Testing the heat dissipation limitation hypothesis: Basal metabolic rates of endotherms decrease with increasing upper and lower critical temperatures

Imran Khaliq Corresp., [1, 2, 3] , **Christian Hof** [2]

[1] Department of Zoology, Ghazi University, Pakistan, Dera Ghazi Khan, Punjab, Pakistan
[2] Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325, Frankfurt, Germany
[3] Institute for Ecology, Evolution and Diversity, Department of Biological Sciences, Johann Wolfgang Goethe Universität Frankfurt am Main, Frankfurt, Germany

Corresponding Author: Imran Khaliq
Email address: imrankhaliq9@hotmail.com

Metabolic critical temperatures define the range of ambient temperatures where endotherms are able to minimize energy allocation to thermogenesis. Examining the relationship between metabolic critical temperatures and basal metabolic rates (BMR) provides a unique opportunity to gain a better understanding of how animals respond to varying ambient climatic conditions. We make use of this opportunity by testing the heat dissipation limit (HDL) theory which hypothesizes that the maximum amount of heat a species can dissipate constrains its energetics. Specifically, we test the theory's prediction that BMR should be lower under higher metabolic critical temperatures. We analysed the relationship of BMR with upper and lower critical temperatures for a large dataset of 146 endotherm species using regression analyses, carefully accounting for phylogenetic relationships and body mass. We show that metabolic critical temperatures are negatively related with BMR in both birds and mammals. Our results confirm the predictions of the HDL theory, suggesting that metabolic critical temperatures and basal metabolic rates respond in concert to ambient climatic conditions.

Testing the heat dissipation limitation hypothesis: basal metabolic rates of endotherms decrease with increasing upper and lower critical temperatures

Short title: Metabolic critical temperatures and metabolic rates in endotherms

Imran Khaliq[*1,2,3] **& Christian Hof**[1]

1: Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt, Germany

2: Institute for Ecology, Evolution and Diversity, Department of Biological Sciences, Goethe University, Max-von-Laue-Straße 13, 60438 Frankfurt, Germany

3: Ghazi University, Dera Ghazi Khan, Punjab, Pakistan

* Corresponding author: Imran Khaliq

e-mail: imrankhaliq9@hotmail.com

phone: +923335849000

Abstract

Metabolic critical temperatures define the range of ambient temperatures where endotherms are able to minimize energy allocation to thermogenesis. Examining the relationship between metabolic critical temperatures and basal metabolic rates (BMR) provides a unique opportunity to gain a better understanding of how animals respond to varying ambient climatic conditions. We make use of this opportunity by testing the heat dissipation limit (HDL) theory which hypothesizes that the maximum amount of heat a species can dissipate constrains its energetics. Specifically, we test the theory's prediction that BMR should be lower under higher metabolic critical temperatures. We analysed the relationship of BMR with upper and lower critical temperatures for a large dataset of 146 endotherm species using regression analyses, carefully accounting for phylogenetic relationships and body mass. We show that metabolic critical temperatures are negatively related with BMR in both birds and mammals. Our results confirm the predictions of the HDL theory, suggesting that metabolic critical temperatures and basal metabolic rates respond in concert to ambient climatic conditions.

Key words: BMR, energy, endogenous heat load, metabolic critical temperatures, macrophysiology, birds, mammals

Introduction

Life history theory predicts that the energy available to organisms is limited and thus has to be utilized economically among different biological processes (McNab, 2012). An endotherm animal (i.e. a bird or a mammal) normally utilizes 30-50% of its daily energy expenditure just to maintain a stable body temperature (homeostasis) (McNab, 2012). This energy is not available for other vital biological processes. From an evolutionary perspective, animals should maximize their energy expenditure for processes ensuring their long-term survival, such as reproduction, dispersal or predator avoidance. Consequently, animals should seek to live in environments with conditions allowing them to keep the energetic cost for homeostasis low and to invest most energy into these processes in order to persist (Kobbe, Nowack & Dausmann, 2014).

