The "minimal boundary curve for endothermy" as a predictor of heterothermy in mammals and birds: a review

Christine E. Cooper[1,2] and Fritz Geiser[2]

[1]Department of Environmental Biology, Curtin University of Technology, POBox U1987 Perth 6845

[2]Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale NSW 2351, Australia

Address for correspondence
C.E. Cooper
Department of Environmental Biology, Curtin University of Technology, POBox U1987 Perth 6845
Ph. (08) 92667965
Fax (08) 9266 2495
E-mail C.Cooper@curtin.edu.au

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Abbreviations:

BMR: basal metabolic rate

T_a: ambient temperature

T_b: body temperature

Abstract

According to the concept of the 'minimal boundary curve for endothermy', mammals and birds with a basal metabolic rate (BMR) that falls below the curve are obligate heterotherms and must enter torpor. We examined the reliability of the boundary curve (on a double log plot transformed to a line) for predicting torpor as a function of body mass and BMR for birds and several groups of mammals. The boundary line correctly predicted heterothermy in 87.5% of marsupials (n = 64), 94% of bats (n = 85) and 82.3% of rodents (n = 157). Our analysis shows that the boundary line is not a reliable predictor for use of torpor. A discriminate analysis using body mass and BMR had a similar predictive power as the boundary line. However, there are sufficient exceptions to both methods of analysis to suggest that the relationship between body mass, BMR and heterothermy is not a causal one. Some homeothermic birds (e.g silvereyes) and rodents (e.g. hopping mice) fall below the boundary line, and there are many examples of heterothermic species that fall above the boundary line. For marsupials and bats, but not for rodents, there was a highly significant phylogenetic pattern for heterothermy, suggesting that taxonomic affiliation is the biggest determinant of heterothermy for these mammalian groups. For rodents, heterothermic species had lower BMRs than homeothermic species. Low BMR and use of torpor both contribute to reducing energy expenditure and both physiological traits appear to be a response to the same selective pressure of fluctuating food supply, increasing fitness in endothermic species that are constrained by limited energy availability. Both the minimal boundary line and discriminate analysis were of little value for predicting the use of daily torpor or

hibernation in heterotherms, presumably as both daily torpor and hibernation are precisely controlled processes, not an inability to thermoregulate.

Introduction

The concept of a “minimal boundary curve for endothermy” in mammals and birds (McNab in 1983) postulates that mammals and birds whose basal metabolic rate (BMR) falls below this allometric curve must use torpor; consequently they are obligate heterotherms. In contrast, species with a BMR above the boundary curve are predicted to be capable of continuous endothermy or, in other words, homeothermic thermoregulation. The minimal boundary curve for endothermy was derived by "placing a linear curve on the left margin of the relation between basal rate and mass for fossorial mammals and hedgehogs" and is described by the equation BMR (mL O_2 h^{-1}) = 15.56 $m(g)^{0.33}$ (McNab 1983) and consequently the double-log plot of this relationship forms a line, henceforth referred to as the boundary line. The boundary line and Kleiber’s (1932) line intersect at a body mass of approximately 80 g, below which the BMR of homeothermic species is predicted to scale according to the boundary line, whereas heterothermic species are thought to scale according to Kleiber’s line. In this way the boundary line claims to provide a clear distinction of the species that should employ torpor and those who do not (McNab 1983). The same concept of a minimal boundary line has been reiterated in recent publications (McNab and Bonaccorso 2001; McNab 2002) and the concept is widely used by other authors.

Some mammals, such as ground squirrels, marmots and large carnivores, have a BMR that falls above the boundary line, but nevertheless use torpor. These exceptions to the boundary line concept have been explained by claiming that seasonal torpor in these hibernating species is "an actively regulated state: it is not an inability to thermoregulate, as tends to be the case for those species whose BMR falls below, especially far below, the boundary curve" (McNab 2002). The implicit assumption here is that species who enter daily torpor (daily heterotherms; with torpor bouts lasting less than 1 day) and hibernators (species capable of prolonged torpor; with torpor bouts that can last longer than 1 day up to several weeks) differ fundamentally in their thermoregulatory ability, and that hibernation is regulated whereas daily torpor is not.

The purpose of our paper is to quantitatively assess the reliability of the boundary line in separating homeothermic and heterothermic mammals and birds, and for heterothermic species, in distinguishing between species that use daily torpor and those that enter prolonged torpor (hibernation). We also explore an alternative method for predicting patterns of heterothermy based on the relationship between mass and BMR, and examine phylogenetic patterns in body temperature regulation.

