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Physiology

Basal metabolic rate, maximum thermogenic capacity and aerobic scope in rodents: interaction between environmental temperature and torpor use

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When torpid animals arouse and warm up to restore normal body temperature (T_b), they produce heat at levels that can reach up to 10 times basal metabolic rate (BMR), close to the cold-induced summit metabolism (VO_2-sum). Because torpor is an adaptation aimed at conserving energy over periods of low ambient temperature (T_a) and food availability, selective forces that have led to the evolution of torpor may have simultaneously favoured high thermogenic capacity (i.e. VO_2-sum) relative to the maintenance costs (i.e. BMR), hence a higher factorial aerobic scope (FAS; the ratio of VO_2-sum to BMR). My objective was to test this adaptive hypothesis using a phylogenetically informed comparative approach with data on BMR and VO_2-sum in rodents. I found a strong negative correlation between FAS and the average of the daily minimum T_a (T_{min}) in species using torpor, which was due to differential effects of T_a on BMR (but not VO_2-sum) in species that use torpor compared with species that do not. In addition, FAS was negatively correlated with the lowest torpid T_b in a subset of nine species. These results suggest that in species using torpor, selective forces may have acted to maximize the efficiency of thermogenic capacity (VO_2-sum) relative to maintenance costs (BMR), resulting in an increasing FAS with decreasing T_a.

1. Introduction

Animals have adapted in many ways to survive periods of cold ambient temperature (T_a) and low food availability, such as food hoarding, migration and hibernation. For many species, torpor (a state of inactivity and reduced responsiveness usually characterized by a reduced body temperature (T_b) and rate of metabolism) is a key physiological adaptation to life in cold environments with insufficient food availability [1]. While torpor allows the animal to conserve energy over protracted periods, it generally requires high levels of metabolic rate during arousals to warm up from torpid to normothermic T_b [2]. In eastern chipmunk (*Tamias striatus*) for example, energy expenditure during arousals can reach up to 10 times the euthermic basal metabolic rate (BMR [3,4]), close to the cold-induced summit metabolism (VO_2-sum) reported in this species [5]. Therefore, selective forces that led to the evolution of torpor may have simultaneously favoured high thermogenic capacity (to warm up quickly from torpor) relative to maintenance costs during torpor (to conserve energy), which itself may be linked to a low BMR during non-torpor periods. Hence, species using torpor should have a higher factorial aerobic scope (FAS; ratio of VO_2-sum to BMR) than homeothermic species.

There have been many comparative studies on the selective forces that led to the evolution of metabolic rates that deviate substantially from allometric predictions [6,7]. Latitude and T_a have been repeatedly shown to be correlated with metabolism, with species living at extreme latitudes and in cold environments

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having higher daily energy expenditure, BMR and VO_2-sum [7–9]. Moreover, species using torpor have lower BMR during non-torpor periods than euthermic species, as suggested by two large (but non-phylogenetic) comparative analyses in 533 bird and 639 mammal species, respectively [10,11]. The relationship between torpor use and VO_2-sum, however, has never been verified. Much less attention has been paid to factors causing interspecific differences in metabolic flexibility. In the only study that did so, the absolute aerobic scope (AAS; mass-specific VO_2-sum minus mass-specific BMR) was significantly correlated with T_a and latitude, but not with torpor use [12]. This is surprising, because metabolic flexibility (i.e. FAS or AAS) should be a particularly important physiological feature of species using torpor (see above).

An overlooked aspect of previous comparative analyses of BMR and VO_2-sum is the potential interaction between torpor use and T_a and/or latitude. While BMR and VO_2-sum generally increase at low T_as or high latitudes [7], it may not necessarily be the case for species using torpor. One may expect that a low metabolic rate during torpor will maximize chances of survival on limited energy stores (body fat or larder hoards). In turn, a low torpid metabolic rate may be linked to low maintenance cost during non-torpor periods (i.e. BMR). By contrast, one may expect that the effect of T_a and/or latitude on VO_2-sum is more pronounced in heterothermic than homeothermic species, because torpid hibernators may want to re-warm from their low T_b in the least possible time, which is limited by the metabolic machinery underlying VO_2-sum [2]. Once combined, the differential effect of T_a and/or latitude on BMR and VO_2-sum should yield large differences in FAS, but only in species using torpor. Here, I used a phylogenetically informed comparative approach [13,14] to test whether rodent species using torpor in cold climates have evolved different metabolic machineries by looking at how torpor use and T_a interact to determine BMR, VO_2-sum and FAS.

