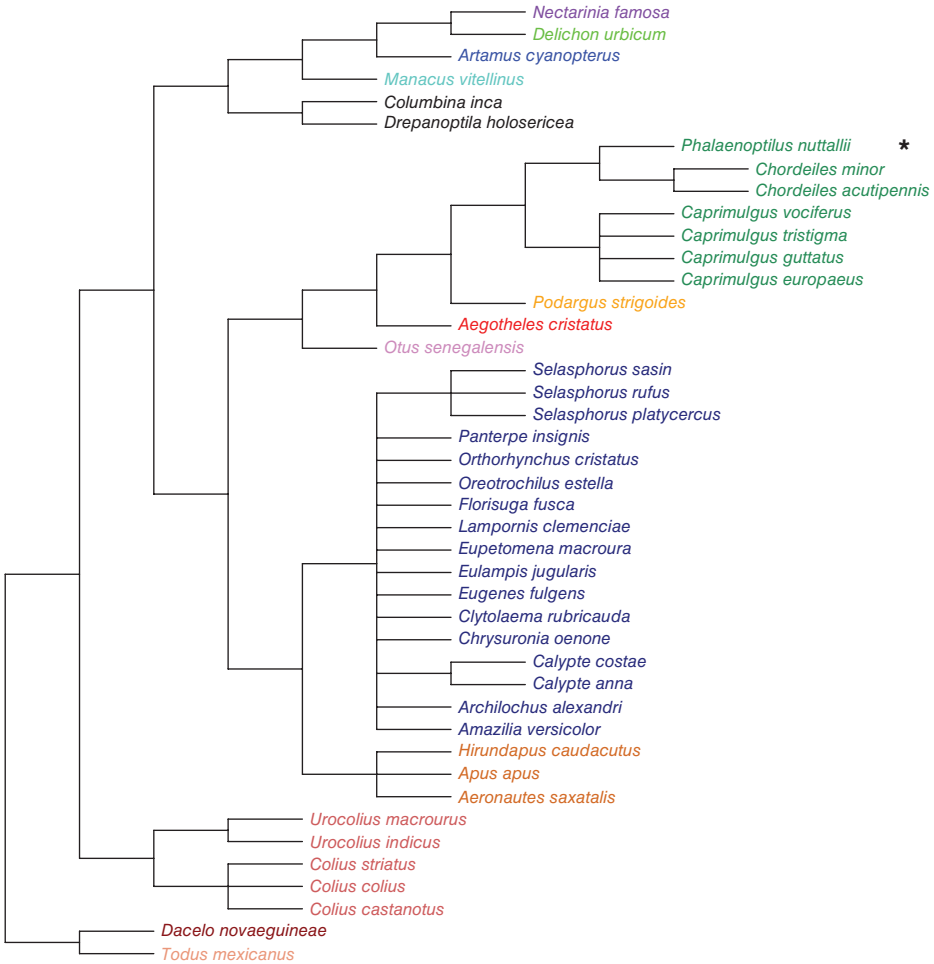

Fig. 1. Phylogenetic tree of the bird species investigated. Different colours indicate the following families (from top to bottom): Nectariniidae, Hirundinidae, Artamidae, Pipridae, Columbidae, Podargidae, Aegothelidae, Strigidae, Trochilidae, Apodidae, Coliidae, Alcedinidae, Todidae. *The single hibernating species among birds was the common poorwill, *Phalaenoptilus nuttallii*.

mass as the predictor, we did not use $T_{\mathrm{b\,min}}$ as an additional covariate, because for many species $T_{\mathrm{b\,min}}$ and $\mathrm{TMR}_{\mathrm{min}}$ were determined in different individuals and/or times.

To obtain approximately linear relationships and normally distributed residuals, body mass was $\log_{10}$-transformed, and in several cases so was the response and other predictor variables. For significant linear PGLS regressions, we report r^2 values as well as intercept, slope and the t and corresponding P-values for the difference between the slope and 0. To compare slopes from separate regressions, we computed their 95% confidence intervals. It should be noted that regression lines in PGLS, due to sample weighting as derived from the phylogeny may differ substantially from 'eye-fitted' lines, i.e. the relationship expected from the data scatterplot. Therefore, we show regression lines from PGLS models even if their slope was not significantly different from zero. As several torpor variables were affected by body mass, and mean masses differed considerably between subgroups, simple group means of variables investigated may reflect the combined effects of both torpor type and body mass differences. Therefore, we additionally give variable values predicted from the regression equations for a 30 g animal of each subgroup (i.e. very close to the overall median body mass of 32 g for all species included in our analysis), which we also call 'adjusted means'. Adjusted means, which arguably are better suited to assess the pure effects of torpor type, are given together with 95% confidence intervals (95% CI) computed from the standard errors of model coefficients. Further 95% CI are also given for the arithmetic mean of all variables. These 95% CI were computed by bootstrapping the data [i.e. generating distributions of 1000 means by random sampling with replacement and determining their 0.025 and 0.975 quantiles (for details see Efron & Tibshirani, 1993)]. For body masses, which were skewed to the right, we also give geometric means. To allow for a comparison of body masses of heterothermic mammals with terrestrial mammals in general (both heterothermic and homeothermic species), we also computed the mean and median, as well as their 95% CI, from the adult body masses of 2636 terrestrial mammal species provided in the PanTHERIA database (Jones *et al.*, 2009). All statistical analyses were carried out using R 3.0.2 (R Development Core Team, 2013).

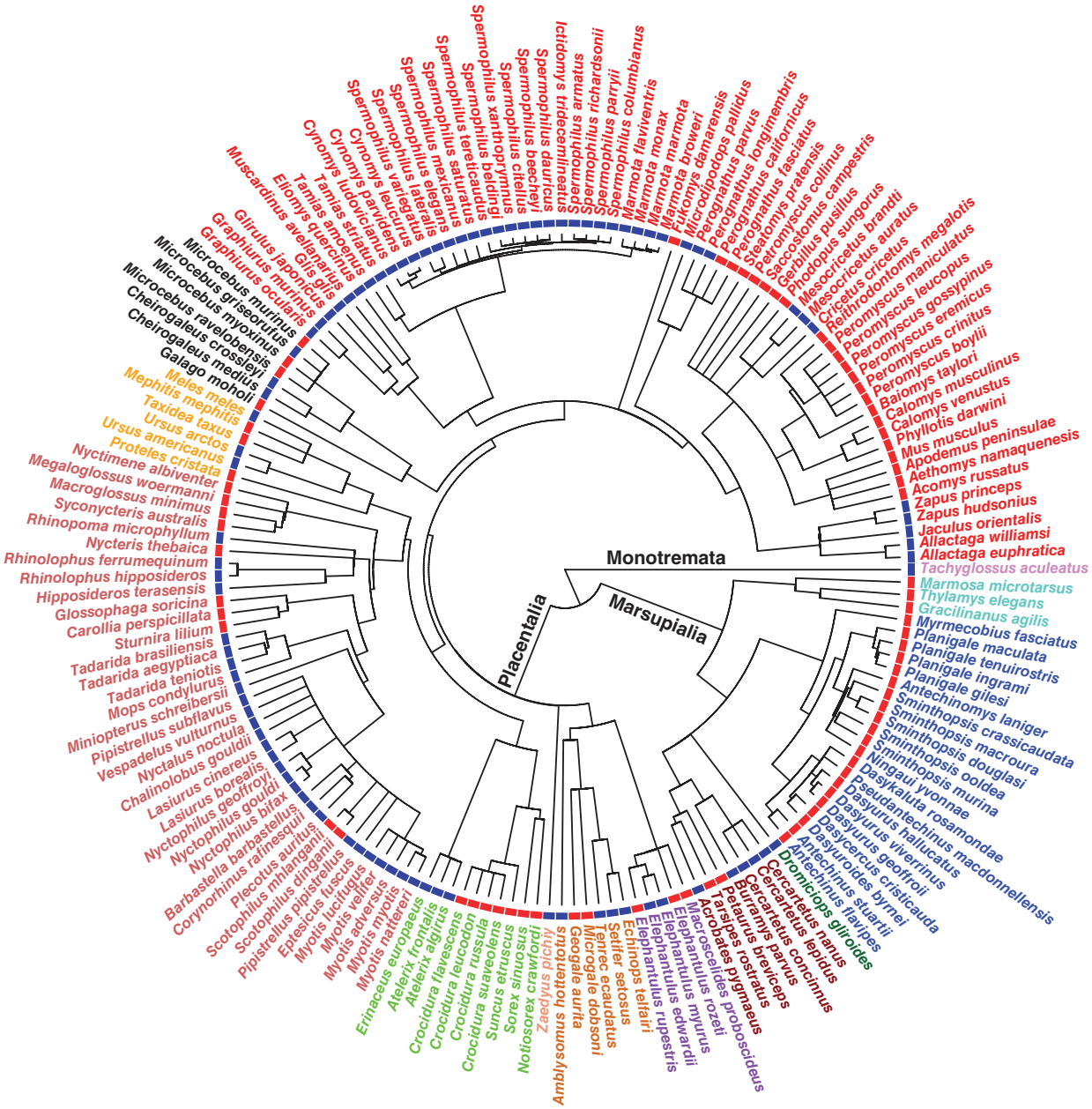

Fig. 2. Phylogenetic tree of the mammal species investigated. Species names in different colours indicate different orders. The coloured blocks next to species names indicate the use of hibernation (blue) or daily torpor (red), according to the traditional definition of heterothermy types.

III. RESULTS

(1) Classification of torpid states

TBD_{max} was the variable that showed the clearest bimodal distribution (Fig. 3). All other variables, except for IBE, also showed distinctly bimodal distributions, however with some overlap between species previously classified as daily heterotherms and hibernators.

Results from Gaussian-mixture cluster analyses unambiguously pointed to the existence of two groups within the species investigated. A two-cluster structure was the best model for all single variables and variable combinations tested ($P < 0.0001$ in all cases). The separation of clusters was strongest when based on TBD_{max} ($\chi^2 = 91.3$), followed by TBD_{mean} ($\chi^2 = 74.1$), a combination of TMR_{min} and $T_{b\,min}$ (Fig. 4; $\chi^2 = 51.0$), TMR_{rel} ($\chi^2 = 36.3$), a combination of TMR_{rel} and $T_{b\,min}$ ($\chi^2 = 32.9$), and $T_{b\,min}$ alone ($\chi^2 = 22.5$). The clusters suggested based on TBD_{max} were virtually identical to our initial classification (99% of species, with only two exceptions, *Elephantulus edwardii* and *Elephantulus myurus*). However, the agreement was also very high when based