Methods

Body mass, BMR and mode of body temperature regulation were taken from original references or from reviews (Hayssen and Lacy 1985; McNab 1988; Geiser and Ruf 1995; McKechnie and Lovegrove 2002; Lovegrove 2003; Geiser 2003, 2004; Cruz-Neto and Jones 2006). We found sufficient and reliable data for homeothermic or heterothermic monotremes (n = 3), marsupials (n = 64), bats (n = 84), rodents (n = 157), and birds (n = 28) for our analysis. Heterothermic species were defined as those whose minimum metabolic rate during torpor is less than BMR and/or minimum body temperature (T_b) >5 ºC below the normothermic resting T_b (Geiser *et al*. 1996). Species with a minimum MR not lower than BMR, or a <5°C T_b reduction were considered to be homeothermic (we recognise that homeothermy in at least some of these species may not withstand vigorous investigation of thermal biology in the field, but these are our best estimates based on available data). BMR and body mass for mammals and birds with known patterns of thermoregulation were plotted along with the minimal boundary line for endothermy. Differences between residuals (obtained by least squares regression of log transformed body mass and BMR data for each of the respective groups) for heterothermic and homeothermic mammals (excluding monotremes) were evaluated using a one-factor ANOVA both before and after correction for phylogenetic history (see below).

Discriminate analysis was used to produce classification functions to separate homeothermic and heterothermic species and for heterotherms, to separate those that use daily torpor and hibernation, using data for log body mass (g; logm) and log BMR (ml O_2 h^{-1}; logBMR). Of the two resulting functions, whichever equation produces the largest value indicates to which category a species belongs. Regression, ANOVA and discriminate analyses were conducted using *statistiXL* v1.6.

The significance of a phylogenetic signal in patterns of heterothermy for each group was assessed by cluster analysis after Vanhooydonck and Van Damme (1999). Random reallocations (1000) of trait categories (daily heterotherm, hibernator or homeotherm) were assessed for fit (minimum cumulative distance of each species with a particular trait to each of the other species sharing that trait) and compared to the actual fit for the phylogenetic tree for each group. Phylogenetically independent residuals were calculated from phylogenetically corrected allometric regressions for each group using independent contrasts (IC; Felsenstein 1985, Garland et al. 1993). Phylogenetic trees for each group were obtained from Withers *et al*. (2006; marsupials), Jones *et al*. (2002; bats) and Lovegrove (2003; rodents). Cluster analyses and IC were conducted using custom-written Visual Basic software (P.C. Withers). Monotremes and birds were excluded from ANOVA, discriminate and phylogenetic analyses because insufficient species numbers or data on torpor use were available for these groups.

Results

Monotremes

Members of the three extant genera of monotremes are large (body mass 1.3 to 10.3 kg) and all have a BMR that lies near or below the marsupial regression, but are above the boundary line because of their large mass (Fig. 1). Long-beaked echidnas (*Zaglossus* spp.) and platypus (*Ornithorhynchus anatinus*) appear to be homeothermic (Grant 1983; Grigg et al. 2003). In contrast, short-beaked echidnas (*Tachyglossus aculeatus*) may hibernate for extended periods in winter and also enter short bouts of torpor in summer (Grigg and Beard 2000; Nicol and Andersen 2000), although their BMR is above the boundary line.

Marsupials

Marsupials have BMRs that conform exceptionally well to an allometric relationship (r^2 = 0.99, n = 64). The residuals from this allometric relationship for heterothermic and homeothermic marsupials do not differ, before or after correction for phylogenetic history ($F_{1,59}$ = 0.81, p = 0.372; $F_{1,59}$ = 0.531, p = 0.469 respectively). The allometric line of BMR for marsupials and the boundary line intercept at a body mass of 87.9 g and a BMR of 67.7 ml O_2 h^{-1}. Heterothermic marsupials range in body mass from ~ 5 g to ~1500 g and have BMRs that fall both above and below the boundary line (Fig. 1). At body masses of less than 87.9 g all marsupials have BMRs that are lower than the boundary line. While all of these species are heterothermic, they include species that use both short-term daily torpor (e.g. dasyurids) and those that undergo prolonged seasonal hibernation (e.g. pygmy-possums, Burramyidae). Eight marsupial species with body masses greater than 87.9 g are known to be heterothermic (*Dasyuroides byrnei*, *Dasyurus geoffroyi*, *D. viverrinus*, *Marmosa robinsoni*, *Monodelphis brevicaudata*, *Myrmecobius fasciatus, Petaurus breviceps, Phascogale tapoatafa*) and, although their BMRs fall above the boundary line, they all enter daily rather than prolonged torpor (Geiser 2003; Cooper and Withers 2004). Therefore the boundary line correctly classifies 87.5% of marsupials as either hetero- or homeothermic (73.3 % of heterothermic and 100% of homeothermic marsupials). However, it fails to distinguish between seasonal hibernators and daily heterotherms.

