Allometry of thermal variables in mammals: consequences of body size and phylogeny

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ABSTRACT

A large number of analyses have examined how basal metabolic rate (BMR) is affected by body mass in mammals. By contrast, the critical ambient temperatures that define the thermo-neutral zone (TNZ), in which BMR is measured, have received much less attention. We provide the first phylogenetic analyses on scaling of lower and upper critical temperatures and the breadth of the TNZ in 204 mammal species from diverse orders. The phylogenetic signal of thermal variables was strong for all variables analysed. Most allometric relationships between thermal variables and body mass were significant and regressions using phylogenetic analyses fitted the data better than conventional regressions. Allometric exponents for all mammals were 0.19 for the lower critical temperature (expressed as body temperature - lower critical temperature), −0.027 for the upper critical temperature, and 0.17 for the breadth of TNZ. The small exponents for the breadth of the TNZ compared to the large exponents for BMR suggest that BMR *per se* affects the influence of body mass on TNZ only marginally. However, the breadth of the TNZ is also related to the apparent thermal conductance and it is therefore possible that BMR at different body masses is a function of both the heat exchange in the TNZ and that encountered below and above the TNZ to permit effective homeothermic thermoregulation.

Key words: allometry, lower critical temperature, mammals, marsupials, thermal neutral zone, upper critical temperature.

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I. INTRODUCTION

An enormous body of literature is available for the basal metabolic rate (BMR) of mammals and how it is related to a multitude of variables such as body mass, body temperature (T_b), geographical distribution and diet (Scholander *et al.*, 1950; Kleiber, 1961; Dawson & Hulbert, 1970; McNab, 1974 2008; Lovegrove, 2003; White & Seymour, 2004; Muñoz-Garcia & Williams, 2005). In recent years, with the advent of analyses that allow statistical consideration of phylogeny, we have seen a renaissance of papers attempting to identify factors that determine BMR (Elgar & Harvey, 1987; Lovegrove, 2000; Withers, Cooper & Larcombe, 2006; White, Blackburn & Seymour, 2009; Capellini, Venditti & Barton, 2010). Surprisingly, however, very little attention has been placed on understanding how thermal variables directly related to BMR are correlated with size and phylogeny.

Metabolic physiologists appreciate that metabolism in endotherms is basal only if thermoregulatory heat production is excluded from measurements (McNab, 1997). Thus BMR is measured in the thermo-neutral zone (TNZ), bordered at the lower end by the lower critical temperature (T_{lc}) where an increase in thermoregulatory heat production commences to compensate for heat loss, and at the upper end by the upper critical temperature (T_{uc}) where metabolism increases largely to dissipate heat to the environment and, in those species that allow T_b to change slightly with ambient temperature (T_a), through a Q_{10} effect on metabolic rate (Bartholomew, 1982; Withers, 1992). These critical temperatures play an important functional and ecological role in thermal biology because they define the T_a over which energy expenditure in normothermic endotherms is minimal and also the T_as at which metabolic rate must increase if a constant T_b is to be maintained.

While it seems that T_b shows no consistent association with size among phylogenetic lineages (Calder, 1984; Clarke & Rothery, 2008), some studies examining the interrelationships of T_{lc} with body mass (Morrison, 1960; McNab, 1970; Peters, 1983) found a weak scaling relationship. However, these studies were based on small sample sizes (e.g. McNab, 1970, maximum $N = 28$) and mainly used calculated rather than measured T_{lc}s. Moreover, there is no published systematic examination of critical temperatures and the TNZ in relation to size and phylogeny of mammals. The few studies examining critical temperatures in mammals used ordinary least-squares (OLS) regression to describe their relationship with body mass. However, not accounting for phylogeny ignores the potential lack of independence among species because of their shared evolutionary history (Felsenstein, 1985; Garland, Harvey & Ives, 1992). Species-related trait values cannot be treated as independent data points in statistical analyses as close

phylogenetic relatives are more likely to be similar than are distantly related species (Felsenstein, 1985; Harvey & Pagel, 1991; Garland *et al.*, 1992 1993; Garland & Ives, 2000). Thus OLS analysis can lead to erroneous results and hence to misleading conclusions, as recently shown for the allometry of BMR and field metabolic rate (FMR) in mammals (Capellini *et al.*, 2010), although this is not always the case.

The purpose of our study therefore was to provide a systematic analysis of how the critical temperatures that define the range of environmental temperatures where metabolism is equivalent to BMR are affected by body mass, how they are affected by phylogeny, and how the allometric exponents might be related to those for BMR and the apparent thermal conductance (C).