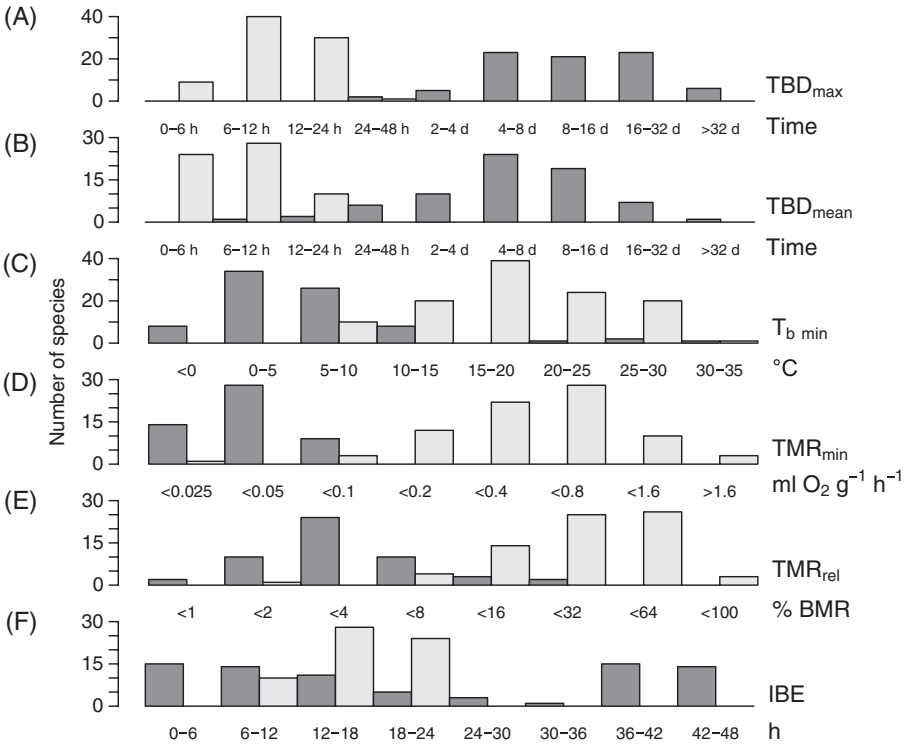

Fig. 3. Frequency distributions of maximum torpor bout duration (A, TBD_{max}), mean torpor bout duration (B, TBD_{mean}), minimum body temperature in torpor (C, $T_{b\,min}$), interbout euthermia duration (F, IBE), minimum metabolic rate in torpor (D, TMR_{min}), and metabolic reduction below basal metabolic rate (E, TMR_{rel}). Dark bars show species traditionally classified (TBD_{max} >24 h) as hibernators, light bars show daily heterotherms (TBD_{max} <24 h). Sample size varied for different variables (see Table 2). Data from mammals and birds were combined.

on other variables, i.e. 97% for $TMR_{min} + T_{b\,min}$, 96% for TBD_{mean}, 95% for TMR_{min}, 93% for TMR_{rel}, 92% for $TMR_{rel} + T_{b\,min}$, and 84% for $T_{b\,min}$. Given that classifying species as daily heterotherms was confirmed by bimodal variable distributions (Fig. 3) as well as cluster analyses, and could be based largely on variables beyond TBD_{max}, such as TMR_{min} and $T_{b\,min}$ alone (Fig. 4), we henceforth simply refer to these groups as 'daily heterotherms' and 'hibernators', and maintain our preliminary classification of species.

(2) Geographical and phylogenetic distribution of species

Centres of species geographic ranges were located in the northern hemisphere in 93 cases (mean latitude: $36.9 \pm 1.3^{\circ}$N) and in the southern hemisphere in 78 cases ($23.1 \pm 1.1^{\circ}$S). The absolute mean latitude of species ranges was very similar for mammalian and avian daily heterotherms (Table 2; overall mean: $24.5 \pm 1.1^{\circ}$). The mean latitude was significantly higher, i.e. $35.0 \pm 1.4^{\circ}$, for mammalian hibernators (Table 2, and 35° for the single avian hibernator). Moreover, these mean latitudes of geographical ranges in heterothermic species were considerably higher than in mammals in general ($17.5 \pm 0.2^{\circ}$; no estimates were available for all birds). Among daily heterotherms, body mass (BM) was unaffected by the species range latitude among both mammals ($\log_{10}BM = -1.66 + 0.003$ Latitude, $t = 0.82$, $P = 0.411$) and birds ($\log_{10}BM = -1.48 + 0.005$ Latitude, $t = 0.18$, $P = 0.858$). However, body mass increased slightly with latitude in mammalian hibernators ($\log_{10}BM = -0.901 + 0.007$ Latitude, $t = 2.18$, $P = 0.0031$). Body mass contained a strong phylogenetic signal in all three subgroups. Pagel's λ was 1.0 (95% CI: 0.93–1; $P_{lower>0} = <0.0001$, $P_{upper<1} = 1$) among avian daily heterotherms, 1.0 (95% CI: 00.86–1; $P_{lower>0} = <0.0001$, $P_{upper<1} = 1$) among mammalian daily heterotherms, and 0.99 (95% CI: 0.95–1; $P_{lower>0} = <0.0001$, $P_{upper<1} = 0.39$) among mammalian hibernators.

The mean body mass was significantly higher in mammalian hibernators than in both mammalian and avian daily heterotherms (Table 2). This was also true when geometric means were compared, to adjust for the skewness in the body mass data (Table 2). Body mass of the single avian hibernator was 0.035 kg. The mean and median body masses of mammalian heterotherms were significantly lower than those of terrestrial mammals in general ($N = 2636$; mean: 24.4 kg, 95% CI: 17.3–32.4 kg; median: 0.134 kg, 95% CI: 0.111–0.165 kg).

Among mammals most orders represented here contained both daily heterotherms and hibernators (Fig. 2), with two exceptions: the carnivorous/omnivorous marsupial orders Dasyuromorphia and Didelphimorphia, for which daily torpor but not hibernation has been reported. In all other

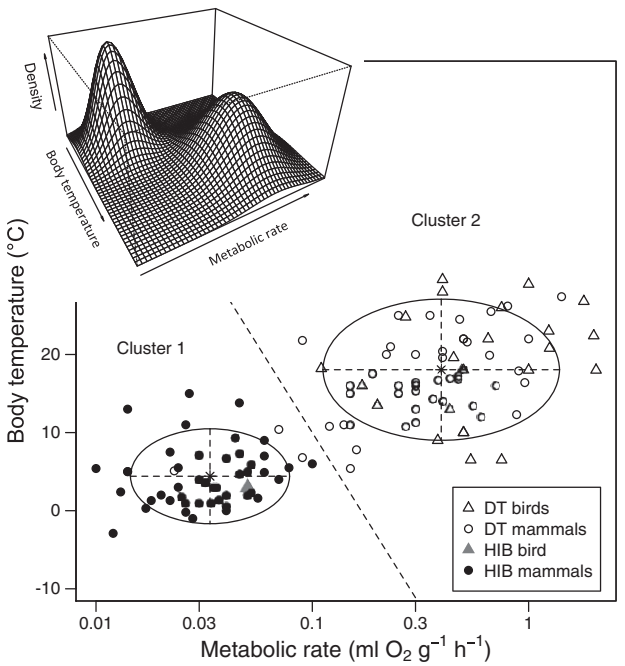

Fig. 4. Results from a cluster analysis based on the traits minimum metabolic rate in torpor (TMR_{min}) and minimum body temperature in torpor ($T_{b\,min}$) indicating the existence of two clusters within heterotherms. Circles represent 95% confidence ellipses for the estimated cluster centres (indicated by asterisks). All species on left of the dashed line were classified as belonging to cluster 1, which was identical to our initial category 'hibernators' (HIB) except for three species (*Elephantulus rozeti*, *Microcebus myoxinus*, *Petaurus breviceps*). Species on the right of the dashed line assigned to cluster 2, which was identical to the traditonal category 'daily heterotherms' (DT) except for one species (*Ursus americanus*). Overall there was a high degree of agreement (117 of 121 species) between this cluster analysis and classical categories. The inset graph shows the density surface computed from the parameters of the Gaussian-mixture model.

orders, the proportion of hibernators (overall 57%) and daily heterotherms (43%) was approximately the same ($\chi^2 = 11.4$, d.f. = 10, $P = 0.325$).

(3) Maximum torpor bout duration

TBD_{max} increased slightly with body mass among mammalian daily heterotherms, but was independent of body mass among both avian daily heterotherms and mammalian hibernators (Fig. 5A); regression slopes did not differ among the three groups. Pagel's λ was 0 (95% CI: 0–0.58; $P_{lower>0} = 1$, $P_{upper<1} = <0.001$) among mammalian daily heterotherms, indicating that a phylogenetic signal in this response variable was absent among mammals using daily torpor. This was also the case for avian daily heterotherms (λ = 0, 95% CI: 0–0.67; $P_{lower>0} = 1$, $P_{upper<1} = <0.0001$). TBD_{max} did contain a significant phylogenetic signal, however, among hibernating mammals (λ = 0.56, 95% CI: 0.13–0.82; $P_{lower>0} = 0.018$, $P_{upper<1} = <0.0001$). TBD_{max} significantly increased with latitude of the species' distribution centre among hibernating mammals, but not among daily heterotherms (Fig. 5B).

Adjusted means of TBD_{max} (calculated for a body mass of 30 g) were ∼10–11 h in both mammalian and avian daily heterotherms, and >200 h in hibernating mammals (Table 2). TBD_{max} was 120 h in the single avian hibernator, the common poorwill (*Phalaenoptilus nuttallii*).

(4) Mean torpor bout duration

TBD_{mean} was independent of body mass in all subgroups of birds and mammals ($t = 1.04$, $P = 0.302$). TBD_{mean} contained no significant phylogenetic signal among mammalian (λ = 0, 95% CI: 0–1; $P_{lower>0} = 1$, $P_{upper<1} = <0.0001$) or avian (λ = 0.53; 95% CI: 0–1; $P_{lower>0} = 0.49$, $P_{upper<1} = 0.21$) daily heterotherms. TBD_{mean} did, however, contain a slight phylogenetic signal in mammalian hibernators (λ = 0.47, 95% CI: 0–0.79; $P_{lower>0} = 0.070$, $P_{upper<1} = <0.0001$). TBD_{mean} increased with increasing latitude of the distribution range among hibernating mammals, but not for daily heterotherms (Fig. 6). The slope for this relationship in hibernators was slightly steeper than that for TBD_{max}.

Adjusted means (to 30 g body mass) of TBD_{mean} were ∼6–7 h in both avian and mammalian daily heterotherms, and >120 h (i.e. >17 times longer) in mammalian hibernators (Table 2). No mean torpor bout length was available for the single avian hibernator. Among mammals traditionally classified as hibernators the shortest TBD_{mean} values were recorded for *Elephantulus myurus* (8.8 h), *Elephantulus edwardii* (17.3 h) and *Atelerix frontalis* (22 h).

(5) Minimum body temperature

$T_{b\,min}$ in daily heterotherms increased with increasing body mass among both mammals and birds (Fig. 7). The slopes of the regression lines did not differ significantly between avian daily heterotherms, mammalian daily heterotherms, and mammalian hibernators. Among hibernators, the regression was heavily influenced by data from three carnivores (*Ursus americanus*, *Ursus arctos*, *Meles meles*, all with $T_{b\,min}$ >28°C). After removing these data points (as well as a $T_{b\,min}$ of 23°C reported for the arid-zone bat *Rhinopoma microphyllum*) the regression slope remained significantly greater than 0. $T_{b\,min}$ contained a strong significant phylogenetic signal among mammals, both among daily heterotherms (λ = 0.68; 95% CI: 0.31–0.88; $P_{lower>0} = <0.001$, $P_{upper<1} = <0.0001$) and among hibernators (λ = 0.78; 95% CI: 0.55–0.91; $P_{lower>0} = <0.0001$, $P_{upper<1} = <0.0001$). Among avian daily heterotherms however, the signal was weak (λ = 0.35; 95% CI: 0–0.87; $P_{lower>0} = 0.271$, $P_{upper<1} = 0.004$).