A discriminate analysis of BMR and mass data for marsupials produced the following equations:

Homeothermic: -31.7 logm + 55.45 logBMR – 26.18

Heterothermic: -35.02 logm + 53.98 logBMR – 15.25

Of all marsupial species 93.5% were correctly classified (97.1 % of homeothermic and 90% of heterothermic species classified correctly). A similar discriminate analysis to separate daily heterotherms from hibernators produced the following equations:

Hibernation: 0.419 logm + 51.83 logBMR –14.78

Daily Torpor: 18.44 logm + 50.88 logBMR –15.02

However this prediction was not robust, with only 47.9 % of species being classified correctly (50% of hibernators and 45.8 % of daily heterotherms).

There was a highly significant ($P < 0.001$) phylogenetic signal for the pattern of heterothermy amongst marsupials, with none of the 1000 reallocations of trait categories fitting the marsupial phylogenetic tree better than the actual pattern *i.e.* the actual pattern of trait characters had a lower minimum cumulative distance of each species with a particular trait to each of the other species sharing that trait, than any of the 1000 random rearrangements.

Bats

The BMR of bats conforms well to an allometric relationship ($r^2 = 0.915$; $n = 85$; Fig 2). There was no significant difference between the residuals from this relationship for heterothermic and homeothermic species, either before or after correction for phylogenetic history ($F_{1,82} = 0.481$, $p = 0.490$; $F_{1,82} = 0.829$, $p = 0.368$ respectively). The boundary line intercepts the allometric equation at a mass of 54.6 g and a BMR of 58.1

ml O_2 h^{-1}. Heterothermic bats have body masses that range from ~4 g to ~74g and have BMRs that fall both above and below the boundary line (Fig 2). Five species of known heterothermic bats (*Anoura caudifer, Artibeus hirsutus*, *Artibeus jamaicensis*, *Dobsonia minor* and *Tonatia sylvicola*) fall above the boundary line (Fig 2), and all five use daily torpor. Two of these (*Dobsonia minor* and *Tonatia sylvicola*) have body masses above 54.6g, whereas the remaining three have body masses less than 54.6 but BMRs that are higher than the boundary line. Both daily heterotherms and species that use long-term hibernation are below the boundary line. No homeothermic bats fall below the boundary line. Thus the boundary line correctly classifies 94% of bats as either hetero- or homeothermic (93 % of heterothermic and 100% of homeothermic bats). However, it fails to distinguish between hibernators and daily heterotherms.

Discriminate analysis of body mass and BMR for bats and insectivores produced the equations:

Homeothermic: $-5.11 \log m + 36.71 \log BMR - 34.69$

Heterothermic: $-12.15 \log m + 32.45 \log BMR - 15.205$

These correctly separated 94% of heterothermic and 93% of homeothermic species (combined success 93%). Daily heterotherms and hibernators were separated using the following discriminate functions

Hibernation: $-8.38 \log m + 29.43 \log BMR - 14.27$

Daily torpor: $-7.65 \log m + 32.36 \log BMR - 19.05$

with 70% of species using hibernation and 70% using daily torpor separated correctly (70% overall correct classification).

There was a highly significant ($P < 0.001$) phylogenetic signal for the pattern of heterothermy amongst bats, with none of the 1000 reallocations of trait categories fitting the bat phylogenetic tree better than the actual pattern.