2. Material and methods

(a) Metabolic and environmental data

I used a recently compiled dataset [7] on VO_2-sum elicited by cold exposure in a mixture of helium and oxygen (i.e. heliox), a widely used method to measure the thermogenic capacity of wild endotherms [15]. In addition to VO_2-sum, this dataset includes a measure of BMR or resting metabolic rate (RMR) in the same population and, when possible, in the same individuals captured in the field or maintained for only a few generations in the laboratory. In this dataset, RMR measures are not significantly higher than BMR measures (see below and [7]); hence the term BMR is used hereafter. Most animals were acclimatized to a season other than winter (it was impossible to control statistically for the effects of seasonality in the analyses because some studies did not specify when animals were actually captured and measured, [7]). The initial dataset included 57 populations of 46 rodent species [7], to which I added a recently published estimate on *T. striatus* (see the electronic supplementary material, table S1, [5]). Naya *et al.* [12] also recently corrected the geographical location for *Chinchilla brevicaudata*.

The initial analysis of this dataset showed that BMR and VO_2-sum varied according to normal daily maximum (T_{max}) and minimum (T_{min}) environmental temperatures (the average of the daily maximum and minimum T_a), latitude, altitude, precipitation (sum of monthly average value) and a broad diet category [7]. These analyses were complicated by the fact that

several environmental variables were inter-correlated, especially T_{min}, T_{max}, latitude and altitude. Here I focused on T_{min} because it is the most relevant variable in light of torpor use and was the best predictor of VO_2-sum (multiple r^2 with body mass = 0.776) and second best of BMR (the correlation between T_{min} and T_{max} is 0.84) [7], but I replicated all analyses using T_{max} and altitude, precipitation, latitude and corrected latitude [12]. I calculated FAS as the ratio of VO_2-sum to BMR and included a new variable coding for torpor use (yes or no) for each species (see the electronic supplementary material, table S1). To this end, I followed categorization by McNab [10] except for eight species that were not in common (see the electronic supplementary material). I found data on both normothermic and minimum torpid T_b on nine of the 12 species considered here as using torpor (see the electronic supplementary material).

(b) Statistical analysis

I analysed log-transformed BMR, log-transformed VO_2-sum and FAS as function of log-transformed body mass (M_b), T_{min}, torpor use and the interaction between T_{min} and torpor use. To take phylogenetic relationships into account, I analysed the data using phylogenetic generalized least squares (PGLS) in Regressionv2.m [14] and a phylogenetic supertree which contained all species in the dataset (see the electronic supplementary material, figure S1). I ran all models using three different transforms: Pagel's λ, Grafen's ρ and Ornstein–Uhlenbeck (see [14] for derived terminology), but retained models using Pagel's λ transform because they fit the data better according to the Akaike information criterion. The final sample size used in each analysis was 58 (i.e. 41 homeothermic and 17 heterothermic species/populations), but for all models, I subtracted one d.f. for every soft polytomy contained in the phylogeny [16]. A variable coding for whether all the requirements were fulfilled for BMR or not (RMR) was not significant for either BMR ($t_{36} = 0.69$, $p = 0.49$) or FAS ($t_{36} = 0.69$, $p = 0.50$) and was excluded from the model.

3. Results

BMR was positively correlated with M_b, but not with T_{min} (table 1a). The main effect of torpor use was significant, indicating that species which use torpor have lower BMR at a T_{min} of 0°C (i.e. intercept; table 1a). The interaction between T_{min} and torpor use was positive but not significant (table 1a). The correlation (r) between mass-residual BMR and T_{min} was -0.53 in species that do not use torpor, but only -0.05 in homeothermic species (figure 1a).

Cold-induced VO_2-sum was positively correlated with M_b (table 1b). In contrast to BMR, VO_2-sum was negatively correlated with T_{min} and the main effect of torpor use was not significant (table 1b). The interaction between T_{min} and torpor use on VO_2-sum was negative but not significant (table 1b). The correlation (r) between mass-residual VO_2-sum and T_{min} was -0.59 in species that do use torpor and -0.55 in homeothermic species (figure 1b).