A non-reproductive endotherm at rest utilizes a minimal amount of energy within its thermal neutral zone (TNZ, McNab, 2002). Under the assumption outlined above, i.e. assuming an energetic trade-off between homeostasis and other biological processes, endotherms should either have a very broad TNZ or live in areas with ambient temperatures falling within the TNZ (Kobbe, Nowack & Dausmann, 2014). However, studies have shown that for the majority of investigated endotherm species neither of these expectations received strong support (Araújo et al., 2013; Khaliq et al., 2014, 2017). This indicates that other physiological and ecological constraints shape the evolution, survival and distribution of endotherm animals (Kearney & Porter, 2009; Fristoe et al., 2015). In fact, in recent decades the identification of the factors that limit the energy availability of animals has become one of the most pursued topics in the field of eco-physiology (Lovegrove, 2003; White et al., 2007; Wiersma et al., 2007; McNab, 2008, 2009; Wiersma, Nowak & Williams, 2012). Researchers have proposed a plethora of factors that influence the energetics of animals, in particular their basal metabolic rate (BMR) which is the minimal level of energy invested for homeostasis. These factors influencing the energy budget of an animal can be categorized as morphological, physiological and environmental (Lovegrove, 2003; White et al., 2007; Wiersma et al., 2007; McNab, 2008, 2009; Kearney & White, 2012; Wiersma, Nowak & Williams, 2012).

Traditionally, most studies have focused on extrinsic factors influencing the energy level in organisms, such as food sources (McNab, 1988, 2009) or environmental conditions (Lovegrove, 2000, 2003; White et al., 2007); however, a few studies have also focused on intrinsic factors (Johnson, Thomson & Speakman, 2001; Wu et al., 2009; Chrzascik et al., 2016). Regarding the latter, two hypotheses have gained attention. First, the central limitation hypothesis predicts that energy intake is constrained by the alimentary canal's capacity to process food, i.e. energy levels should be directly linked to the efficiency of the alimentary canal to convert food into energy (Drent & Daan; Peterson, Nagy & Diamondt, 1990). In other words, available energy is constrained at the level of energy creation. However, this hypothesis has been questioned because it was shown that under cold conditions animals can elevate energy levels beyond the upper limits set by the central limitation hypothesis (Król & Speakman, 2003). Secondly, the peripheral limitation hypothesis predicts that it is the internal organs' capacity to expend energy that constrains the energy level in animals (Hammond & Diamond, 1997; Bacigalupe & Bozinovic, 2002). However, this hypothesis has also been found not to explain the increase of energy level within the same individual animal (containing the same organs) under cold conditions (Król & Speakman, 2003).

Recently, the heat dissipation limit (HDL) hypothesis has been put forward (Speakman & Król, 2010). It has received support from different lines of evidence, like from the ability of endotherms to raise energy levels under cold conditions (Król & Speakman, 2003), the negative relationship of ambient temperatures with basal metabolic rates (White et al., 2007), or the negative relationship of ambient temperatures with field metabolic rate (Speakman, 1997). These findings point towards the role of animals' heat dissipation capacity in limiting their energy levels. However, the idea is not entirely new and has previously been discussed with empirical evidence. McNab & Morrison (1963) have shown that mammals inhabiting hotter environments are confronted with the endogenous heat load challenge due to their inefficiency to dissipate heat. When ambient temperatures rise, the difference between body and ambient temperatures decreases and it becomes increasingly difficult for endotherms to dissipate heat from the body. Consequently, it becomes a challenge to keep body temperatures constant. As temperatures rise beyond the upper limit of the TNZ (upper critical temperature, T_{uc}), the amount of heat generated at BMR exceeds the capacity of the body to dissipate heat passively, and other cooling mechanisms (e.g. evaporative cooling) must be employed to maintain body temperature and avoid hyperthermia.