II. METHODS

(1) Database

Data from published studies on 204 species from diverse orders of mammals were available for the present analysis (Table 1; single species data with the corresponding references are available online as supplementary material, Appendix S1). The data set comprised 204 observations on T_{lc} and body mass, 93 on T_{uc} and 93 on the breadth of the TNZ (calculated as T_{uc}-T_{lc}). In our study T_{lc} and T_{uc} are assumed to reflect the intercept between C and BMR, and heat stress coefficient and BMR, respectively.

Species ranged from some of the smallest mammals, such as the masked shrew (*Sorex cinereus*) weighing 3.5 g to large species such as the bison (*Bison bison*) weighing 800 kg. While we do not claim the study to be exhaustive, an effort was made to include all available studies that recorded T_{lc}, T_{uc}, T_b and body mass from the same animals. If body mass was not provided in the same publication, the additional information was taken from other publications. If T_b measured in the TNZ for a certain species was not given in the source paper (placentals, $N = 45$; marsupials, $N = 7$), T_b was either taken from the table published by Clarke, Rothery & Isaac (2010) or the mean T_b of the respective systematic group was assumed.

When data on a species were provided by more than one source, only one study was included, based on data quality and the number of observations, resulting in one data point per species. For analyses values for all traits were log_{10}-transformed to linearize their relationship with T_{lc} expressed as $log_{10}(T_b$-$T_{lc})$, since T_{lc} can be calculated as $T_{lc} = T_b - BMR/C$ which yields T_b-$T_{lc} = BMR/C$ (Peters, 1983). T_{lc} is also provided on a linear scale to allow easy visual assessment of how it is affected by body mass. All analyses were performed for all species and separately for placentals and marsupials.

Table 1. Summary of range of body mass, lower critical temperature (T_{lc}), upper critical temperature (T_{uc}) and the breadth of the thermo-neutral zone (TNZ) in various mammalian orders included in the present analysis (see online Appendix S1 for species data)

Order	Body mass (g)		T_{lc} (°C)		T_{uc} (°C)		Breadth of TNZ (°C)	
	Range	$\mathcal{N}$	Range	$\mathcal{N}$	Range	$\mathcal{N}$	Range	$\mathcal{N}$
Monotremata	1601–3000	2	20–24	2	30	1	10	1
Didelphimorphia	13–1500	12	22–29	12	35–36	7	7–14	7
Dasyuromorphia	7–552	7	28–33	7	34	1	2.7	1
Peramelemorphia	645–1551	5	27–30	5	35	1	8	1
Diprotodontia	10–26400	18	10–34	18	20–35	15	1.1–14.6	15
Microbiotheria	40.2	1	29	1	—	0	—	0
Chiroptera	4–464	48	24–35	48	33–43	30	1.5–12.7	30
Rodentia	7.3–6000	56	7–33	56	25–36	17	2.5–18	17
Macroscelidea	39–50	2	33–35	2	36	1	3.5	1
Lagomorpha	432–3000	5	10–20	5	26	1	8	1
Hyracoidea	2000–2750	3	10–24	3	—	0	—	0
Erinaceomorpha	67–749	4	28–31	4	—	0	—	0
Soricomorpha	3.5–55	12	24–35	12	28–36	7	3–8.5	7
Perissodactyla	500000	1	5	1	25	1	20	1
Cetartiodactyla	21000–800000	9	−40 to 9	9	20–30	3	11–21	3
Carnivora	540–165000	14	−30 to 26	14	33–35	3	8–10	3
Primates	105–5000	5	24–32	5	25–35	5	3–7.5	5

(2) Phylogeny

The phylogenies in Newick format were derived from the recently published mammalian supertree which includes 4510 species with branch lengths derived from dated estimates of divergence times (Bininda-Emonds et al., 2007, 2008). The supertree for mammals in Newick format (Bininda-Emonds et al., 2008) was pruned to include only the species used in this study using the 'Analysis in phylogenetics and evolution' (APE) package (Paradis, Claude & Strimmer, 2004) and the 'Analysis of evolutionary diversification' (GEIGER) package (Harmon et al., 2008) in R (Ihaka & Gentleman, 1996). The phylogeny including all mammals used in the present study, from which the trees for the different datasets were derived, is available as online supplementary material (Appendix S2).

(3) Phylogenetic signals

To detect phylogenetic signals individually across traits, K- and P-values were calculated following Blomberg, Garland & Ives (2003) using the 'R tools for integrating phylogenies and ecology' (PICANTE) package (Kembel et al., 2010) in R. The calculation of K essentially involves the observed and expected ratios of the mean squared error of the tip data (measured from the phylogenetically corrected mean) and the mean squared error of the data calculated using the variance-covariance matrix (derived from the candidate tree). A detailed description of the calculation is given in Blomberg et al. (2003). In brief, a $K < 1$ for a certain trait implies that relatives resemble each other less than expected under Brownian motion evolution along the candidate tree and a $K > 1$ implies that close relatives are more similar than expected (Blomberg et al., 2003).