The predicted $T_{b\,min}$ for a 30 g avian daily heterotherm was ∼22°C, which was only slightly higher than in a mammalian daily heterotherm of the same body mass (17°C; Table 2). Adjusted mean $T_{b\,min}$ in mammalian hibernators was ∼4°C, i.e. significantly lower than in the other subgroups

Table 2. Central tendencies of variables of torpor as well as of body mass and the absolute value of latitude of species geographic ranges in mammals and birds. Adjusted means are values for a 30 g animal (the overall median body mass in the dataset) predicted from the regression of variables against body mass

	Avian daily heterotherms	Mammalian daily heterotherms	Mammalian hibernators
Body mass (kg)			
Mean	0.052	0.336	2.410
95% CI	0.028–0.083	0.069–0.706	0.350–5.413
Geometric mean	0.020	0.033	0.093
95% CI	0.013–0.030	0.024–0.049	0.061–0.147
Median	0.026	0.026	0.068
N	42	78	93
Latitude (°)			
Mean	23.1	25.3	35.0
95% CI	19.1–27.1	22.5–27.8	32.3–37.4
Median	24.0	26.2	38.1
N	42	78	93
TBD_{max} (h)			
Adjusted mean	10.1	11.2	266.6
95% CI	9.7–10.6	10.6–11.8	111.7–636.6
Mean	10.1	12.9	391.9
95% CI	9.0–11.2	11.4–14.5	303.9–479.9
Median	10	12.3	288
N	23	57	82
TBD_{mean} (h)			
Adjusted mean	6.1	6.0	123.9
95% CI	3.0–12.4	3.0–12.4	51.7–297.2
Mean	6.3	8.2	198.0
95% CI	4.9–7.6	7.0–9.3	158.2–233.8
Median	6.3	7.4	161
N	12	50	70
$T_{b\,min}$ (°C)			
Adjusted mean	21.8	16.9	3.9
95% CI	17.5–26.1	11.4–22.5	2.9–10.7
Mean	20.2	18.1	6.2
95% CI	18.0–22.1	16.6–19.4	4.8–7.7
Median	20.8	17.9	5.0
N	41	73	79
TMR_{min} ($ml\,O_2\,g^{-1}\,h^{-1}$)			
Adjusted mean	0.585	0.237	0.039
95% CI	0.302–1.134	0.100–0.600	0.036–0.040
Mean	0.740	0.430	0.037
95% CI	0.557–0.951	0.352–0.509	0.032–0.043
Median	0.500	0.370	0.035
N	25	54	50
TMR_{rel} (% BMR)			
Adjusted mean	35.3	18.8	4.3
95% CI	16.0–78.0	7.5–47.2	2.1–8.7
Mean	30.5	29.9	4.4
95% CI	22.0–39.8	26.1–34.4	3.5–5.6
Median	24.0	28.0	3.0
N	19	54	50
IBE (h)			
Adjusted mean	17.2	14.1	6.9
95% CI	13.9–21.4	10.1–19.7	3.5–13.4
Mean	17.7	15.8	12.0
95% CI	16.4–19.0	14.6–16.8	9.8–14.4
Median	17.7	16.6	10.3
N	12	50	49

$T_{b\,min}$, minimum body temperature in torpor; TBD_{max}, maximum torpor bout duration; TBD_{mean}, mean torpor bout duration; IBE, interbout euthermia duration; TMR_{min}, minimum MR in torpor; TMR_{rel}, metabolic reduction below basal metabolic rate (BMR). Note that IBE in daily heterotherms was estimated as $24\,h - TBD_{mean}$.

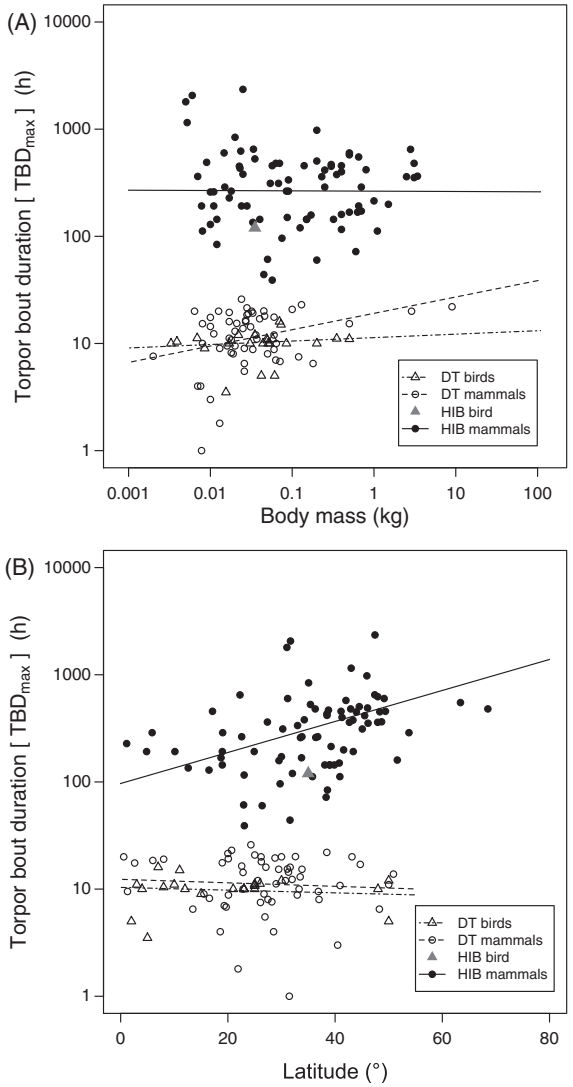

Fig. 5. (A) Maximum torpor bout duration (TBD_{max}) in relation to body mass (BM). In mammalian daily heterotherms (DT) TBD increased slightly with body mass ($\log_{10}TBD_{max} = 1.28 + 0.152\ \log_{10}BM$, $t = 2.56$, $P = 0.013$, $r^2 = 0.10$). In mammalian hibernators (HIB) TBD_{max} was independent of body mass ($P = 0.968$) and this was also the case for avian daily heterotherms ($P = 0.55$). (B) TBD_{max} in relation to absolute latitude of the species distribution centre. For mammalian daily heterotherms the regression was not significant ($t = -0.49$, $P = 0.621$). Among mammalian hibernators maximum torpor bout duration increased with latitude ($\log_{10}$duration $= 1.985 + 0.0144$ latitude, $t = 5.05$, $P < 0.0001$, $r^2 = 0.12$). There was no significant relationship in avian daily heterotherms ($t = -0.73$, $P = 0.471$).

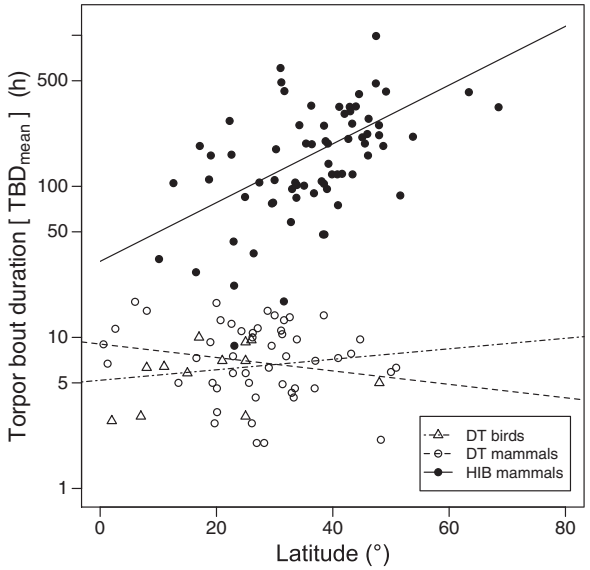

Fig. 6. Mean torpor bout duration (TBD_{mean}) in relation to absolute latitude of the species distribution centre. There were no significant relationships in avian ($t = 0.73$, $P = 0.487$) or mammalian ($t = -1.49$, $P = 0.140$) daily heterotherms (DT). Mean torpor bout duration increased with latitude in mammalian hibernators (HIB) ($\log_{10}TBD_{mean} = 1.503 + 0.019$ latitude, $t = 5.36$, $P < 0.0001$, $r^2 = 0.26$).

(Table 2). Interestingly, eight mammalian hibernators had $T_{b\,min} \leq 0^{\circ}C$; three of these had $T_{b\,min} \leq -2^{\circ}C$.

(6) Minimum metabolic rate

Mass-specific TMR_{min} decreased with increasing body mass in both daily heterotherms and hibernators (Fig. 8A). Among daily heterotherms the slopes of the regression lines for these relationships in both mammals and birds were not statistically different from that for BMR within the same group. In hibernating mammals, however, the slope of TMR_{min} as a function of body mass was significantly lower ($P < 0.05$) than that for mammalian or avian BMR. Notably, the decrease in TMR_{min} of hibernators with increasing body mass was statistically significant both with and without the largest hibernator (*Ursus americanus*; Fig. 8A). After excluding the black bear, the regression equation was $TMR = -1.651 - 0.156\ \log_{10}BM$ ($t = -3.43$, $P = 0.0012$, $r^2 = 0.17$).

BMR contained a significant phylogenetic signal among mammals ($\lambda = 0.61$; 95% CI: 0.18–0.87; $P_{lower>0} = <0.001$, $P_{upper<1} = <0.0001$), but not among birds ($\lambda = 0$; 95% CI: 0–1; $P_{lower>0} = 1$, $P_{upper<1} = 0.117$). TMR_{min} during daily torpor in mammals was affected by phylogeny ($\lambda = 0.81$; 95% CI: 0.44–0.96; $P_{lower>0} = 0.003$, $P_{upper<1} = 0.004$). There was no evidence for a phylogenetic signal in TMR_{min} among hibernating mammals ($\lambda = 0$; 95% CI: 0–0.48; $P_{lower>0} = 1$, $P_{upper<1} = <0.0001$) or birds using daily torpor ($\lambda = 52$; 95% CI: 0–1; $P_{lower>0} = 0.312$, $P_{upper<1} = <0.134$).

The predicted, mass-specific BMR for 30 g animals was 1.060 ml O_2 $g^{-1}\,h^{-1}$ (95% CI: 0.757–1.48 ml O_2 $g^{-1}\,h^{-1}$) for mammals and 1.628 ml O_2 $g^{-1}\,h^{-1}$ (95% CI 0.993–2.671 ml O_2 $g^{-1}\,h^{-1}$) for birds. In mammalian daily heterotherms the predicted TMR_{min} at a body mass of 30 g was 60% lower than in avian daily heterotherms, but the 95% CI of the estimates overlapped (Table 2). The adjusted mean TMR_{min} in mammalian hibernators (~0.04 ml O_2 $g^{-1}\,h^{-1}$) was only 17% of that in mammalian

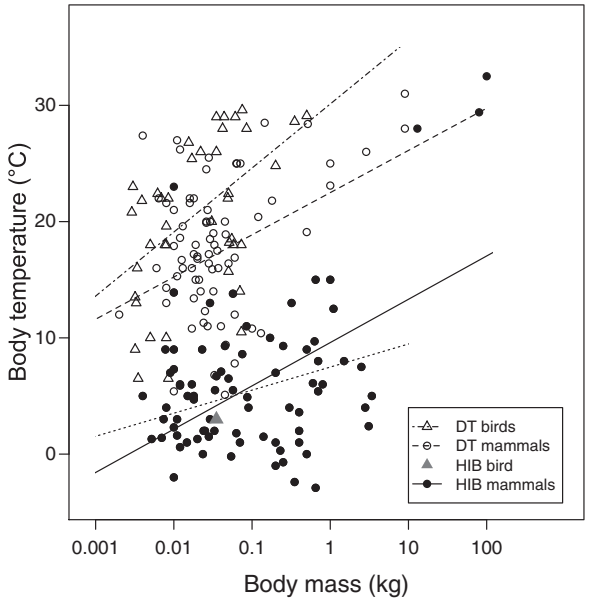

Fig. 7. Minimum body temperature in torpor ($T_{b\,min}$) as a function of body mass (BM). $T_{b\,min}$ increased with mass among mammalian daily heterotherms (DT) ($T_{b\,min} = 22.5 + 3.63\ \log_{10}BM$, $t = 3.56$, $P < 0.001$, $r^2 = 0.14$) and avian daily heterotherms ($T_{b\,min} = 21.8 + 5.53\ \log_{10}BM$, $t = 2.84$, $P = 0.007$, $r^2 = 0.26$). $T_{b\,min}$ also increased with body mass among mammalian hibernators (HIB) ($T_{b\,min} = 9.6 + 3.72\ \log_{10}BM$, $t = 3.98$, $P < 0.001$, $r^2 = 0.20$). After removing data from hibernators with $T_{b\,min} > 20^{\circ}C$ ($N = 4$) the regression equation was $T_{b\,min} = 7.5 + 1.98\ \log_{10}BM$, $t = 2.18$, $P = 0.032$, $r^2 = 0.02$ (dotted line).

daily heterotherms (~0.24 ml O_2 g^{-1} h^{-1}); this difference was significant (Table 2).