To avoid an increased risk of hyperthermia under increasing temperatures, endotherms may have two non-exclusive avenues of adaptation: changes in their thermal conductance (i.e. the ability to passively dissipate heat) or changes in their BMR as one crucial source of endogenous heat (Naya et al., 2013). All else being equal, to keep their body temperatures constant, species with a relatively high BMR must invoke active cooling mechanisms at a lower environmental temperature, i.e. have a lower T_{uc}, than species with a relatively low BMR. Similarly, species with a relatively high thermal conductance are able to dissipate more heat at a given environmental temperature than species with low thermal conductance. Thus, by increasing thermal conductance, decreasing BMR, or both, endotherms may increase their T_{uc}, hence being able to cope better with rising global temperatures (Kobbe, Nowack & Dausmann, 2014). Similarly, when environmental temperatures decrease, the difference between body temperatures and environmental temperatures increases and as a consequence the animal loses heat. When environmental temperatures reach the lower critical temperature (T_{lc}), the heat generated at the BMR level is not sufficient to keep body temperatures constant; therefore, the animal must invoke active heat generation (e.g. by increasing its food intake). Animals with relatively high BMR should therefore be able to extend their T_{lc} towards low temperatures.

The HDL theory proposes that the overall energetics of endotherms are dependent on their abilities to dissipate heat from the body (Speakman & Król, 2010). However, there is a lack of consensus about the generality of the HDL theory (Petit, Vézina & Piersma, 2010; Wiersma, Nowak & Williams, 2012), and studies that empirically support the HDL theory remain scarce (Speakman & Król, 2010; White & Kearney, 2013). Tests of the effects of heat dissipation limitations on BMR are even rarer (but see Naya et al. 2013). Here, we test this prediction, using a global data set of T_{uc}, T_{lc} body mass, and BMR of endotherms, i.e. mammals and birds, in order to evaluate the influence of heat dissipation limits on species' metabolism. Following the above line of arguments we expect, if heat dissipation is a limiting factor of endotherm energy levels (i.e. BMR), a negative relationship between critical temperatures and BMR.

Materials and methods

Data

Data for T_{uc}, T_{lc} , BMR and body mass for birds and mammals were compiled from published sources (see Khaliq et al. 2014, 2015 for a detailed description). The compiled data were obtained from physiological experiments conducted to measure BMR under different temperature conditions. Data quality and suitability for macro-physiological analyses have been extensively debated recently (McKechnie et al., 2016; Hof et al., 2017a,b; Wolf et al., 2017). Here, the focus on critical temperatures and BMR requires the use of data fulfilling the strictest quality criteria, i.e. with sufficient sample size and enough temperature range to estimate critical temperatures (see Table S1 in Hof et al., 2017 for details). Thus, the dataset used here consists of 58 bird species (28 migrants and 30 residents) belonging to 28 families and 12 orders, ~~and~~ 88 mammal species belonging to 40 families and 16 order (see supplementary table S1). To account for the evolutionary non-independence of data in comparative analysis, phylogenetic information for all species were compiled from published supertrees for birds (Jetz et al., 2012) and mammals (Fritz, Bininda-Emonds & Purvis, 2009; Kuhn, Mooers & Thomas, 2011).

Analyses

To evaluate the influence of body mass on metabolic critical temperatures and to account for the joint evolutionary history of species, we used phylogenetic generalized least squares (PGLS) regression using the package *caper* (Orme et al., 2012) in R (R Core Team, 2013). This approach estimates a parameter λ (Pagel's lambda, Pagel 1999), which indicates the amount of phylogenetic influence on the phenotype and applies a correction (Martins, Hansen & Url, 1997; Freckleton, Harvey & Pagel, 2002). We modeled T_{uc} and T_{lc} separately, using PGLS, as a function of log-transformed body mass while estimating λ by a maximum likelihood approach.

To test for the influence of heat dissipation on BMR, we modeled BMR as a function of body mass and then individually added T_{uc} or T_{lc} to the PGLS model. T_{uc} and T_{lc} were used as proxies for species' heat dissipation abilities, assuming that species with lower metabolic critical temperatures should be able to dissipate heat more efficiently than species with higher critical temperatures. To evaluate the robustness of the analysis across phylogenetic trees, we sampled 100 trees from the pseudo-posterior distribution of the used supertrees (Kuhn, Mooers & Thomas, 2011; Jetz et al., 2012) and ran the analyses for these 100 trees. For the final analysis we generated a maximum clade credibility (MCC) tree, using TreeAnnotator (included in BEAST v.1.7.5, Drummond & Rambaut 2007).