(4) Phylogenetic generalized least squares

The method of phylogenetic generalized least squares (PGLS; Grafen, 1989; Martins & Hansen, 1997; Garland & Ives, 2000; Rohlf, 2001) was implemented for the available trait data using BayesTraits (Pagel, Meade & Barker, 2004). PGLS allows for flexibility in the underlying evolutionary assumptions (Martins & Hansen, 1997). While phylogenetic independent contrasts (PIC, Felsenstein, 1985) analysis is a special case of PGLS assuming a 'Brownian motion' model of evolution where the variation in the trait data is fully explained by the phylogeny, PGLS analysis allows more flexibility through the use of a parameter (λ) which can be interpreted as a measure of evolutionary constraint acting on the phenotypes. The parameter λ is determined by maximum likelihood (ML) and can range between 0 (no phylogenetic signal, similar to OLS analysis) and 1 (pattern of trait data variation is fully explained by the phylogeny, similar to PIC analysis). Intermediate values of λ indicate that the trait evolution is phylogenetically correlated, but does not follow fully a Brownian motion model (Pagel, 1999; Freckleton, Harvey & Pagel, 2002; White et al., 2009). A more in-depth description and further mathematical details on PGLS analysis can be found in Pagel (1999), Garland & Ives (2000) and Freckleton et al. (2002).

In order to detect outliers, residual values corrected for phylogeny generated by the PGLS analyses were extracted and standardized by dividing by their square root of their variance. Outliers were defined and removed when standardized residuals were $> \pm 3$ (Jones & Purvis, 1997). Thus, four outliers were removed from the T_{lc} dataset for placentals (*Heterohyrax brucei, Apodemus mystacinus, Alopex lagopus, Peropteryx macrotis*), five from the T_{uc} dataset for all mammals (*Natalus tumidirostris, Tadarida brasiliensis, Nasua narica, Dobsonia praedatrix, Aepyprymnus rufescens*), two from the T_{uc} dataset for

Table 2. Phylogenetic signals (K-values) for the difference between body temperature and lower critical temperature ($T_b - T_{lc}$), upper critical temperature (T_{uc}), the breadth of the thermo-neutral zone (TNZ), and body mass (BM) for the corresponding datasets for mammals included in the present study [computed after the method of Blomberg *et al*. (2003), see text for details]

| | K-values | | | | | |
Species	BM for T_b-T_{lc}	BM for T_{uc}	BM for TNZ	T_b-T_{lc}	T_{uc}	TNZ
All	1.034***	1.203***	1.165***	0.390***	0.414***	0.272*
Marsupials	1.064***	0.817**	0.822*	0.642***	0.989**	0.754*
Placentals	1.493***	1.339***	1.279***	0.571***	0.647***	0.297*

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

marsupials (*Petauroides volans, Bettongia gaimardi*), two from the TNZ dataset for all mammals and for placentals (*Cercopithecus mitis, Aotus trivergatus*) and two from the TNZ dataset for marsupials (*Aepyprymnus rufescens, Tarsipes rostratus*).

(5) Model fit

To identify the best fitting model, we compared OLS ($\lambda = 0$) and PIC ($\lambda = 1$) models to the PGLS ($\lambda = $ ML) model using BayesTraits (Pagel *et al*., 2004). We used likelihood ratio (LR) tests, as described in Capellini *et al*. (2010), with LR $= 2 \times [Lh$ (better-fitting model) $- Lh$ (worse-fitting model)], with the best-fitting model having the highest log-likelihood score (Lh). The significance was tested with a chi-square distribution with 1 degree of freedom (Pagel, 1997 1999; Freckleton *et al*., 2002).

III. RESULTS

(1) Phylogenetic signals and model fit

Phylogenetic signals (i.e. K-values) for body mass were significant ($P < 0.05$) for all datasets and clades (Table 2). K-values for body mass were generally >1 indicating that close relatives are more similar than expected under the Brownian motion model of evolution, except for marsupials. Testing the three different thermal variables (i.e. $T_b - T_{lc}$, T_{uc}, and the breadth of the TNZ) separately for their phylogenetic signal resulted in K-values <1 for all traits and clades, suggesting that close relatives resemble each other less than expected under Brownian motion evolution. Phylogenetic signals were also significant for thermal traits in all clades ($P < 0.001$).

Results on estimated ML λ for the association between body mass and thermal variables using PGLS regression analysis, showed that ML λ had an intermediate value (i.e. $0 < \lambda < 1$) for all relationships and thus required phylogenetic correction (Table 3). However, the evolution of all relative thermal variables (i.e. their association with body mass) was not consistent with Brownian motion and thus significantly different to PIC in all clades, except for the breadth of TNZ and T_{uc} in marsupials, where PGLS was not significantly different from PIC. PGLS was also significantly different from OLS analysis for all datasets and clades, emphasizing the need for a phylogenetic correction of the trait data. PGLS models provided a better fit to the data than either OLS or PIC, except for T_{uc} and TNZ in marsupials, where ML λ was not statistically different from 1.