There was a significant relationship between TMR_{min} and TBD_{max} among hibernators with short TBD_{max} being associated with high mass-specific TMR_{min} (Fig. 8B). A similar, but much weaker relationship between these traits was also detectable in mammalian, but not in avian daily heterotherms (Fig. 8B). At the median TMR_{min} across all subgroups (0.09 ml O_2 g^{-1} h^{-1}), the predicted TBD_{max} was significantly higher for mammalian hibernators (133.2 h; 95% CI: 52.4–338.2 h) than among mammalian (13.2 h; 95% CI: 10.2–16.8 h) and avian daily heterotherms (13.0 h; 95% CI: 7.0–23.9 h).

(7) Relative torpor metabolic rate

TMR_{rel} (i.e. TMR_{min} expressed as a percentage of BMR) was variable among daily heterotherms and showed a tendency to increase with body mass, but not significantly so (Fig. 9). In mammalian hibernators the increase of TMR_{rel} with body mass was statistically significant.

There was evidence for a phylogenetic signal in TMR_{rel} among mammalian daily heterotherms ($\lambda = 0.86$; 95% CI: 0.49–0.99; $P_{lower>0} = 0.002$, $P_{upper<1} = 0.035$) but only a tendency for a signal among avian daily heterotherms ($\lambda = 0.70$; 95% CI: 0–1; $P_{lower>0} = 0.104$,

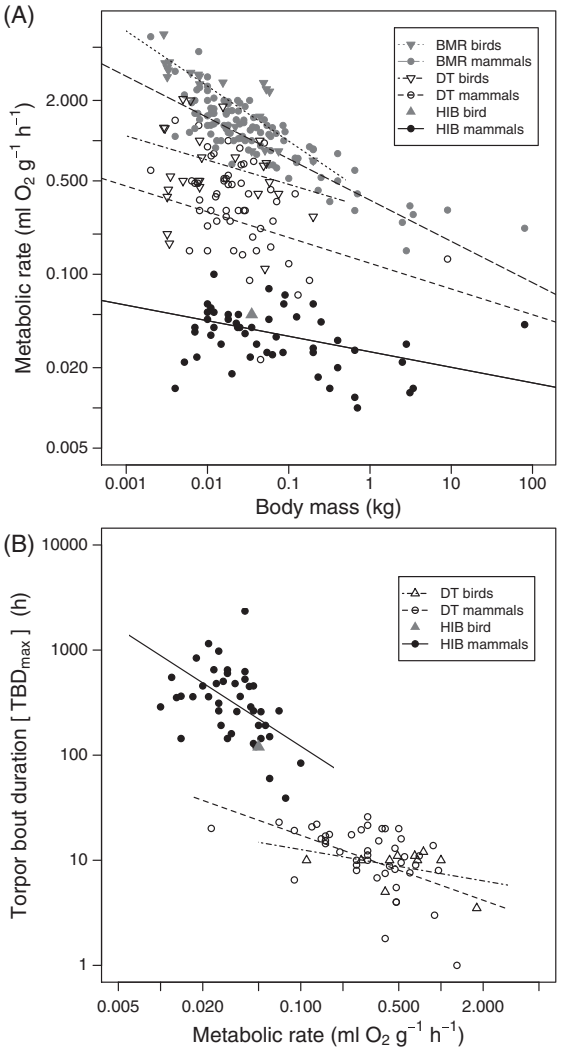

Fig. 8. (A) Basal (BMR) and minimum metabolic rate during torpor (TMR_{min}) as a function of body mass (BM). Regression equations for mass-specific BMR are $\log_{10}BMR = -0.444 - 0.308\ \log_{10}BM$ ($t = -13.9$, $P < 0.0001$, $r^2 = 0.73$) among mammals and $\log_{10}BMR = -0.415 - 0.412\ \log_{10}BM$ ($t = -4.33$, $P < 0.001$, $r^2 = 0.66$) among birds. TMR_{min} also decreased as body mass increased in mammalian daily heterotherms (DT) ($\log_{10}TMR_{min} = -0.917 - 0.192\ \log_{10}BM$, $t = -2.30$, $P = 0.025$, $r^2 = 0.19$). In avian daily heterotherms the slope of this regression was not significantly different from zero ($t = -1.17$, $P = 0.25$). Among hibernating (HIB) mammals the decrease in TMR_{min} with body mass was not pronounced but was statistically significant ($\log_{10}TMR_{min} = -1.579 - 0.116\ \log_{10}BM$, $t = -4.41$, $P = 0.0001$, $r^2 = 0.13$). (B) The relationship between TMR_{min} and maximum torpor bout duration (TBD_{max}). TBD_{max} decreased with increasing TMR_{min} among mammalian hibernators ($\log_{10}TBD_{max} = 1.22 - 0.862\ \log_{10}TMR_{min}$, $t = -4.56$, $P < 0.0001$, $r^2 = 0.20$). A weaker relationship in the same direction was also detectable among mammalian daily heterotherms ($\log_{10}TBD_{max} = 0.76 - 0.475\ \log_{10}TMR_{min}$, $t = -3.92$, $P < 0.001$, $r^2 = 0.27$), but not in avian daily heterotherms ($t = -1.37$, $P = 0.205$).

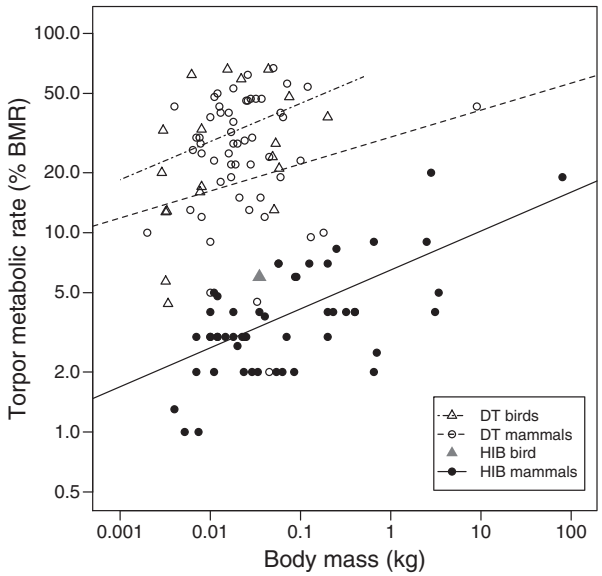

Fig. 9. Metabolic reduction (TMR_{rel} expressed as percentage basal metabolic rate, BMR) as a function of body mass (BM). Slight increases of TMR_{rel} among daily heterothems (DT) were non-significant (birds: $t = 1.12$, $P = 0.275$; mammals: $t = 1.59$, $P = 0.117$). Among hibernating mammals there was a significant relationship between TMR_{rel} and body mass ($\log_{10}TMR_{rel} = 0.81 + 0.20 \log_{10}BM$, $t = 5.40$, $P < 0.0001$, $r^2 = 0.42$).

$P_{upper<1} = 0.171$). No phylogenetic signal was detectable among hibernating mammals ($\lambda = 0$; 95% CI: 0–0.52; $P_{lower>0} = 1$, $P_{upper<1} = <0.0001$).

Adjusted means to 30 g body mass for TMR_{rel} were ~40 and 20% for avian and mammalian daily heterotherms, respectively, but with overlapping 95% CI (Table 2). Among birds, the lowest TMR_{rel} during daily torpor were observed in *Calypte anna* (4.4%) and *Archilochus alexandri* (5.7%); among mammals the lowest values for daily torpor were reported for *Elephantulus rozeti* (2.0%), *Microcebus myoxinus* (4.5%) and *Tarsipes rostratus* (5.0%). Among hibernators, the adjusted mean TMR_{rel} was 4.3% for all species (Table 2) and 4.0% (95% CI: 1.4–6.6) when the two largest values were excluded. The lowest TMR_{rel} was found in a bat, *Vespadelus vulturnus* (1.3%). TMR_{rel} in the single avian hibernator, *Phalaenoptilus nuttallii*, was 6%.

(8) Interbout euthermia

IBE was more variable in hibernators (range 1.5–44 h) than in daily heterotherms (6.8–22 h; Fig. 3, Table 2). IBE was not affected by body mass in either avian or daily heterotherms, but increased significantly with body mass in mammalian hibernators (Fig. 10A). IBE decreased significantly as mass-specific BMR increased among mammalian hibernators (Fig. 10B), but no such relationship was present in daily heterotherms (not shown on graph). IBE contained a phylogenetic signal in mammalian hibernators ($\lambda = 0.77$; 95% CI: 0.19–0.95; $P_{lower>0} = 0.028$, $P_{upper<1} = <0.0001$), but

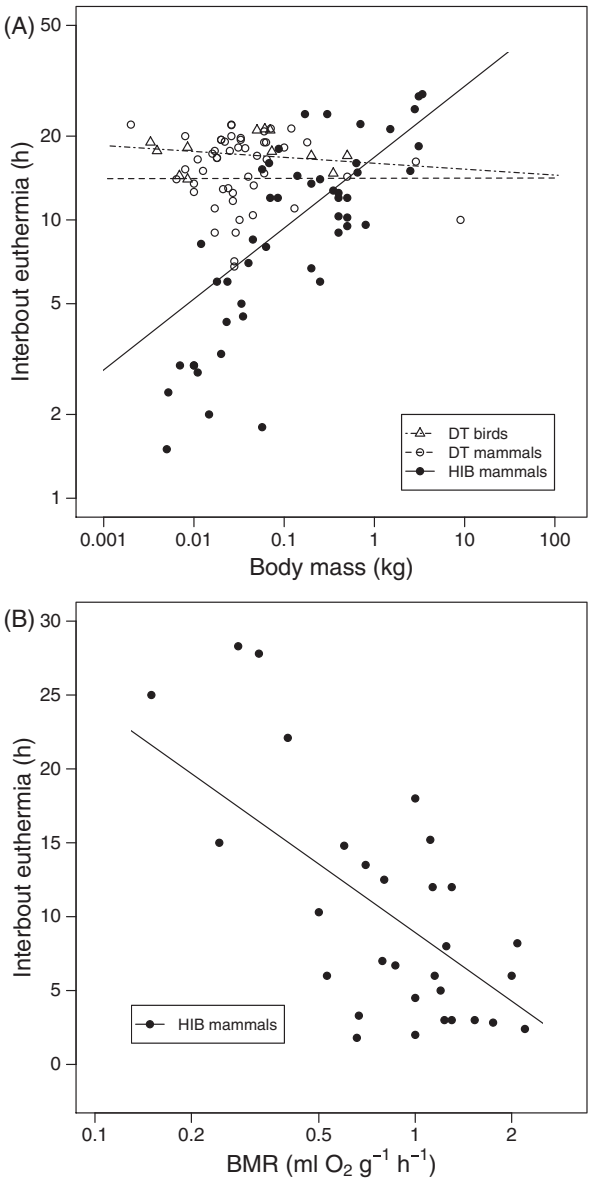

Fig. 10. (A) Duration of interbout euthermia (IBE) as a function of body mass (BM). There was no significant relationship with body mass in avian ($t = -0.59$, $P = 0.562$) or mammalian ($t = 0.01$, $P = 0.987$) daily heterotherms (DT), but the duration of euthermia episodes increased with body mass among mammalian hibernators (HIB) ($\log_{10}IBE = 1.22 + 0.255 \log_{10}BM$, $t = 4.59$, $P < 0.0001$, $r^2 = 0.66$). (B) The relationship between basal metabolic rate (BMR) and IBE in mammalian hibernators ($IBE = 8.92 - 15.39 \log_{10}BMR$, $t = -3.80$, $P < 0.001$, $r^2 = 0.50$). There was no significant relationship in daily heterotherms (data not shown for clarity).

the signal was non-significant among mammalian ($\lambda = 0.63$; 95% CI: 0–0.94; $P_{lower>0} = 0.310$, $P_{upper<1} = <0.0001$) and avian daily heterotherms ($\lambda = 0.53$; 95% CI: 0–1; $P_{lower>0} = 0.394$, $P_{upper<1} = 0.182$). There was no significant relationship between IBE and the latitude of the species' geographical range (all $t \leq 1.1$, $P \geq 0.275$).