Results

T_{lc} and T_{uc} co-varied with body mass (M), with the exception of bird T_{uc} (Mammals: $T_{lc} = M^{-0.04}$, lambda = 1, t = -3.002, p = 0.003, n =88; $T_{uc} = M^{-0.02}$, lambda = 0, t = -4.6, $p < 0.001$, n = 58; Birds: $T_{lc} = M^{-0.07}$, lambda = 0, t = -3.13, $p < 0.001$, n = 58; $T_{uc} = M^{-0.001}$, lambda = 0, t = -0.16, p = 0.87, n = 58). 8% of the variation in T_{lc} and 19% of the variation in T_{uc} of mammals could be explained by body mass. A higher amount of variation (13%) in T_{lc} was explained by body mass in case of birds. As expected, body mass is positively related with BMR both in birds and mammals (Mammals: $BMR = M^{0.69}$, lambda = 0.91, t = 37.3, $p < 0.001$, n = 88; Birds: $BMR = M^{0.71}$, lambda = 0.66, t = 19.2, $p < 0.001$, n = 58). After accounting for the effect of body mass, T_{lc} and T_{uc} are negatively related with BMR both in mammals and birds (Table 1, Fig. 1). The lambda values for the majority of the models on the relationship between T_{lc} or T_{uc} and BMR were zero, indicating no phylogenetic signal in the regression model residuals.

Discussion

Our results show that endotherm species with higher mass-independent critical temperature values tend to have lower mass-independent BMR values (Fig. 1), which is in accordance with our expectations. In order to manage endogenous heat load under warm and dry conditions, endotherm species that experience ambient temperatures above T_{uc} are likely to require increasing amounts of water for the increased rates of evaporative cooling that are required to dissipate metabolic heat from the body (Williams & Tieleman, 2002). By attaining higher T_{uc} levels and decreasing mass-independent BMR under rising temperatures, endotherms can reduce endogenous heat load and thus avoid hyperthermia with lower efforts of evaporative cooling (McNab & Morrison, 1963; Speakman & Król, 2010). Similarly, under decreasing ambient temperatures below T_{lc} levels, endotherms lose heat rapidly and require heat generation above BMR levels to maintain body temperatures. Endotherm animals would thus have two non-exclusive avenues to cope with lower temperatures: higher BMR levels or lower thermal conductance, e.g. via insulation. As a consequence, lower levels of T_{lc} can be expected (Scholander et al., 1950a; Scholander, 1955).

Large endotherms tend to dissipate or lose metabolic heat slowly because of their small surface area relative to their body volume (Scholander et al., 1950c; Riek & Geiser, 2013). Thermal conductance scales with body mass with an exponent around 0.57, while both BMR and body surface area scale with body mass with exponents around 0.67 (Riek & Geiser, 2013). This indicates that thermal conductance increases more slowly with body mass than BMR. Therefore, larger endotherms are better able to withstand colder temperatures than smaller endotherms (Scholander et al., 1950b). Similarly, small-bodied endotherms have a higher thermal conductance than larger species. Therefore, small endotherms may be able to cope better with rising ambient temperatures than larger species (Scholander et al., 1950b). Hence, to occupy a variety of environmental conditions, apart from body size, endotherms rely on BMR and heat dissipation, (Fristoe et al., 2015).

The findings of the present study support the hypothesis that the capacity to dissipate heat is an important constraint for the energetics of endotherms (Speakman & Król, 2010). Recently, Naya et al. (2013) highlighted the importance of rodents' ability to dissipate heat in order to manage endogenous heat load and suggested that endotherm species (particularly non-tropical rodents) tend to increase their thermal conductance during the summer season. Such an increase in conductance should also be a means to increase their T_{uc}. Other studies also suggest that endotherm species do indeed raise their T_{uc} during warmer months (Wilson, Brown & Downs, 2011). Without such plastic changes in T_{uc}, endotherms may find it difficult to cope with the temporal variability in dry and hot conditions and as a result would frequently experience hyperthermia, which may have serious consequences for their survival (McKechnie & Wolf, 2010; Speakman & Król, 2010). Therefore, hot and dry conditions would probably favour species with lower mass-independent BMR and higher T_{uc}.