Table 3. Summary of tests for model fit, comparing phylogenetic generalized least squares (PGLS) models (λ estimated by maximum likelihood, ML) with ordinary least square (OLS) models ($\lambda = 0$) and phylogenetic independent contrasts (PIC, $\lambda = 1$) for the difference between body temperature and lower critical temperature ($T_b - T_{lc}$), upper critical temperature (T_{uc}) and breadth of the thermo-neutral zone (TNZ) in mammals included in the present study

| | | | | | | PGLS *versus* PIC | | PGLS *versus* OLS | |
Species	N	ML λ	*Lh* PGLS	*Lh* PIC	*Lh* OLS	LR	P	LR	P
$T_b - T_{lc}$									
All	204	0.66	88.08	35.93	58.36	104.30	<0.001	59.44	<0.001
Marsupials	43	0.52	23.68	14.96	18.86	17.44	<0.001	9.64	0.002
Placentals	155	0.50	65.09	23.70	55.38	82.78	<0.001	19.42	<0.001
T_{uc}									
All	88	0.57	141.39	127.51	136.23	27.76	<0.001	10.32	<0.001
Marsupials	22	0.69	50.60	49.72	47.05	1.76	n.s.	7.10	0.008
Placentals	68	0.55	119.58	106.91	111.83	25.34	<0.001	15.50	<0.001
TNZ									
All	91	0.29	22.85	−8.55	20.13	62.80	<0.001	5.44	0.019
Marsupials	22	0.86	11.77	11.54	7.77	0.46	n.s.	8.00	0.005
Placentals	66	0.15	18.96	−8.08	15.70	54.08	<0.001	6.52	0.011

ML $\lambda = $ maximum likelihood for λ; Lh $= $ log-likelihood score for models with ML $= \lambda$, $0 = \lambda$ or 1λ; LR $= $ likelihood ratio.

Table 4. Phylogenetic generalized least-squares models for the allometry of the difference between body temperature and lower critical temperature ($T_b - T_{lc}$), upper critical temperature (T_{uc}) and the breadth of the thermo-neutral zone (TNZ) for mammals included in the present study, with the maximum likelihood (ML) λ value for the relationship between trait (i.e. $T_b - T_{lc}$, T_{uc} and breadth of TNZ) and body mass and with the slope (b), intercept, r^2 and n-statistics of the model

Species	N	MLλ	b (S.E.)	log intercept (S.E.)	F	$d.f.$	P	r^2
$T_b - T_{lc}$								
All	204	0.66	0.194 (0.016)	0.497 (0.092)	160.0	202	<0.001	0.44
Marsupials	43	0.52	0.161 (0.027)	0.514 (0.083)	36.6	41	<0.001	0.47
Placentals	155	0.50	0.208 (0.018)	0.574 (0.061)	128.8	153	<0.001	0.46
T_{uc}								
All	88	0.57	−0.027 (0.006)	1.566 (0.030)	20.7	86	<0.001	0.19
Marsupials	22	0.69	0.006 (0.006)	1.522 (0.017)	0.95	19	n.s.	0.05
Placentals	68	0.55	−0.030 (0.007)	1.559 (0.019)	21.5	66	<0.001	0.24
TNZ								
All	91	0.29	0.170 (0.020)	0.411 (0.079)	64.2	89	<0.001	0.42
Marsupials	22	0.86	0.333 (0.040)	0.021 (0.121)	68.5	19	<0.001	0.78
Placentals	66	0.15	0.142 (0.023)	0.483 (0.057)	37.0	64	<0.001	0.36

(2) Allometric relationships

Allometric relationships between thermal variables and body mass were significant ($P < 0.05$) except for T_{uc} in marsupials (Table 4). PGLS models showed that allometric exponents varied between marsupials and placentals for $T_b - T_{lc}$, T_{uc} and TNZ as a function of body mass. The allometric exponent for relative $T_b - T_{lc}$ in marsupials (0.16) was lower than for placentals (0.21), however the difference was not significant (ANOVA, $F_{1, 196} = 3.0$, $P = 0.09$; Table 4). Our results show that T_{lc} decreases with body mass and that the allometric relationship between body mass and T_{lc} for all mammals can be described as T_{lc} (°C) $= T_b$ (°C) $- 3.14$ body mass (g)$^{0.19}$ (Fig. 1). The ML λ for T_{uc} as a function of body mass was high for marsupials (0.69) and somewhat lower for placentals (0.55). The allometric exponent for T_{uc} of placentals was significantly ($P < 0.01$) lower than for marsupials, with body mass explaining 24% in placentals and only 5% in marsupials (Table 4, Fig. 2). In placentals T_{uc} decreased with increasing body mass, whereas in marsupials T_{uc} remained constant over the body mass range examined. The allometric exponent for the breadth of TNZ was significantly ($P < 0.01$) greater in marsupials (0.33) than in placentals (0.14), with an intermediate exponent for all mammals (0.17, Table 4, Fig. 3). The allometric relationship was described by the function TNZ (°C) $= 1.05$ body mass (g)$^{0.33}$ for marsupials, and TNZ (°C) $= 3.04$ body mass (g)$^{0.14}$ for placentals (Table 4). Furthermore, body mass explained 78% of the variation in the breadth of TNZ in marsupials, whereas in placentals body mass explained only 36 %.