IV. DISCUSSION

(1) The classification of types of heterothermy

Our results show that the classical distinction between hibernation and daily torpor is supported by clear differences in most torpor traits. Even traits that showed considerable overlap between the two groups (e.g. $T_{b\,min}$, Fig. 3), when combined with other characteristics such as TMR_{min}, can be used to predict whether a species uses daily torpor or hibernation to a reasonable degree of certainty (Fig. 4). Our results also show that allometric relationships of daily torpor and hibernation characteristics show distinct elevations and slopes if phylogeny is taken into account. Thus, previous analyses that indicated the validity of this distinction of heterothermy types (e.g. Geiser & Ruf, 1995) were not affected by a lack of accounting for similar characteristics of closely related species. The fact that $T_{b\,min}$ was the variable least suited (using cluster analysis) to differentiate between daily torpor and hibernation may also explain why a recent comprehensive study (Boyles *et al.*, 2013), using T_b-based indices of heterothermy, found only very weak evidence to support this classical division. In view of our current analysis, it seems clear that this outcome of Boyles *et al.* (2013) does not identify the absence of distinct types of torpor but merely underlines the problems inherent in focusing on T_b, or T_b-based indices, which, to a greater extent than other variables, are affected by confounding factors such as body mass. Another reason why Boyles *et al.* (2013) found no clear subgroups among heterotherms was probably due to the fact that in their study, data were not restricted to extreme values, i.e. estimates of a species maximum physiological capability. Further, one of the indices used by Boyles *et al.* (2013), the heterothermy index, is intrinsically unable to distinguish between deep/short and long/shallow torpor bouts; given the high predictive value of torpor bout duration indicated by our analyses, this questions the usefulness of the heterothermy index for the purpose of testing for the existence of physiologically distinct subgroups. This also applies to another recently suggested measure, the thermoregulatory index (Muñoz-Garcia *et al.*, 2013) that requires simultaneous measurements of T_b, T_a, and MR, currently limiting its use largely to laboratory situations. While this index may be a sensible measure of the degree of heterothermy at any point in time, it does not include the duration of torpor bouts, which, according to our analysis, was the most prominent distinctive characteristic of torpor types. For these reasons, the avoidance of arbitrary thresholds, which was the major rationale behind the development of the above indices of heterothermy, may also limit their usefulness, at least for classification purposes.

(2) Torpor bout duration and interbout euthermia

Our results show that classifying endotherms as daily heterotherms or hibernators based on a TBD_{max} below or above 24 h, respectively, is highly reliable. The average TBD_{max} for a 30 g hibernator was >30 times greater than in a 30 g daily heterotherm. In our dataset comprising 214 species, there was only one ambiguous species, *Sminthopsis macroura*, which was previously classified as a daily heterotherm despite a TBD_{max} of 25.9 h. However, as pointed out by the authors (Körtner & Geiser, 2009) this maximum duration was measured in a highly unusual torpor bout for this species, which usually had TBDs of 11 h.

As mentioned before, hibernators may express bouts of torpor lasting for less than 24 h. Nevertheless, there are several reasons why hibernation and daily torpor should be considered as two distinct physiological states. Firstly, only one species previously classified as a daily heterotherm (*Elephantulus myurus*) has the capability to exhibit multiday torpor bouts (Fig. 3). Secondly, as demonstrated above, it is possible to separate the vast majority of hibernators from daily heterotherms based on a combination of $T_{b\,min}$ and TMR_{min} alone. It remains to be seen whether those species with both low $T_{b\,min}$ and low TMR_{min} (e.g. *Elephantulus rozeti*) were simply misclassified (based on TBD_{max} alone) and will be found to exhibit multiday torpor in future studies. On the other hand, reliance on extreme characteristics carries the danger of artefacts from unusual laboratory conditions, such as unusually low T_a (Tomlinson, Withers & Cooper, 2007; Lovegrove, 2012*b*), which may have been the case in *E. rozeti*. Very few species were difficult to classify *via* cluster analysis based on TBD_{max}, namely *Elephantulus edwardii* and *E. myurus*, both traditionally viewed as hibernators. At least in the latter species even free-ranging animals occasionally show torpor bouts lasting more than 24 h (Mzilikazi & Lovegrove, 2004). These exceptional cases seem insufficient to question the dichotomy between daily torpor and hibernation, or to postulate a third type of heterothermy (for which there was no evidence in our statistical analyses).

A third, and very important argument for differentiating between the two types of torpor is supported by studies showing that daily torpor is an extension of the circadian rhythm of T_b, and free-runs, i.e. continues with an endogenous period that deviates slightly from 24 h, under constant lighting conditions (Lynch, Bunin & Schneider, 1980; Ruf, Steinlechner & Heldmaier, 1989; Kirsch, Ouarour & Pevet, 1991; Körtner & Geiser, 2000*b*). This is not the case, however, in hibernators, in which the circadian clock seems at least strongly suppressed, although it may still exert some influence on torpor/arousal cycles (e.g. Daan, 1973; Pohl, 1987; Grahn *et al.*, 1994). Some studies suggest that the circadian clock actually is arrested and is restarted only after the hibernation season, at least when hibernators experience naturally low T_a (Hut, Barnes & Daan, 2002*a*; Hut *et al.*, 2002*b*; Ruby, 2003; Malan, 2010). Also, there is evidence that genes involved in the molecular mechanism of the circadian clock, such as *Per1*, *Per2* and *Bmal1*, are expressed constantly, rather than rhythmically, during hibernation (Revel *et al.*, 2007). Hence, although mechanisms of hypothalamic control of T_b or metabolic reduction may be similar in daily heterotherms and hibernators (while T_b

set-points and the degrees of metabolic reduction differ), at least those physiological mechanisms that govern the temporal structure of heterothermy are clearly different between daily torpor and hibernation. Therefore, we concur with Sheriff *et al.* (2012) who suggested that short, shallow torpor bouts (<24 h), which hibernators often exhibit just prior to the hibernation season, physiologically resemble consecutive multiday torpor and should be called 'short torpor', but not 'daily torpor'.

An early attempt to explain variation in TBD was a metabolism-dependent, so-called 'hourglass mechanism' that may control torpor/euthermia cycles. This hypothesis assumes the development of a metabolic imbalance during torpor (e.g. the accumulation or depletion of metabolites or the accretion of cellular damage) that can be eliminated only in the euthermic state (Fisher, 1964; French, 1985). This idea seemed to be supported by a decrease of TBD with body mass (and, by inference, MR), albeit in a very limited sample of mammals (French, 1985). Subsequent, more comprehensive comparisons showed no evidence for such a relationship between TBD and body mass (e.g. Geiser & Ruf, 1995; Malan, 2010), as was confirmed by the present study (Fig. 5A). The absence of an effect of body mass on TBD has been used to argue that torpor–arousal cycles are not governed by metabolism, and to dismiss the hypothesis that arousal from hibernation is driven by an hourglass mechanism (Malan, 2010). A problem with this argument, however, is that in torpid hibernators the dependency of MR on body mass is drastically reduced (Fig. 8A), which renders body mass a very poor proxy for metabolic processes during deep torpor. Therefore, a more direct test of the hourglass hypothesis is evaluating the relationship between MR in torpor (rather than body mass) and the duration of torpor episodes. Our finding of a significant decrease of TBD_{max} with increasing TMR_{min} among hibernators (Fig. 8B), as well as a decrease of IBE with metabolic rate (Fig. 10), is fully compatible with the idea of an hourglass mechanism. If arousal is due to a metabolic imbalance, this imbalance will progress faster at high TMR, and can be eliminated more rapidly at high euthermic MR. Such a mechanism seems a more parsimonious explanation than the assumption of a specialized, non-temperature-compensated circadian torpor–arousal clock, as suggested by Malan (2010). However, the two mechanisms may not be entirely mutually exclusive, because any metabolism-driven hourglass may still be modulated by an endogeneous clock that influences the probability of actual arousal, once a certain metabolic imbalance is reached during torpor. In any case, it should be noted that such an endogenous clock modulating TBD in hibernators, if it exists, must differ anatomically and functionally from the central circadian clock controlling daily torpor (Ruby, 2003; Malan, 2010).

Arguably, the differences between clock mechanisms and respective temporal structures constitute the fundamental difference between daily torpor and hibernation, which has subsequently led to distinct levels of minimum T_b and degree of metabolic reduction. They may explain the fact that most traits showed little overlap between daily heterotherms and hibernators (Fig. 3). As outlined in greater detail previously (Geiser & Ruf, 1995), the advantages of keeping entrained with the light–dark cycle should select against multiday torpor bouts in animals that continue to remain active and forage above ground, i.e. daily heterotherms. Species that opt to employ multiday torpor, on the other hand, should benefit from a larger body mass facilitating higher body energy stores, and from reaching lower TMR_{min} to maximise energy savings. These differences may well have led to disruptive selection and hence to the absence of intermediate types of torpor.

Obviously, further research is necessary to clarify if it is indeed the clock mechanism governing the temporal control of torpor that separates hibernators from daily heterotherms. For instance, it would be interesting to see whether the constant, arrhythmic expression of clock genes in the central circadian pacemaker, which to our knowledge has been demonstrated only in one mammal (Revel *et al.*, 2007), is a general feature of hibernating mammals. We would predict that the massive suppression of clock genes in the central circadian pacemaker is a prerequisite of the capability for consecutive multiday torpor. However, a group of species that may be particularly important to study in this context, because some residual circadian clock activity may be adaptive for them, are those hibernators that occasionally show above-ground activity during winter, such as hedgehogs (Morris, 1973) which may be exposed to light/dark cycles. Since our present analysis supports the hypothesis of an hourglass mechanism driving torpor–arousal cycles in hibernators, it points to a need for a renewed search for the nature of the 'metabolic imbalance' that seems to accumulate during torpor (e.g. Fisher, 1964; French, 1985). It may be promising to concentrate this search on physiological functions that are paramount for survival at low T_b, and that have been previously suggested to play a role in the induction of arousals, namely brain and heart function (Daan, Beersma & Borbély, 1984; Carey, Andrews & Martin, 2003; Ruf & Arnold, 2008; Giroud *et al.*, 2013). Advanced methods of genomics, transcriptomics and proteomics could help to identify molecular targets whose accumulation or depletion rates correlate with the durations of torpor bouts and interbout euthermia. Finally, another possible (albeit time-consuming) approach to clarify better the physiological differences between daily torpor and hibernation are artificial selection regimes designed to select either for or against long/deep torpor (again, along with genomics/transcriptomics or proteomics studies to identify molecular factors that may differ between selection lines). The most promising models for such a project may be those species with torpor characteristics that seem to be borderline between daily torpor and hibernation, such as *Elephantulus* spp.