FAS was not significantly correlated with M_b, but negatively correlated with T_{min} (table 1c). The main effect of torpor use was significant, indicating that species using torpor have higher FAS at a T_{min} of 0°C (i.e. intercept; table 1c). There was a significant interaction between torpor use and T_{min} on FAS (table 1c). While FAS is independent of T_{min} in homeothermic species ($r = -0.09$), it increases steeply with decreasing T_{min} in species that use torpor ($r = -0.76$; figure 1c). Similar results are obtained with T_{max}, (i.e. significant interaction with torpor use; electronic

Table 1. Phylogenetic least squares models of (a) basal metabolic rate (BMR), (b) maximum cold-induced summit metabolism (VO_2-sum) and (c) factorial aerobic scope (FAS; VO_2-sum divided by BMR) as function of body mass (M_b), year-round average of daily minimum air temperature (T_{min}), torpor use (yes or no) and the interaction between T_{min} and torpor use in 58 populations of 49 rodent species. (p-values are calculated on a test statistic (t) with 37 degrees of freedom to account for the polytomies in the phylogeny.)

| term	(a) log BMR			(b) log VO_2-sum			(c) FAS		
	estimate ± s.e.	t	p	estimate ± s.e.	t	p	estimate ± s.e.	t	p
log M_b	0.666 ± 0.039	17.24	0	0.694 ± 0.042	16.34	0	0.363 ± 0.540	0.67	0.5056
T_{min}	0.001 ± 0.003	0.16	0.8751	−0.012 ± 0.004	3.13	0.0034	−0.170 ± 0.046	3.67	0.0008
torpor$_{(yes)}$	−0.097 ± 0.046	2.11	0.0418	0.030 ± 0.052	0.58	0.5636	1.651 ± 0.646	2.56	0.0148
T_{min} × torpor$_{(yes)}$	0.006 ± 0.004	1.62	0.1138	−0.003 ± 0.005	0.72	0.4737	−0.124 ± 0.056	2.23	0.0321
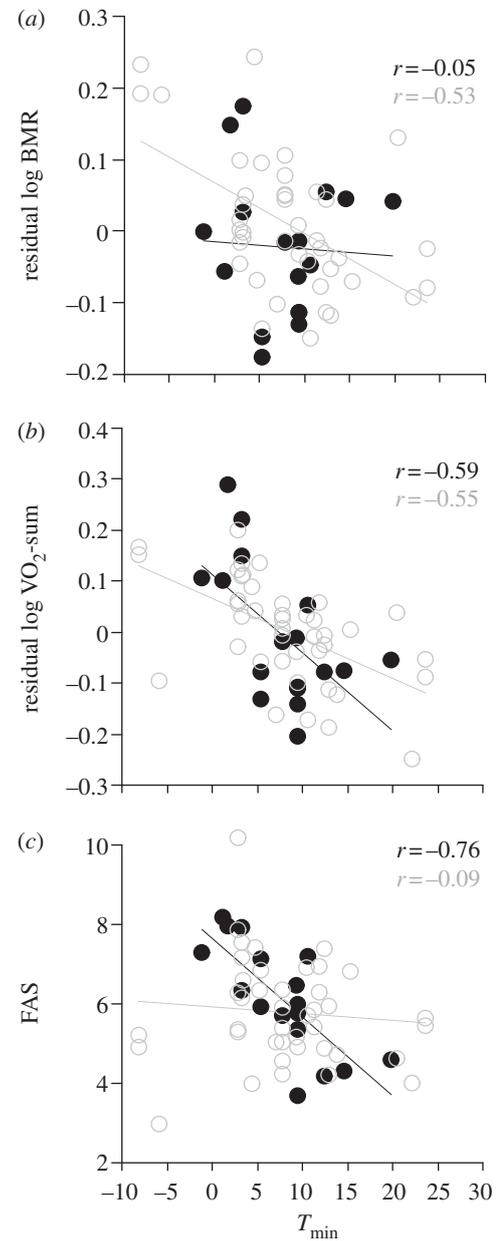
Figure 1. The interaction between torpor use and minimum air temperature (T_{min}) on (a) basal metabolic rate (BMR), (b) cold-induced summit metabolism (VO_2-sum) and (c) factorial aerobic scope (FAS; ratio of VO_2-sum to BMR) in 58 populations of 49 rodent species. Log-transformed BMR and VO_2-sum are plotted as residuals from a regression against log-transformed body mass. Also shown are the correlation coefficients (uncorrected for phylogeny) in homeothermic (grey circles) and heterothermic (black circles) species.

supplementary material, table S2). However, neither altitude, latitude nor precipitation significantly interacted with torpor use to influence FAS, although the interaction with latitude corrected for altitude was marginally non-significant (see the electronic supplementary material, table S2).