IV. DISCUSSION

(1) Model fit and phylogenetic signals

Our study is the first describing the relationship between body mass and thermal variables using phylogenetic analysis. Our results show that PGLS models, which take the phylogenetic signal in the data into account, always fit the data better than OLS models and thus should be preferred when analysing thermal variables. As our results show, phylogenetic correction was warranted due to the significant differences between PGLS and OLS models, with PGLS models always having the higher log-likelihood scores. However, the strength of the phylogenetic signal for the relationship between thermal variables and body mass, estimated by the ML λ was in all cases intermediate (i.e. $0 < \lambda < 1$), and thus also significantly different from 1 for most relationships (except for T_{uc} and the breadth of the TNZ in marsupials), indicating that the evolution of these relationships was less than expected under the Brownian motion model. This emphasises that assuming a value for λ such as in PIC ($\lambda = 1$) or OLS ($\lambda = 0$) over-or under-estimates the influence of shared evolution, respectively, and will likely lead to erroneous results and conclusions (Capellini *et al.*, 2010).

Analysing body mass and thermal variables separately for their phylogenetic signal showed that mass had a strong and exaggerated phylogenetic signal ($K > 1$), indicating that relatives resemble each other generally more in mass than expected under the Brownian motion model (Blomberg *et al.*, 2003). The phylogenetic signal was also significant for all physiological traits examined in the present study (i.e. $T_b - T_{lc}$, T_{uc}, and breadth of the TNZ). However, the signal for physiological traits was less than expected ($K < 1$) under Brownian motion, which is in accordance with other physiological variables such as T_b, C and evaporative water loss (Withers *et al.*, 2006).

(2) Lower critical temperature

Our study is the first incorporating measured T_{lc} and body mass values from a large number of mammalian species ($N = 204$) of diverse orders. The data set includes sufficient numbers to divide it into marsupials and placentals, which is important because, on average, marsupials have a lower BMR and use different mechanisms for thermogenesis than placentals (Dawson & Hulbert, 1970; McNab, 1974;
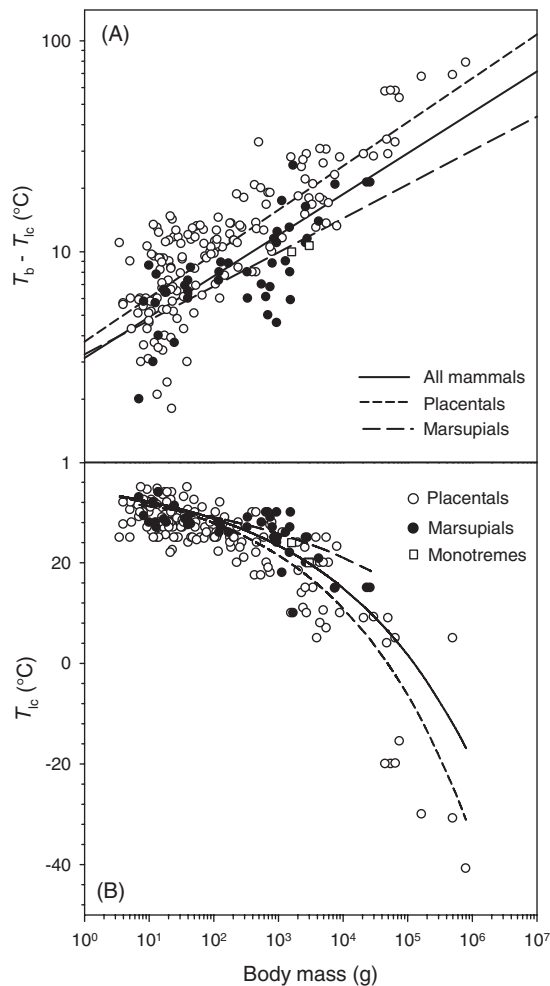
Fig. 1. Relationship between the lower critical temperature (T_{lc}) and body mass in mammals. Circles are placentals, dots are marsupials and squares are monotremes. Fitted lines in A have been derived from the phylogenetic least-squares (PGLS) models from linearized relationships by expressing T_{lc} as $T_b - T_{lc}$ for all mammals (solid line), placentals (short dashed line) and marsupials (long dashed line), where the *y*-intercept was calculated by forcing the regression line through the estimate for the root of the tree, following Garland *et al.* (1993) and Garland & Ives (2000). Fitted lines in B have been derived by the model $T_{lc} = T_b - a$ body mass^b. Model fit and allometric equations are given in Tables 3 and 4 and in Section III.