There are further differences apart from circadian system functionality in winter, mainly concerning the seasonal control of torpor, that appear generally to differ between hibernators and daily heterotherms. For instance, several hibernators make use of an endogenous circannual clock

that drives the onset and termination of the hibernation season (Pengelley & Fisher, 1963; Pengelley & Asmundson, 1969; review in Körtner & Geiser, 2000*a*), whereas the seasonal occurrence of daily torpor is often triggered by short photoperiods (e.g. Lynch *et al.*, 1978; Ruf *et al.*, 1993), shortage of food or low ambient temperatures (e.g. Hainsworth, Collins & Wolf, 1977; Hudson & Scott, 1979; Ruf *et al.*, 1993; Silva-Duran & Bozinovic, 1999). Hibernation and daily torpor also differ in that the former typically relies on the availability of substantial energy reserves, either body fat or food stores, whereas daily torpor is accompanied by continued foraging. This factor likely contributed to our finding of a significant difference in body mass between daily heterotherms and hibernators. Although this variable showed the largest overlap between the two types of torpor, mean and median body mass was several times larger in hibernators. As pointed out previously (Lindstedt & Boyce, 1985; Calder, 1996), small body mass constrains the size of body fat stores, not just absolute storage amounts but also in terms of the proportion of body fat. Hence hibernators, which seem to rely mostly on endogenous energy stores, i.e. body fat (Humphries, Thomas & Kramer, 2003*b*), will benefit from larger body sizes. Daily heterotherms, on the other hand, which continue to forage, should benefit from a functional circadian system that keeps them entrained with the light–dark cycle and serves to optimize times of daily activity and rest. The need to continue foraging also explains why both TBD_{mean} and TBD_{max} among daily heterotherms peaked well below 24 h (Fig. 3; means: ~7 h for TBD_{mean} and ~10 h for TBD_{max}; Table 2) as this average duration of daily torpor leaves sufficient time for foraging within the daily cycle.

Continued foraging *versus* reliance on energy stores would also help to explain why, on average, species using daily torpor have distribution ranges at lower latitudes, whereas hibernators extend geographic ranges closer to the poles. This result – which, to our knowledge, has not been reported previously – almost certainly reflects adaptations to increasing seasonality of habitats at higher latitudes and the absence of food resources in the environment during winter, favouring physiological responses that rely on energy reserves. The fact that among hibernators, and only in this subgroup, body mass increases with latitude can also be understood in terms of increased capacity for body fat stores in larger animals. However, this effect may also be explained in terms of Bergmann's rule (Bergmann, 1848), i.e. the concept that colder climates select for increased body sizes because the associated decrease of relative body surface area reduces heat loss. For a more detailed discussion of the effects of environmental conditions on body mass in hibernators see Gür (2010) and Ozgul *et al.* (2010).

The absolute latitude of the species' geographic range was also a significant predictor of TBD_{max}, and even more so of TBD_{mean}, among hibernators (Figs 5 and 6). To our knowledge this is also a novel finding, as the effects of latitude on hibernation characteristics have not been investigated previously (but see Boyles *et al.*, 2013, for effects of latitude on the general degree of heterothermy). TBD was not associated with latitude, however, among daily heterotherms (Figs 5 and 6). The absence of this effect among daily heterotherms, as outlined above, is most likely due to the fact that TBD_{max} is constrained to <24 h in order to maintain entrainment with the light–dark cycle. Mean and maximum TBD in hibernators increased towards higher latitudes, indicating that most hibernating mammals prolong torpor (even if it does increase energy savings) only if environmental conditions dictate such a behaviour. In some cases, species that hibernate for several months at higher latitudes may remain euthermic and even reproduce during winter in warmer parts of their geographical distribution range (e.g. the garden dormouse, Gil-Delgado *et al.*, 2006). Striking differences in the use of torpor and hibernation, likely due to local climatic conditions, may even occur on a small geographical scale (Lehmer *et al.*, 2006). Incidentally, this degree of flexibility in the use of prolonged torpor also questions the validity of the terms 'obligate' *versus* 'facultative' hibernator.

It is evident that the coldest winter habitats at extreme latitudes require the most profound energy savings. This would explain why hibernators lengthen TBD with decreasing T_a and T_b in torpor (e.g. French, 1982; Hut *et al.*, 2002*a*; Bieber & Ruf, 2009). This seems the most straightforward proximate physiological mechanism that links low hibernaculum temperatures, *via* $T_{b\,min}$, to decreased energy expenditure. On the other hand, high-latitude geographical ranges are also characterized by long periods of low food availability, which also should promote the use of energy stores and hibernation, independent of cold load. It has long been recognized that factors other than low T_a can be a major selective force favouring hibernation, such as seasonal droughts, which often occur even in subtropical and tropical environments (Darwin, 1845).

Even when adjusted for the effect of latitude, there was still a large residual variation in both maximum and mean TBD in our analyses, likely caused by species-specific factors not accounted for here. It appears that TBD_{max} and other characteristics of hibernation (or torpor in general) result from both the benefits and costs of hypometabolic states (Humphries, Kramer & Thomas, 2003*a*; Humphries *et al.*, 2003*b*). The costs of prolonged torpor are evident from the fact that within a species, animals overwintering in mild winters apparently avoid its use (e.g. Gil-Delgado *et al.*, 2006; Lehmer *et al.*, 2006). Further, supplemental feeding of food-hoarding hibernators can significantly reduce their use of torpor (Humphries *et al.*, 2003*a*) and individuals with high body energy reserves among fat-storing hibernators reduce torpor use and increase euthermic episodes during winter (Zervanos, Maher & Florant, 2013; Bieber *et al.*, 2014). While these observations indicate that torpor use is minimized whenever possible, the physiological mechanisms generating costs are not as easy to pinpoint. One physiological function that may be impaired is memory (Millesi *et al.*, 2001), but this effect may be species specific (Clemens, Heldmaier & Exner, 2009). It has also been hypothesized that torpor may represent a state of sleep deprivation, but there was little

experimental support for this hypothesis (review in Kräuchi & Deboer, 2011). Further, torpor at low T_b is associated with extreme immune-suppression that is reversed during periodic arousals (Burton & Reichman, 1999; Prendergast *et al.*, 2002; Bouma, Carey & Kroese, 2010). Generally, immune-suppression during torpor is probably beneficial as it saves energy, protects from inflammatory processes, and typically has little risks since most microbes proliferate very slowly at low temperatures (Ma *et al.*, 2005; Bouma *et al.*, 2010). However, impaired immune function during hibernation may increase the risk of contracting certain viral or fungal diseases that can be lethal (Prendergast *et al.*, 2002; Bouma *et al.*, 2010). Torpor also seems to be associated with increased oxidative stress and the potentially costly up-regulation of antioxidant defences (Buzadžić *et al.*, 1997; Carey, Frank & Seifert, 2000; Ni & Storey, 2010). Recent evidence from edible dormice (*Glis glis*) suggests that despite up-regulated antioxidant defences, arousals from deep hibernation are associated with cellular damage in terms of shortening of telomeres, i.e. the repeated sections of DNA that ensure the integrity of the ends of chromosomes (Turbill *et al.*, 2013). This effect may be directly related to rewarming from low T_b as the use of daily torpor in Djungarian hamsters (*Phodopus sungorus*; with much higher $T_{b\,min}$), was found to have a positive effect on relative telomere lengths (Turbill *et al.*, 2012).

The benefits of torpor are easier to characterize, because they were the focus of past research. In particular, it has been known for some time that hibernation and daily torpor result in significant energy savings (Hall, 1832; Darwin, 1839; Wyss, 1932; Kayser, 1939). However, recent data identify several other beneficial functions of torpor. Torpor facilitates migration in certain birds; it is an integral part of reproductive strategies that involve sperm storage in certain bats and other mammals; it can primarily serve as a water-conservation mechanism; and it was found to lower the risk of extinction (review in Geiser & Brigham, 2012). The latter finding is due to the fact that hibernation, which typically is associated with retreat into underground burrows and other secluded areas, decreases predation risk and, although often assumed otherwise, leads to much higher survival rates than during the active season in the same species (review in Turbill, Bieber & Ruf, 2011). The fact that torpor indirectly facilitates predator avoidance may help to explain why both hibernators and daily heterotherms have relatively low body masses, compared to terrestrial mammals on average: large mammals have fewer predators and extrinsic mortality decreases as body mass increases (Owen-Smith & Mills, 2008; Ricklefs, 2008). Further, large animals seem unable to dig underground burrows, which prohibits this avenue of predator avoidance, but maintain high alertness and fast flight, which are incompatible with deep torpor. Obviously, further important energetic reasons, related to T_b and TMR_{min} (see Section IV.3) may account for the finding that hibernation and daily torpor become exceedingly rare as body size increases.

(3) Minimum body temperature in torpor

The $T_{b\,min}$ of a typical 30 g mammal was 13°C lower in hibernators than in mammalian daily heterotherms (and 18°C lower than in birds showing daily torpor). However, there was also considerable overlap between these subgroups (Figs 3 and 7) confirming the earlier conclusion that $T_{b\,min}$ alone is not well suited to discriminate between hibernation and daily torpor (Geiser & Ruf, 1995).

$T_{b\,min}$ increased significantly with body mass in all groups, whether apparent outliers (i.e. large carnivores with $T_{b\,min}$ >20°C) were included or not. This differs from euthermic mammals, in which resting T_b shows no allometric relationship with body mass (Lovegrove, 2012*c*). Our present result also differs from previous analyses of smaller samples that did not find an effect of body mass on $T_{b\,min}$ among hibernators (Geiser & Ruf, 1995). One might be tempted to attribute this increase of $T_{b\,min}$ to effects of thermal conductance decreasing as body mass increases. However, based on the allometric equation for conductance in mammals (Bradley & Deavers, 1980) the increase of $T_{b\,min}$ (in animals at steady state with identical TMR_{min}) would only be 2.5°C for an increase in body mass from 10 g to 10 kg. The observed effect was much larger (+6°C) over this body mass range among mammalian hibernators even after removal of outliers, and even larger (+11 to 17°C) in daily heterotherms (Fig. 7). Moreover, whereas large body size and the ensuing greater heat capacity may create time constraints for entrance into and rewarming from daily torpor, this factor should be negligible in hibernators that may stay torpid for several weeks. Therefore, we suggest that small animals, with higher mass-specific metabolic rates, select a low $T_{b\,min}$ in order to reach TMR_{min} similar to those achieved by larger animals. Lower $T_{b\,min}$ will always be associated with lower TMR_{min} irrespective of whether metabolic reduction results from active metabolic depression (with decreasing $T_{b\,min}$ as a side effect) or from temperature effects (*cf*. Carey *et al.*, 2003). The finding that many large animals maintain relatively high $T_{b\,min}$ provides further support for the view that the torpid state appears to be associated with risks or physiologically adverse effects, making the regulated depth of torpor the evolved result of a trade-off between its costs and benefits. Since the use of energy reserves, namely body fat stores, to cover energy expenditure inevitably will be lower in small animals (Calder, 1996), it is not surprising that they are apparently forced to undergo extremely deep torpor bouts, and to risk adverse consequences such as cellular damage during arousals (Turbill *et al.*, 2013).

Another factor associated with very low $T_{b\,min}$ during hibernation is very low ambient temperatures, down to ~ −20°C in hibernacula of the Arctic ground squirrel (*Spermophilus parryii*) (Barnes, 1989). Whereas several species may reach $T_{b\,min}$ below 0°C at low T_a, supercooling seems limited to $T_{b\,min}$ above −3°C (Table 1). This is probably because in the supercooled state, animals are vulnerable to ice nucleation and freezing (Boyer & Barnes, 1999), and ice formation is much slower at high subzero temperatures

(Storey & Storey, 2013), which also may allow hibernators to escape freezing by arousal.