All else being equal, it should be advantageous for endotherms to achieve extreme metabolic critical temperatures (i.e. very low T_{lc} and very high T_{uc}) because wide thermal limits will allow endotherms to maintain BMR across a wide range of environmental temperatures, and thereby conserve energy (Scholander et al., 1950b,c). However, TNZs in endotherms are not infinitely wide (Riek & Geiser, 2013; Araújo et al., 2013; Khaliq et al., 2014), which may be due to a constraint that is difficult to overcome: T_{lc} and T_{uc} are positively correlated, i.e. possibilities are limited to change between low minimum conductance and high maximum conductance and thereby to alter the TNZ dynamically to suit prevailing conditions. In simple words, in order to tolerate cold temperatures an endotherm requires a high energy level and low thermal conductance which is disadvantageous under higher ambient temperatures (McNab, 2012). This trade-off is supported by findings that the breadth of the TNZ of small endotherms varies seasonally which could be inferred as a mechanism to conserve energy (Wilson, Brown & Downs, 2011; Kobbe, Nowack & Dausmann, 2014).

Conclusions

The relationship of metabolic critical temperatures with BMR contributes a novel aspect to a better understanding of the relationships between species' energy budget and their environment, especially under changing climatic conditions. To off-set the negative effects of rising temperatures, endotherms may have at least two avenues for adaptation: (i) the alteration of heat dissipation capacities e.g. via altering body insulation (Scholander et al., 1950a), or (ii) achieving higher levels of metabolic critical temperatures. Endothermic species, particularly those in the tropics, might face the challenge of hyperthermia during periods of high ambient temperatures (see also Khaliq et al. 2014). Therefore, considering the heat dissipation capacities of endotherms may significantly improve assessments of species' vulnerability to climatic change.

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Table 1(on next page)

Table 1: Phylogenetic generalized least squares models of BMR as a function of body mass and either upper or lower critical temperature (T_{lc} or T_{uc}).

BMR was first modeled using phylogenetic generalized least squares (*PGLS)*, as a function of body mass while Pagel's λ was estimated, and set it to its maximum likelihood value (see Methods). After controlling for phylogeny and body mass, we individually added either T_{UC}, T_{LC} in the model. Bold values indicate associations where estimated parameters (B) are significantly different from 0. BMR, body mass was log-transformed. n = sample size, B = estimated parameter ±SE, λ = Pagel's Lambda, set to its maximum likelihood value.

Table 1: Phylogenetic generalized least squares models of BMR as a function of body mass and either upper or lower critical temperature (T_{lc} or T_{uc}).