Fleming, 1980; Geiser & Körtner, 2004; Jastroch *et al.*, 2008). For example, while for many placental mammalian species brown adipose tissue (BAT) is the main source for non-shivering thermogenesis (Himms-Hagen, 1984; Jastroch *et al.*, 2008), marsupials are able to use vasoconstrictor-induced non-shivering and shivering thermogenesis in skeletal muscles (Eldershaw *et al.*, 1996). The role of BAT as a source for non-shivering thermogenesis in marsupials remains controversial with some studies showing that BAT is absent or non-functional (Nicol, Pavlides & Andersen, 1997; Rose *et al.*, 1999) and others showing that BAT is present in some marsupials (Hope *et al.*, 1997).
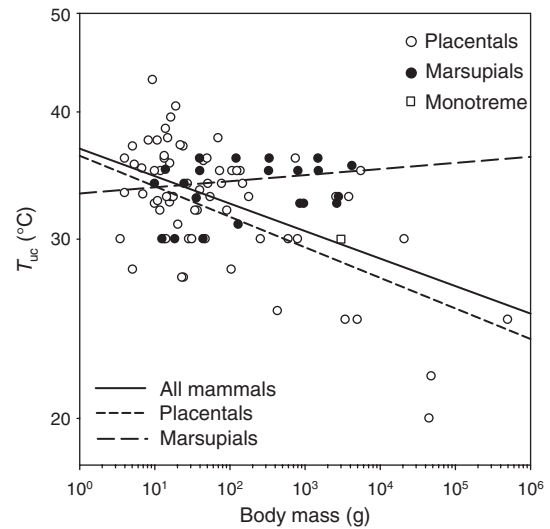

Fig. 2. Relationship between the upper critical temperature (T_{uc}) and body mass in mammals. Circles are placentals, dots are marsupials and the square is a monotreme. Fitted lines have been derived from the phylogenetic least-squares (PGLS) models for all mammals (solid line), placentals (short dashed line) and marsupials (long dashed line), where the *y*-intercept was calculated by forcing the regression line through the estimate for the root of the tree, following Garland *et al.* (1993) and Garland & Ives (2000). Model fit and allometric equations are given in Tables 3 and 4.
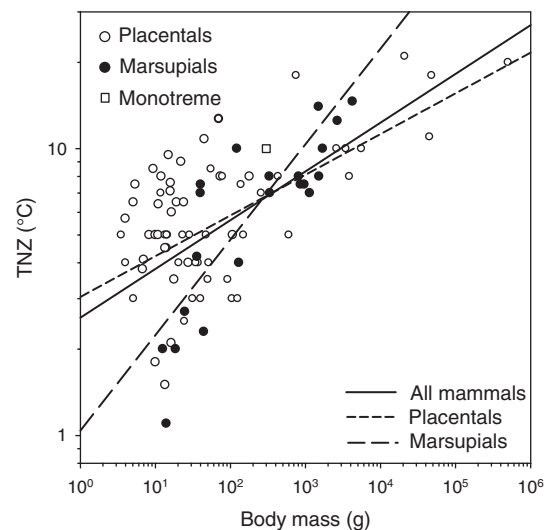

Fig. 3. Relationship between the breadth of the thermo-neutral zone (TNZ, expressed as the difference between upper critical temperature and lower critical temperature) and body mass in mammals. Circles are placentals, dots are marsupials and the square is a monotreme. Fitted lines have been derived from the phylogenetic least-squares (PGLS) models for all mammals (solid line), placentals (short dashed line) and marsupials (long dashed line), where the *y*-intercept was calculated by forcing the regression line through the estimate for the root of the tree, following Garland *et al.* (1993) and Garland & Ives (2000). Model fit and allometric equations are given in Tables 3 and 4.