The highest $T_{b\,min}$ during torpor, on the other hand, are maintained by large carnivores (*Meles meles*, *Ursus americanus*, *Ursus arctos*). This differentiates them from other hibernators more than the TMR (although data on TMR_{min} are currently available only for *U. americanus*). This suggests that adverse effects of torpor may be due to, in particular, low $T_{b\,min}$. Black bears and other large carnivores seem to avoid adverse effects of low T_b by maintaining body temperatures >28°C (Fowler & Racey, 1988; Tøien *et al.*, 2011). Notably, in *U. americanus*, even at this high T_b, TMR_{min} reached a level (0.042 ml O_2 g^{-1} h^{-1}) that was within the 95% confidence interval of the mean among hibernators (0.036–0.043 ml O_2 g^{-1} h^{-1}). Arguably then, an efficient type of torpor that combines metabolic reduction typical for hibernation with an almost euthermic T_b, has evolved in these large carnivores. It remains to be clarified, however, whether torpor in these 'denning' species is a separate type of heterothermy or simply represents an extreme in a continuum of hypometabolic states, and resulting body-mass-related T_b reductions among hibernators. In any case, the fact that high T_b apparently does not constrain the TMR_{min} argues against the usefulness of the term 'deep hibernator' sometimes used in the literature to characterize species. Neither our analysis of $T_{b\,min}$ nor that of TMR_{min} or TMR_{rel} point to the existence of distinct subgroups within hibernators.

Adverse effects of a reduction in T_b, even if decreases in T_b are small as in bears, may also explain the conspicuous absence of torpor and hibernation in its typical form in certain taxonomic groups such as the ungulates. Even under extremely harsh environmental conditions, as experienced for instance by the Svalbard reindeer (*Rangifer tarandus*), these animals do not use torpor but remain euthermic throughout winter (Blix, 1989). In the past, drastic reductions of food intake during winter were thought to be primarily due to a marked reduction in locomotor activity, a behaviour called 'Arctic resignation' (Blix, 1989). There is, however, increasing evidence that both Cetartiodactyla and Perissodactyla are also capable of profound hypometabolism in winter (Arnold *et al.*, 2004; Kuntz *et al.*, 2006; Signer, Ruf & Arnold, 2011). Importantly however, such reductions in winter metabolic rate in red deer (*Cervus elaphus*), horses (*Equus ferus przewalskii*), or alpine ibex (*Capra ibex*) were associated with reduced peripheral tissue temperatures, rather than core temperatures (e.g. Arnold *et al.*, 2011). It remains to be seen how many endothermic species (perhaps including marine mammals) use this type of hypometabolism, which is much less conspicuous than hibernation or daily torpor, as an alternative over-wintering strategy. As suggested by Lovegrove (2012*c*) one reason for the maintenance of high euthermic T_b and the avoidance of torpor may be a cursorial lifestyle, e.g. in several Lagomorpha, Artiodactyla, Perissodactyla and Carnivora, which requires high T_b for maximum muscle function and high running speed (Clarke & Pörtner, 2010; Rojas, Körtner & Geiser, 2012). An interesting open question in this context is however, whether even cursorial animals when using peripheral cooling may sacrifice some flight or hunting capability for energy savings under harsh winter conditions.

(4) Metabolic reduction

TMR, both in terms of absolute and relative MR, was another trait that clearly separated daily heterotherms from hibernators. For a 30 g mammal, TMR_{min} in hibernators was only 16.7% of that in daily heterotherms, and there was little overlap in TMR_{min} between these subgroups (Fig. 8). The degree of reduction of TMR_{min} below BMR was similar in avian and mammalian daily heterotherms (Fig. 8), resulting in statistically equivalent TMR_{rel} in these groups (Fig. 9).

TMR_{min} decreased with increasing body mass in both mammalian daily heterotherms and hibernators (Fig. 8). Among hibernators, the slope of this relationship was only −0.116, but was significantly different from 0. In a smaller subsample of hibernators TMR_{min} previously appeared to be body-mass independent (Geiser & Ruf, 1995), but a slope (−0.128) very similar to our present findings was reported previously (Geiser, 2004), suggesting that TMR_{min} in hibernators does indeed decrease slightly with body mass.

This observation raises the question why small mammalian hibernators do not reduce TMR_{min} further? We hypothesize that there may be at least two reasons: (*i*) high thermal conductance forces small mammals to spend more energy to maintain a certain $T_b - T_a$ gradient in torpor than larger animals. (*ii*) Small species, which have to reduce MR when entering torpor from a high mass-specific BMR, may be limited by the extent of possible TMR reductions. For instance, one component of the 'metabolic machinery' that generates higher BMR in small animals is mitochondrial basal proton leak, which is associated with increased membrane polyunsaturated fatty acid content (reviews in Hulbert & Else, 2005; Polymeropoulos *et al.*, 2012). Although proton leak decreases with T_b (Polymeropoulos *et al.*, 2012), and seems to be actively suppressed during hibernation (Barger *et al.*, 2003), it is most likely never entirely absent. Hence, differences in membrane composition and proton leak that affect BMR may well still be present in the torpid state and could at least partly explain the mass dependency of TMR_{min}.

The relative reduction of metabolic rate TMR_{rel} (i.e. TMR_{min} expressed as a percentage of BMR) was highly variable among both avian and mammalian daily heterotherms (Fig. 9). This can be attributed partly to measurement error in both BMR and TMR_{min}, used to compute TMR_{rel}. In very small mammals and birds, it may be almost impossible to obtain 'true' values of BMR, because these animals are rarely in a genuinely post-absorptive, euthermic state at rest. Among mammalian hibernators, however, there was less variation in TMR_{rel}, and after the removal of two apparent outliers it was best described by a constant, i.e. 4% of BMR. Some of the variability in species displaying daily torpor may also be due to the maintenance of large $T_b - T_a$ gradients in some daily heterotherms, while, at least in most hibernators, T_b typically is very close to T_a (e.g. Heldmaier & Ruf, 1992; Arnold, 1993; Bieber & Ruf, 2009).

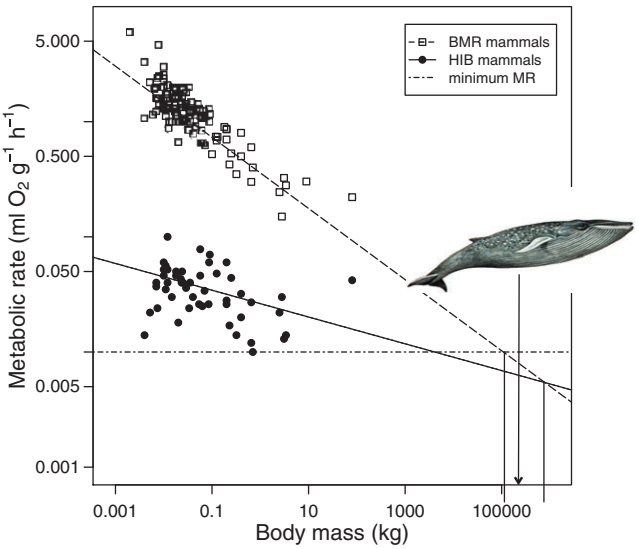

Fig. 11. Basal (BMR) and hibernation (HIB) metabolic rates among mammals intersect at a body mass close to that of the largest animal known to have existed, the blue whale *Balaenoptera musculus*. Body mass of endotherms may reach an upper limit due to excess heat production if BMR cannot be reduced below the minimum metabolic rate (MR) reached during hibernation.

Interestingly, the degree of metabolic reduction during mammalian hibernation is similar to the extent of metabolic depression reported in many other animals (e.g. molluscs, crustaceans, or reptiles; Guppy & Withers, 1999). However, much lower metabolic rates and degrees of depression can be reached by invertebrates under conditions such as desiccation, freezing, supercooling, and oxygen deficiency, down to a virtually complete absence of metabolism in diapaused eggs of brine-shrimps (Clegg, 1997). In mammals, the lowest MR_{min} reported was 0.01 ml O_2 g^{-1} h^{-1} in the hedgehog (*Erinaceus europaeus*) (Thäti, 1978). Conceivably, this may be close to the absolute minimum metabolic rate attainable by mammals, or even endothermic vertebrates in general. If this is true, this minimum metabolic rate would be identical to the predicted BMR for an animal of a body mass of 115 tonnes, intriguingly close to the mass of the largest known animal, the blue whale (*Balaenoptera musculus*; weighing up to 170 tonnes; Fig. 11). Even if mammals could decrease their cellular metabolism further, as predicted by the regression for TMR_{min}, minimum metabolism would be equal to BMR at a body mass of 750 tonnes, still within the same order of magnitude (Fig. 11). Thus, an absolute lower limit of MR around or slightly below 0.01 ml O_2 g^{-1} h^{-1} may well constrain the upper limit of body mass that can be reached by a mammal. This is because BMR generates just sufficient heat at thermoneutrality to keep T_b at euthermic levels. It seems that blue whales always live at temperatures within or above their thermoneutral zone (Lavigne *et al.*, 1990), and arguably will face thermoregulatory problems when heat production is elevated due to locomotion or lactation (Hokkanen, 1990). Of course, specialized heat-dissipation mechanisms, such as increased blood flow to body appendages may have co-evolved with larger body size. Still, even with such adaptations, there may be a maximum body mass at which endotherms are unable to dissipate the excess heat generated by their BMR plus other processes, and overheat with detrimental consequences (Speakman & Król, 2010).

(5) Phylogeny, torpor use, and its apparent absence in certain taxa

Many of the variables investigated here contained a significant phylogenetic signal. This underlines the need for phylogenetically informed statistics in this context, although it seems that using these methods has only confirmed the classical view that daily torpor and hibernation are distinct adaptations (e.g. Geiser & Ruf, 1995). Differences in the strength of a phylogenetic signal between traits and subgroups can be partly explained by differences in the variation of torpor variables. For instance, coefficients of variation (CV, i.e. SD/mean) were very low for TBD_{max} in avian (0.27) and mammalian (0.47) daily heterotherms, in which the timing of bouts is controlled by the circadian system. Not surprisingly then, there was no significant phylogenetic signal in this variable. In mammalian hibernators, on the other hand, TBD_{max} varied considerably (CV = 1.58), and included a strong phylogenetic signal. Overall there was a significant correlation between the coefficient of variation of a variable and Pagel's λ (Spearman's rho = 0.68, $P < 0.002$, $N = 18$), indicating that phylogenetically close species had similar characteristics whenever variation was not constrained. Notably, several variables, such as $T_{b\,min}$ in mammals, contained a strong phylogenetic signal even when the effect of body mass on these variables was statistically eliminated. Thus, phylogenetic signals in torpor variables were not just due to the fact that closely related species typically have similar body masses.

The finding that closely related species showed similar torpor characteristics is fully compatible with a plesiomorphic origin of heterothermy. The view that torpor is an ancestral trait dates back at least to the 19th century (reviewed in Johnson, 1931) and was subsequently reinforced by several authors, based on different arguments (e.g. Eisentraut, 1956; Kayser, 1961; Grigg, Beard & Augee, 1990, 2004; Augee & Gooden, 1992; Malan, 1996; Lovegrove, 2012*b*). There also seems to be a prevailing view that daily torpor, i.e. 'circadian heterothermy' (Malan, 1996), represents the ancient trait, whereas prolonged hibernation, especially in cold environments, is viewed as an advanced, secondary adaptation (Malan, 1996; Grigg *et al.*, 2004; Lovegrove, 2012*b*). However, our present phylogenetic analysis does not rule out that heterothermy may have evolved independently in birds and mammals (*cf*. Geiser, 1998). Also, significant phylogenetic signals in torpor characteristics could be detectable if heterothermy evolved more than once in separate mammalian clades, e.g. in marsupials and placentals (discussed in Geiser, 2008). It seems entirely unlikely, however, that heterothermy involved independently in at least 11 mammalian orders (Fig. 2). Thus, a single origin of heterothermy, with subsequent adaptive adjustments

depending on the biology of each species, seems the most parsimonious view, and this explanation has recently gained some evidence from a phylogenetic statistical analysis (Lovegrove, 2012*a*).