Rodents

The relationship between BMR and body mass for rodents ($r^2 = 0.69$; n = 242; data from Hayssen and Lacy 1985; Lovegrove 2000a) is not as strong as for marsupials and bats. The residuals from the allometric line of BMR for rodents are significantly lower for known heterothermic species than those for homeothermic rodents both before and after phylogenetic correction ($F_{1,156} = 9.1$, $P = 0.003$; $F_{1,156} = 10.1$, $P = 0.002$ respectively). The intercept between the allometric line of BMR (data from Lovegrove 2000a) and the boundary line occurs at a body mass of 32.2 g and a BMR of 48.9 ml O_2 h^{-1}. Both daily heterotherms and seasonal hibernators have BMRs that fall below as well as above the boundary line; ~53% of heterothermic rodents are above the boundary line (Fig 3). An extreme case is the woodmouse (*Apodemus flavicollis*), which has a BMR that is well above the boundary line but enters daily torpor (Aeschimann *et al*. 1998). The Siberian hamster (*Phodopus sungorus*) is a daily heterotherm with strongly seasonal torpor. It has a BMR that is above the boundary line both in summer and winter, but the species enters torpor only in winter (Heldmaier and Steinlechner 1981b).

The BMR of the majority of homeothermic rodents appears to scale with the boundary line (Fig.3). However, unlike for marsupials, the BMR of a few species of rodent considered to be homeothermic (the spinifex and fawn hopping mice, *Notomys alexis* and

N. cervinus; MacMillen and Lee 1970; Withers *et al.* 1979; Dawson and Dawson 1982) and the swamp rat (*Rattus lutreolus*; Collins 1973) fall under the boundary line (residuals –28.6, -8.0 and -9.3 ml O_2 h^{-1} respectively; Fig. 3). Overall, the boundary line correctly classifies 82.3% of rodents as either hetero- or homeothermic (51.2% of heterotherms and 98.1 % of homeotherms), whereas the line separates 65.9% of hibernators and 83.3% of daily heterotherms correctly.

The discriminate functions for hetero- and homeothermic rodents were

Homeothermic: 19.21 logm + 39.52 logBMR –20.79

Heterothermic: 17.21 logm + 36.22 logBMR – 16.87

These correctly separated 68% of rodents into the two categories (66.5 % of homeothermic and 69.5% of heterothermic rodents correctly). Daily heterotherms and hibernators were separated using the following discriminate functions

Hibernation: 17.69 logm + 28.2 logBMR –18.91

Daily torpor: 14.11 logm + 27.54 logBMR –13.61

with 92.5% of species using daily torpor and 71.9% using hibernation separated correctly (81.7% overall correct classification).

There was no significant phylogenetic pattern (P = 0.766) for heterothermy in rodents. Of the 1000 reallocations of trait categories, 766 fitted the rodent phylogenetic tree better than the actual pattern.

Birds

Heterothermic birds range in mass from ~3 g to ~500 g (Schleucher 2001; McKechnie and Lovegrove 2002) and have BMRs that fall both above and below the boundary line in similar proportions (Fig. 4). The BMR of the poorwill (*Phalaenoptilus nuttallii*) falls below the boundary line. The poorwill is the only known avian hibernator and enters prolonged torpor bouts in winter but also short bouts of torpor in summer (Jaeger 1948; Bartholomew *et al*. 1957; French 1993; Brigham *et al*. 2006).

Some birds considered to be homeothermic have BMRs below the boundary line (Fig 4). For example, silvereyes (*Zosterops australis*) can maintain a normothermic T_b at an effective ambient temperature (T_a) as low as -40 ºC, have a circadian variation in T_b of only 3-4 ºC and do not enter torpor (Maddocks and Geiser 1999) despite their BMR (both in summer and winter) falling below the boundary line (mean residual = -8.8 mL O_2 h^{-1}; Fig. 4). Todies (*Todus mexicanus*) have a BMR that is well below the boundary line (residual = -20.8 mL O_2 h^{-1}), and whereas females enter torpor as predicted, males appear to be homeothermic. (Merola-Zwartjes and Ligon 2000).

Discussion

Our analyses suggest that McNab's (1983) minimal boundary line for endothermy is not a reliable predictor of heterothermy and homeothermy in endotherms. Although classifying a high proportion of species correctly, we identify examples of heterothermic species, from a range of taxonomic groups with BMRs above this line, and there are some examples of apparently strictly homeothermic rodents and birds that fall below the boundary line. The classification functions produced by our discriminate analysis to distinguish between heterothermic and homeothermic species (based also on body mass and BMR) had an overall similar success rate to McNab's (1983) boundary line, being slightly better for marsupials, similar for bats and appreciably worse for rodents. However, neither method proved reliable for distinguishing between daily heterotherms and those that enter prolonged torpor. For marsupials and bats, patterns of heterothermy are best predicted by phylogenetic history, although there is no significant phylogenetic pattern in heterothermy for rodents. We discuss further the relationship between body mass, BMR and heterothermy, and examine the limitations of using this relationship to predict heterothermy in endotherms.