Although FAS was not correlated with normothermic T_b ($t_{14} = 0.74$; $p = 0.47$), it was significantly negatively correlated with torpid T_b (PGLS estimate ± s.e. = $-0.11 ± 0.05$; $t_{14} = 2.25$; $p = 0.041$; figure 2).

4. Discussion

Given that torpor is a physiological adaptation aimed at conserving energy, but involves high levels of thermogenesis during
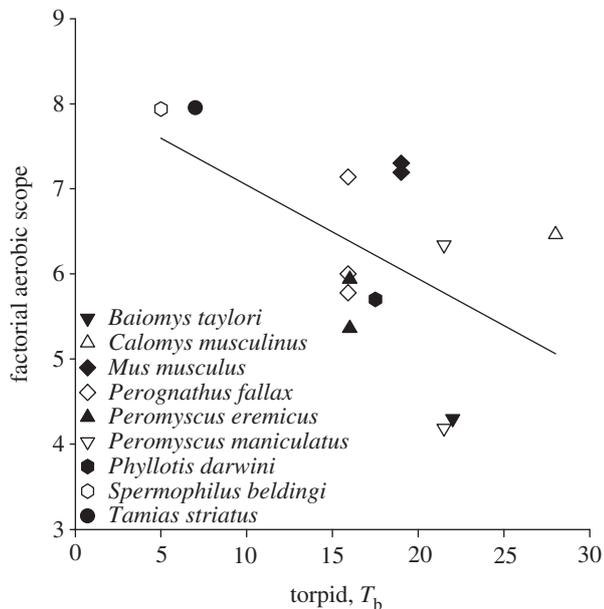
Figure 2. Factorial aerobic scope (ratio of cold-induced summit metabolism to basal metabolic rate) as function of torpid body temperature (T_b) in nine rodent species.

arousals [2], it is intuitive to think that it requires high thermogenic capacity (VO_2-sum) relative to maintenance costs (BMR), leading to a high FAS. Analysing FAS yielded results otherwise undetectable from the individual analyses of its components (i.e. BMR and VO_2-sum). In homeothermic species, both BMR and VO_2-sum were negatively correlated with T_{min}, hence there was no correlation between T_{min} and FAS. In heterothermic species using torpor, BMR was independent of T_{min} while the correlation was still present with VO_2-sum. Once combined, these effects yielded a strong negative relationship between T_{min} and FAS in heterothermic species ($r^2 = 0.57$; figure 1c). The different effect of T_{min} on BMR and FAS in heterothermic versus homeothermic species may reflect the presence of selective forces that acted on the metabolic machinery of heterothermic species using torpor in cold climates.

The comparative method cannot unambiguously demonstrate 'adaptation,' meaning the tailoring of an ancestral condition to allow it to meet the needs of a new physical environment [13]. It is possible that high FAS in species using torpor in cold climates simply represents phenotypic plasticity, whereby individuals adjust their FAS in response to local environments. Further studies are needed to differentiate genetic and population-level adaptations from phenotypic plasticity. An interesting avenue for future research would be to test if factors that negatively affect FAS also reduce survival in species using torpor in cold climates. Parasites for example, are known to increase RMR, decrease VO_2-sum and consequently FAS in free-ranging eastern chipmunks [5]. Perhaps not coincidentally, parasites also reduce overwinter survival in juvenile chipmunks during a year of low food abundance [17]. Moreover, in a captive chipmunk population, BMR during periods of normothermic arousal (i.e. between torpor bouts) was negatively correlated with total number of torpor bouts exhibited throughout the winter [4]. Given that a high FAS was associated with a low torpid T_b across rodent species (figure 2), the current empirical evidence suggests that torpor is an energy conservation mechanism that simultaneously requires low maintenance costs and high thermogenic capacity. Another interesting avenue for future research will be to test whether BMR during non-torpor periods is linked to metabolism while torpid.

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