If heterothermy indeed is a plesiomorphic trait, this raises the question why it is absent in many extant endotherms. As pointed out previously, there may well be physiological specializations and ecological conditions within certain taxa that preclude modes of energy conservation involving large drops in core T_b (*cf*. Ruf *et al.*, 2012; Lovegrove, 2012*b*). Adverse effects of torpor, such as memory loss (Millesi *et al.*, 2001) or impaired muscle function (Clarke & Pörtner, 2010; Rojas *et al.*, 2012) may have selected against torpor whenever environmental conditions in terms of climate and food availability permit continued euthermia. This view is supported by the observation that certain species may make extensive use of heterothermy under harsh, but to a much lesser extent or not at all under mild winter conditions (e.g. Lehmer & Biggins, 2005; Gil-Delgado *et al.*, 2006; Dunbar & Brigham, 2010). Even in cold climates, costs associated with torpor may have favoured the evolution of alternatives such as increased body size (e.g., Secord *et al.*, 2012), which lowers heat loss due to a reduced relative body surface area and additionally facilitates the development of long, well-insulating fur (Scholander *et al.*, 1950). Surprisingly then, at least at first glance, many small mammals save energy by a reduction of body mass towards winter. Because such a reduction of body size is typically accompanied by moulting to winter fur with improved insulation, the net effect is a decrease of total energy expenditure (review in Heldmaier, 1989). Small endotherms also show various other adaptations that allow overwintering under harsh conditions without torpor. In several species of shrews, tree squirrels or moles, for instance, these adaptations include the use of elaborate nests, thermally buffered burrow systems, reliance on abundant, energy-rich prey, and food hoarding (e.g., Thompson & Thompson, 1980; Genoud, 1985; Merritt, 1986; Larsen *et al.*, 1997). In grey squirrels (*Sciurus carolinensis*), the hoarding strategy is further augmented by specialized cognitive functions that allow for very high rates of recovery of cached food (Jacobs & Liman, 1991). Another adaptation of both small and large endotherms that significantly decreases energy expenditure is reduced activity during the coldest winter periods (e.g. Merritt, 1986; Blix, 1989). There are of course further avenues by which endotherms, depending on their ecology, may avoid torpor even under severe climatic conditions.

However, even considering adverse effects of torpor and alternative adaptations, the number of heterotherms (171 mammalian, 43 avian species) examined here appears to represent a stunningly small minority of all mammals (>5000 species) and birds (>10000 species). As noted by McKechnie & Lovegrove (2002) for birds, the limited number of orders and families with species known to use heterothermy is surprising. There are of course a number of species for which some indication of heterothermy has been observed (for examples of such cases, see Lovegrove, 2012*b*), but not enough quantitative information was available for inclusion in our present analysis. Even so, the number of known heterotherms remains very limited. One might be tempted to conclude that this is simply related to the fact that the vast majority of species live in the tropics. Indeed, the mean geographical distribution range of all terrestrial mammals is located at an absolute latitude of approximately 17.5°, considerably lower than that of daily heterotherms (25°) or hibernators (35°) alone. The same holds for birds for which species richness peaks in the tropical band (0–5°, Kissling, Sekercioglu & Jetz, 2012), while heterothermic birds had geographical ranges at a mean latitude of 23°. However, heterothermic species – at least in certain taxa – commonly occur even in the tropics (e.g. McKechnie & Lovegrove, 2002; Dausmann, Glos & Heldmaier, 2009; Geiser & Stawski, 2011). Relatively low numbers of known tropical heterotherms – as in the dataset examined here – are, to a certain degree, likely caused by a bias in the distribution of researchers and their preferred study species (Lovegrove, 2000). To some degree, this may have also biased our results on the latitudinal distribution of heterotherms. Another reason for the limited overall number of known heterothermic species may be the fact that only a relatively small fraction of species and families have been investigated systematically with regard to torpor use (Geiser & Körtner, 2010; Lovegrove, 2012*b*).

An additional cause for the apparent absence of heterothermy in some species may be the use of captive individuals in investigations, perhaps not necessarily reflecting the biology of free-ranging individuals. Animals in captivity are often stressed and may not behave like their free-ranging conspecifics with regard to torpor use. This seems to be especially pronounced in birds. For instance, in captivity, frogmouths (*Podargus strigoides*) and kookaburras (*Dacelo novaeguinea*) maintain stable euthermic T_b even at low T_a (McNab & Bonaccorso, 1995; Bech & Nicol, 1999; Buttemer, Nicol & Sharman, 2003), whereas free-ranging individuals regularly reduce T_b by up to 10°C on cold winter nights (Körtner, Brigham & Geiser, 2000; Cooper *et al.*, 2008). Moreover, under laboratory conditions, substantial decreases in T_b have been recorded only in small birds and often only after severe starvation (Marshall, 1955; Lasiewski & Dawson, 1964; Peiponen, 1965; Dawson & Fisher, 1969). In the field, some of the same species frequently enter torpor even under apparently favourable environmental conditions (Brigham, 1992; McKechnie & Lovegrove, 2002; Doucette *et al.*, 2012). Therefore, we expect that even among birds, which typically can avoid periods of unfavourable conditions by migration, future studies will uncover many more heterothermic species that express not only daily torpor but perhaps also hibernation.

Mammals also may resist entering torpor in captivity. Free-ranging echidnas (*Tachyglossus aculeatus*) hibernate in many areas of Australia, including warm habitats (Grigg, Beard & Augee, 1989; Nicol & Andersen, 1996). By contrast, they are reluctant to do so in captivity. In sugar gliders (*Petaurus breviceps*), daily torpor is shallow and rare in captivity, whereas deep and frequent torpor bouts occur in the wild

under similar environmental conditions (Geiser, Holloway & Körtner, 2007). Moreover, edible dormice (*Glis glis*) are extremely reluctant to hibernate in captivity unless they are allowed to dig their own hibernacula or are provided with elaborate artificial burrows (Wilz & Heldmaier, 2000; Bieber & Ruf, 2009). Finally, species or entire groups may be misclassified as homoeothermic based on non-systematic, short-term investigations of torpor use. This was the case, for example, for shrews and pteropodid bats, which were regularly described as being entirely homeothermic (Stoddart, 1979; Ransome, 1990), although experimental evidence clearly shows otherwise (Table 1). Especially among bats, there are probably a much larger number of heterothermic species than currently known (Geiser & Stawski, 2011; Lovegrove, 2012*a*,*b*). Similar incorrect conclusions were drawn from early evolutionary examinations on murid rodents including the house mouse (*Mus musculus*) (Cade, 1964) and the rock elephant shrew (*Elephantulus edwardii*) (Leon, Shkolnik & Shkolnik, 1983). Thus, it is likely that with an increasing number of studies on free-living animals and more systematic work on the thermal biology of mammals and birds, the number of known heterotherms will increase enormously.

V. CONCLUSIONS

(1) Daily torpor and hibernation are distinct physiological adaptations, and species employing these two types of metabolic reduction differ particularly in their maximum (and mean) torpor bout duration, as well as their capacity for absolute and relative reduction of metabolic rate. Hibernators, on average, reach lower $T_{\mathrm{b\,min}}$ than daily heterotherms, have higher body masses, and live at geographical ranges closer to the poles.

(2) Arguably, a fundamental difference between daily heterotherms and hibernators is the temporal structure of torpor patterns. Daily heterotherms employ the circadian system to control torpor timing in order to stay entrained with the light–dark cycle, which facilitates continued foraging. By contrast, hibernators appear to have uncoupled their temporal control of torpor from the circadian system to allow prolonged bouts of hypometabolism and reliance on energy stores.

(3) Within each functional group, most torpor traits ($T_{\mathrm{b\,min}}$, $\mathrm{TMR_{min}}$, $\mathrm{TMR_{rel}}$) are significantly affected by body mass, suggesting a dependence on metabolic processes. Even though torpor bout duration is independent of body mass, it decreases with an increase in mass-specific TMR among hibernators. Moreover, the duration of euthermic intervals between hibernation torpor bouts decreases as euthermic metabolic rate (BMR) increases. These observations support the classical hypothesis that torpor–arousal cycles in hibernators (but not in daily heterotherms) are driven by a metabolism-dependent imbalance that accumulates during torpor and is eliminated during interbout euthermic phases.

(4) The degree of metabolic reduction during mammalian hibernation is similar to the extent of metabolic depression in many other animal groups (e.g. molluscs, crustaceans or reptiles). We suggest that the absolute minimum MR observed in hibernators ($\sim$0.01 ml O_2 g^{-1} h^{-1}) may constrain the maximum body mass of mammals – or even of endotherms in general – because this MR will generate excessive heat load under thermoneutrality at body masses exceeding approximately 100 tonnes.

(5) Most torpor traits, if they are not constrained for ecological (i.e. $\mathrm{TBD_{max}}$ in daily heterotherms) or physiological (i.e. $\mathrm{TMR_{min}}$ in hibernators) reasons, contain a significant phylogenetic signal, that is, closely related species often show similar characteristics. This supports the view of a plesiomorphic origin of torpor, with adaptive adjustments to the environmental conditions and ecology of each species.

(6) Species-specific adaptations to certain habitats or resources may, on the other hand, also lead to the avoidance of torpid states that are associated with low core T_{b}. This is because decreased T_{b} also has adverse effects, such as an impairment of muscle function and maximum running speed. These costs of torpor may explain why many endotherms even in harsh environments employ alternative avenues of overwintering, such as food hoarding, building of elaborate nests, reducing activity or, particularly in large endotherms, regional heterothermy.

(7) Possible adverse effects of torpor alone do not sufficiently explain however, why the occurrence of torpid states has been demonstrated only in several hundred out of >15000 bird and mammal species. We largely attribute this fact to a scarcity of studies on undisturbed, free-ranging animals. Given the availability of new devices to measure T_{b} and/or MR in the field, we expect that the number of species known to exhibit torpor will increase substantially.

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VIII. APPENDIX: DEFINITIONS OF KEY TERMS

Daily heterotherms

Endothermic species of mammals and birds that use daily torpor.

Daily torpor

A period of controlled reduction of metabolism and body temperature in daily heterotherms lasting for less than one day, typically less than 12 h. The timing and duration of daily torpor is controlled by the circadian clock which ensures that bouts of torpor alternate with the resumption of euthermic functions such as activity, foraging, and sleep within the 24 h daily cycle.

Ectotherm

An organism whose metabolic heat production is low and therefore its body temperature is usually close to that of the environment. Ectotherms generally lack insulation.

Endotherm

An organism with the capacity for high metabolic heat production by the use of shivering and/or non-shivering thermogenesis.

Eutherm (=normotherm)

The physiological state during which a heterothermic endotherm displays high (typically $>>30^{\circ}$C) body temperatures. These terms are used pragmatically, without intending to suggest that high body temperatures are always beneficial (the greek 'eu') or normal (as torpor can be considered the normal state for many hibernators).

Heterothermic endotherm

An organism that is capable of homeothermic thermoregulation, but at certain times of the day or the year enters a state of torpor.

Hibernation or multiday torpor

A sequence of multiday torpor bouts, during which metabolism decreases significantly below basal metabolic rate and body temperature is often lowered, typically interrupted by periodic arousal episodes.

Homeotherm

An organism that maintains a more or less constant body temperature either *via* appropriate heat production or heat loss, or by living in a thermally stable environment.

Hypometabolism

A reduction of metabolic rate below basal metabolic rate that often is associated with decreased core body temperature but may be also associated with regional heterothermy only.

Hypothermia

A reduction of body temperature significantly below euthermia. Commonly viewed as an uncontrolled pathological reduction of body temperature often due to drugs or extreme cold exposure.

Metabolic rate

A measure of the total metabolic energy use. Can be quantified indirectly by measuring oxygen consumption or carbon dioxide production or heart rate, or directly by measuring metabolic heat production.

Torpor

A period of controlled reduction of metabolism, core body temperature, and other physiological processes. Torpor is a general term and can be daily or multiday.

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