Allometric equations for the estimation of T_{lc} have been reported previously for mammals (Scholander *et al.*, 1950; Morrison, 1960; McNab, 1970 1974). However, unlike in our analyses, these equations were based on low numbers of species and importantly, were not corrected for phylogeny, although, as our results show, phylogenetic correction for relative T_{lc} is warranted due to the strong phylogenetic signal in the data. Furthermore previous equations were mainly derived by the combination of logistic equations for BMR and C rather than from measured T_{lc} and body mass values. Although T_{lc} can be calculated from C, BMR and T_b as $T_{lc} = T_b - \text{BMR}/C$, it must be noted that all three parameters characterising T_{lc} (i.e. T_b, BMR and C) can vary independently from each other. Calculating T_{lc} from literature data on thermal conductance, BMR and T_b yields the equation $T_{lc} = T_b - 4.15$ body mass$^{0.18}$ (Peters, 1983) for mammals, which differs somewhat from that determined in our study from measured T_{lc} data controlled for phylogeny ($T_{lc} = T_b - 3.14$ body mass$^{0.19}$). The present findings however confirm that absolute T_{lc} decreases with increasing body size (Scholander *et al.*, 1950). The T_{lc} of an animal is reached when BMR equals the homeostatic heat requirement to compensate for heat loss at a T_a below T_b. However, T_{lc} depends on an interaction between the minimal C and BMR as well as on T_b. Therefore, the reason for the lower T_{lc}s of larger mammals is due to a lower C (Bradley & Deavers, 1980) and a relatively higher total BMR (Capellini *et al.*, 2010) compared to smaller mammals. Since T_b is relatively independent from size (Calder, 1984; Clarke & Rothery, 2008), T_{lc} will decline with size, which means that small homeotherms need to increase their metabolism to offset heat loss at higher T_as than large homeotherms. This also enables larger mammals to decrease their heat loss and thus maintain a constant T_b at lower T_as better than smaller mammals. Furthermore, larger mammals have usually thicker fur than small mammals and thus are better protected against heat loss, since fur traps a stationary layer of air close to the skin which acts as a good thermal insulator (Schmidt-Nielsen, 1984; Speakman & Thomas, 2003). This is one of the reasons why some large heavily furred mammals like the wolf or brown bear can tolerate T_as below -20 °C or even below -40 °C in the case of the bison, without increasing their heat production (Scholander *et al.*, 1950; Phillips & Heath, 1995). Smaller mammals on the other hand cannot afford to be heavily furred because the thick fur would hinder their manoeuvrability. This also explains to some extent why there are fewer small species in colder climates than in warmer climates.

Comparing our two allometric equations for T_{lc} of placentals and marsupials reveals that the exponent for marsupials (0.16) is lower than that for placentals (0.21). This difference was not significant, however it indicates that the T_{lc} in marsupials falls less rapidly with increasing body mass than it does in placentals. This difference maybe explained by the lower BMR of marsupials (Dawson & Hulbert, 1970) which apparently is not offset by a lower C. Another reason could be the distribution range of marsupials in relatively warm areas or their smaller upper size range compared to placentals. Fleming (1980) derived an equation for the estimation of T_{lc} in marsupials from logistic equations for standard metabolic rate and mass-specific C of Dawson & Hulbert (1970) and Kinnear & Shield (1975). The derived equation ($T_{lc} = T_b - 3.20$ body mass$^{0.17}$) is similar to that found for marsupials in our study ($T_{lc} = T_b - 3.27$ body mass$^{0.16}$).

(3) Upper critical temperature

Unlike T_{lc}, T_{uc} cannot be calculated from C, BMR and T_b. To our knowledge the present study is the first to try to explain the relationship between T_{uc} and body mass in mammals. The present results suggest a negative relationship between body mass and T_{uc} in mammals in general, i.e. a decrease in T_{uc} with increasing body mass. Body mass explained only 19% of the variation in T_{uc} for all mammals when corrected for phylogeny and 24% in placentals, but was not significant for marsupials. Thus T_{uc} is far less affected by body mass than T_{lc} in marsupials. The negative relationship between T_{uc} and body mass in placentals can be explained by the fact, that, as outlined above, large mammals are usually more heavily furred than small mammals and thus cannot dissipate heat as easily. Moreover, the relative small surface area to volume ratio means that the volume of heat-producing tissue in large mammals is proportionally much greater than the surface area used for heat dissipation. Were it not for the low mass-specific heat production of large mammals they would therefore overheat. This is emphasised by a recent model that predicts that heat dissipation constraints influence the scaling of metabolic rate (Speakman & Król, 2010). The so-called heat dissipation limit theory postulates that in endothermic animals the upper boundary for total energy expenditure is not so much defined by the supply of energy but rather by the maximum capacity to dissipate body heat to avoid hyperthermia. The heat dissipation limit theory predicts that the scope to increase metabolism declines with increasing size of the animal. Our results on T_{uc} support this view, because T_{uc} and body mass show a negative relationship overall.