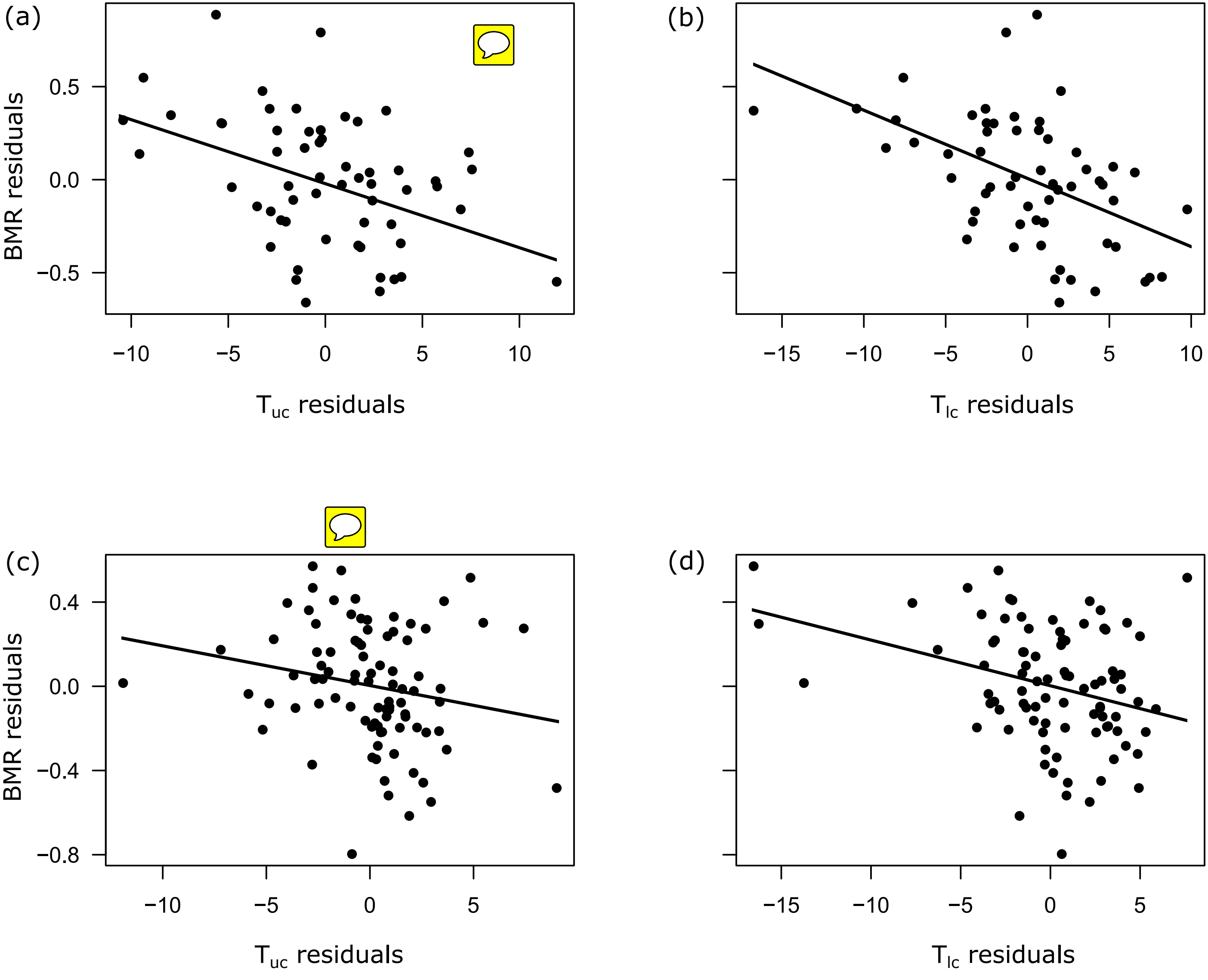
	Birds (n = 58)				Mammals (n = 88)			
	B	λ	R^2	*P*	B	λ	R^2	*P*
Mass	**0.70 (±0.03)**	**----**	**----**	**<0.001**	**0.68 (±0.01)**	**---**	**----**	**<0.001**
T_{UC}	**-0.1.07(±0.25)**	**0.66**	**0.89**	**<0.001**	**-0.57 (±0.23)**	**0.91**	**0.94**	**0.01**
Mass	**0.68 (±0.03)**	**----**	**----**	**<0.001**	**0.67 (±0.01)**	**----**	**----**	**<0.001**
T_{LC}	**-0.31 (±0.13)**	**0.59**	**0.88**	**0.02**	**-0.32 (±0.12)**	**0.90**	**0.94**	**0.008**

BMR was first modeled using phylogenetic generalized least squares (*PGLS)*, as a function of body mass while Pagel's λ was estimated, and set it to its maximum likelihood value (see Methods). After controlling for phylogeny and body mass, we individually added either T_{UC}, T_{LC} in the model. Bold values indicate associations where estimated parameters (B) are significantly different from 0. BMR, body mass was log-transformed. n = sample size, B = estimated parameter ±SE, λ = Pagel's Lambda, set to its maximum likelihood value.

Figure 1(on next page)

Figure 1: Relationship between BMR and upper and lower critical temperatures in birds (a, b) and mammals (c, d)

(a, b) birds, (c, d) mammals. BMR residuals are calculated as the log BMR minus log BMR as predicted by log mass; and the T_{lc} and T_{uc} residuals are calculated as the T_{lc} or T_{uc} minus T_{lc} or T_{uc} as predicted by log mass.


(a)
(b)
(c)
(d)
BMR residuals
0.5
0.0
−0.5
0.4
0.0
−0.4
−0.8
−10
−5
0
5
10
−15
T_{uc} residuals
T_{lc} residuals