Body mass is clearly a major factor influencing heterothermy. Torpor is a mechanism important for both energy and water conservation, and is particularly important for small species (Morrison 1960; Bartholomew 1972; Barnes and Carey 2004). A small body mass enhances heat loss, due to a high surface area to volume ratio, so the relative advantages of heterothermy are especially pronounced for small endotherms. Small species cool faster, have a high mass-specific energy requirement, have a greater reduction of metabolic rate in comparison to normothermic values, and the overall energetic costs of rewarming are smaller due to reduced thermal inertia at smaller body masses (Bradshaw 2003; Speakman and Thomas 2003).

Whereas some species that use torpor do have a significantly lower BMR than those that do not (e.g. rodents) this is not true for marsupials and bats. There are sufficient exceptions amongst all groups to suggest that not all small species with a low BMR are obligate heterotherms, and that a high BMR is due not only to the cost of homeothermic regulation. Several examples presented here (e.g. silvereyes, hopping mice) indicate that small endotherms, with low BMRs (below the boundary line) are capable of maintaining a high and stable T_b during cold exposure. Such examples are few however, due to the prevalence of heterothermy in small species (Geiser and Ruf 1995). In addition, not all small species with a high BMR (*e.g.* bats, rodents) are homeothermic, suggesting that a high BMR in small species is not inextricably linked to the cost of permanent homeothermy. *A priori* one might even predict that species with a high BMR and the associated high costs of energy expenditure during normothermia are more likely to enter torpor, to compensate for this high energy expenditure. However species with a low BMR often live in an environment that requires frugal use of energy and presumably use torpor for the same reason. A low BMR has been associated with environments with low primary productivity (e.g. deserts) and with diets with a low net energy yield (e.g. myrmecophages, folivores). Heterothermy, which is important for the conservation of both energy and water, is an important additional strategy for species occupying low-energy niches (Lovegrove 2000b). Thus, species with a low BMR may also enter daily torpor because they have a lifestyle that requires a frugal use of energy during the inactive phase of the day or year when fuels are not replenished. Thus any association of a low BMR and heterothermy need not be causal.

Although both the boundary line or our discriminate analysis were reasonably successful in discriminating heterotherms and homeotherms, a number of species were not correctly classified by either method. The limitations of both are presumably due to factors other than the influence of the relationship between body mass and BMR on patterns of heterothermy. For marsupials and bats, the pattern of heterothermy is strongly related to phylogeny. For marsupials, all dasyurids studied to date use daily torpor, and all of the Burramyidae (pygmy-possums) use prolonged hibernation (Geiser 2003; Geiser and Körtner 2004). Species of these two groups are heterothermic regardless of whether their BMR falls above or below the boundary line. Other marsupials (e.g. peramelids, macropodids) are all larger than the 87.9 g intercept of the BMR/boundary lines but are all presumably homeothermic due to phylogenetic affiliation rather than a relationship between mass and BMR. The Tasmanian devil (*Sarcophilus harrisii*) is the largest extant dasyurid, and although it has been suggested that it uses daily torpor (Nicol and Maskrey 1980), its thermal biology has not been investigated in sufficient detail to confirm torpor. The use of torpor by this largest extant dasyurid would confirm a strong phylogenetic rather than mass/BMR influence on heterothermy. For bats, there are also strong phylogenetic patterns. Vespertilionids show a predominance of hibernation, small pteropodids are daily heterotherms and large pteropodids apparently are characterised by homeothermy. For these groups, phylogenetic history and size are better predictors of patterns of heterothermy than a relationship between mass and BMR.