(4) Breadth of the thermo-neutral zone

The TNZ of an animal is defined as the range of T_a in which T_b is regulated only by the control of sensible heat loss (IUPS Thermal Commission, 1987). Thus, regulatory changes in metabolic heat production or evaporative heat loss only occur outside the TNZ, which is characterised as $T_a > T_{lc}$ and $T_a < T_{uc}$. In our study the T_a range of the TNZ varied among species from as low as 1.1°C (*Acrobates pygmaeus*) to as high as 21°C (*Capra hircus*). Body mass had a moderate effect ($r^2 = 0.42$) on the breadth of TNZ for all mammals. However, when separating the data set into placentals and marsupials, the TNZ of marsupials was highly influenced by body mass ($r^2 = 0.78$), but less in placentals ($r^2 = 0.36$). This is most likely explained by the slightly positive slope for the T_{uc} in marsupials in comparison to the negative
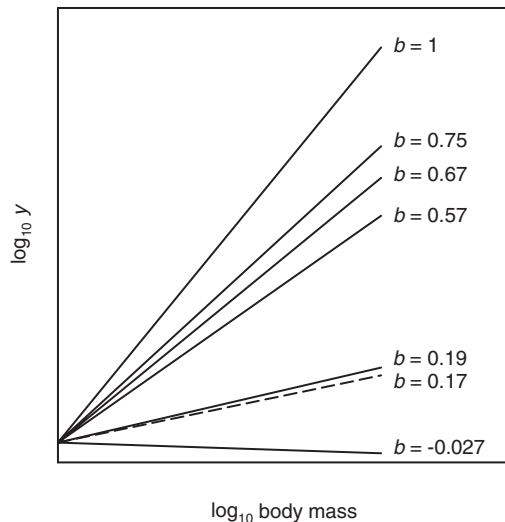
Fig. 4. Scaling exponents (*b*) between body mass and metabolic and thermal variables: $b = 1$ directly proportional relationship, $b = 0.75$ (basal metabolic rate, BMR, Kleiber, 1961), $b = 0.67$ (BMR, White & Seymour, 2003), $b = 0.57$ (apparent thermal conductance, *C*, Bradley & Deavers, 1980), $b = 0.19$ (lower critical temperature, T_{lc}), $b = 0.17$ (breadth of thermo-neutral zone, TNZ), $b = -0.027$ (upper critical temperature, T_{uc}).

slope for the T_{uc} in placentals and a similar effect of body mass on T_{lc}. Obviously, the breadth of the TNZ is not only affected by the size of the animal, but also by the extent they use insulation. As we have seen, good insulation using fur substantially decreases the T_{lc} of mammals and reduces heat loss at low T_a. The disadvantage of thick fur is its relative inflexibility at high T_a, resulting in a lowering of the T_{uc} in large placentals.

(5) Thermal variables in relation to BMR and apparent thermal conductance

Our analyses show that the breadth of the TNZ scales with body mass with an exponent of 0.17 in all mammals. As the TNZ is defined as the range of T_a in which BMR can be basal and BMR in turn affects the T_{lc} and T_{uc} to some extent, the question arises why the scaling exponent differs so substantially from that for BMR (Fig. 4). Proposed allometric exponents for BMR differ among 0.75 (Kleiber, 1961), 0.67 (White & Seymour, 2003), and more recently 0.72 (Capellini *et al.*, 2010). The scaling exponent of 0.17 for the breadth of the TNZ suggests that BMR *per se* explains only a small part of the change of TNZ with body mass. However, the total *C* is also a variable that is related to the TNZ, but its exponent (0.57, Bradley & Deavers, 1980) is also below that for BMR. Interestingly, the sum of the exponents for *C* and the breadth of the TNZ is 0.74, close to the BMR exponents. Is it therefore possible that BMR is a compromise, that is selected so that T_{uc} occurs at a maximal high level and T_{lc} at a minimum low level at a given body mass/insulation, but that nevertheless is idling high enough to allow it to be adequately up-regulated when required during cold exposure?

V. CONCLUSIONS

(1) To our knowledge, the present study is the first to investigate critical temperatures in a large dataset of mammals ($N = 204$) using phylogeny. Our results show that the critical temperatures defining the TNZ (i.e. T_{lc} and T_{uc}), key criteria for measuring BMR, and the breadth of the TNZ are all influenced by phylogeny.

(2) However, while T_{lc} is clearly body-mass-dependent in both marsupials and placentals, T_{uc} is only body-mass-dependent in placentals.

(3) The breadth of the TNZ, defined as the difference between T_{uc} and T_{lc}, is strongly correlated with body mass in marsupials, but less in placentals because in the latter both T_{lc} and T_{uc} fall with body mass.

VI. ACKNOWLEDGEMENTS

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Body mass, body temperature, lower critical temperature, upper critical temperature and the breadth of the thermo-neutral zone of mammalian species included in the analysis.

Appendix S2. Phylogeny in Newick format including all mammals used in the present study.