For rodents the relationship between phylogeny and heterothermy is not significant and the occurrence or otherwise of heterothermy is complex, presumably further influenced by a suite of habitat, climate and life history factors such as diet. Most homeothermic species are above the boundary line, but the exceptions suggest that species with a BMR below the boundary line are not necessarily obligate heterotherms, and that species above the line may not necessarily be homeothermic. For *Phodopus sungorus* BMR is above the boundary line both in summer and winter, although the species only enters daily torpor in winter. Winter acclimatised *P. sungorus* are capable of maintaining a homeothermic T_b at T_a as low as -69 ºC. Nevertheless, *P. sungorus* enter spontaneous (food ad libitum) torpor in winter, even at mild, thermoneutral T_a of 23 ºC (Heldmaier and Steinlechner 1981a; Geiser and Heldmaier 1995). In summer, *P. sungorus* does not enter spontaneous torpor, although its thermogenic capacity is substantially reduced to about 70% of the winter capacity (Heldmaier and Steinlechner 1981a,b). Thus data on thermoenergetics of *P. sungorus* do not support a link between BMR and torpor use, nor a link between thermoregulation and thermogenic capacity and torpor. For birds insufficient data are available to fully understand the relationship between BMR, body mass and heterothermy, and the use of torpor by birds in general is an area that requires further investigation. Presumably, heterothermy in rodents and birds is primarily determined by adaptation to fluctuating energy and/or water availability (Lovegrove 2000b), with is turn is related to factors including distribution, habitat, climate and life history traits such as diet.

For heterothermic species, both the boundary line and our discriminate analysis have substantial limitations for predicting patterns of torpor. Heterothermic species with a BMR above the boundary line are not restricted to hibernators, contradicting McNab's

(1983; 2002) suggestion; many of the species are daily heterotherms, which use daily torpor exclusively. In fact, all of the heterothermic marsupial, bat and bird species with a BMR above the boundary line use daily torpor, whereas all hibernators fall below the boundary line. For rodents, the BMRs of a mix of daily heterotherms and seasonal hibernators fall above and below the boundary line. Our discriminate analysis had a similar low success rate to the boundary line in separating species that use daily torpor and those that use hibernation. The inability of these techniques to separate these two groups of heterotherms is presumably due to a conceptual weakness - daily torpor is not a reflection of poor thermoregulatory ability or failure of heat production, and there appears to be no physiological reason for these two groups to be divided based on the relationship between body mass and BMR.

Both daily torpor and hibernation are precisely controlled processes and there is no known physiological difference in proportional thermoregulation during daily torpor and seasonal hibernation. Although T_b in both groups may vary over a wide temperature range when torpid individuals are thermoconforming, T_b in all species investigated so far is regulated above a species- or population-specific set point by proportional thermogenesis as during normothermia, albeit at a lower T_b (Heller and Hammel 1972). There are examples of thermoregulation during torpor by daily heterotherms for birds (e.g. hummingbirds; Hainsworth and Wolf 1970; Hiebert 1990), marsupials (e.g. dunnarts and kowaris; Geiser and Baudinette 1987) and placentals (e.g. Siberian hamsters, shrews; Heldmaier and Steinlechner 1981b; Nagel 1985) as well as for thermoregulation during hibernation from several mammalian orders, including marsupials (e.g. pygmy-possums; Song et al. 1997), rodents (e.g. ground squirrels, dormice; Wyss 1932; Heller and Hammel 1972), bats (Hock 1951), and insectivores (Fowler and Racey 1990). Although the average minimum T_b for hibernators is ~6 ºC and is ~17 ºC for daily heterotherms, T_b minima show substantial overlap between the two groups (Geiser and Ruf 1995), some daily heterotherms have a T_b minimum <10 ºC (e.g. honey possum *Tarsipes rostratus*; Withers *et al*. 1990, hummingbird *Oreotrichilus estella*; Carpenter 1974), and some hibernators have a T_b minimum >10 ºC (e.g. tenrecs *Tenrec ecaudatus, Setifer setosus*; Kayser 1964, Hildwein 1970) and consequently T_b minima are not a reliable trait for separating the two groups of heterotherms. To our knowledge differences in thermogenic capacity between daily heterotherms and hibernators have not been investigated, but maximum rewarming rates from torpor are indistinguishable between daily heterotherms and hibernators (Geiser and Baudinette 1990) suggesting that, as for thermoregulation, thermogenic capacity does not differ between the two groups of heterotherms.

Our analyses raise the question as to why BMR should be a predictor for torpor use. Torpor is predominantly employed by small species in which BMR comprises only a small component of daily energy expenditure. Consequently, BMR is not likely to have a strong selective pressure on torpor use by various birds and mammals. Body mass, together with phylogenetic history is a significant determinant of heterothermy for marsupials and bats, but not rodents. For rodents, it is highly likely that body mass combined with habitat or food availability will provide strong selective pressures on torpor use as well as on BMR. Thus, our analysis suggest that it is not simply the relationship between BMR and body mass alone, but rather a combination of factors including body mass, phylogeny, diet, climate and other life history traits that determine whether or not a species is heterothermic.

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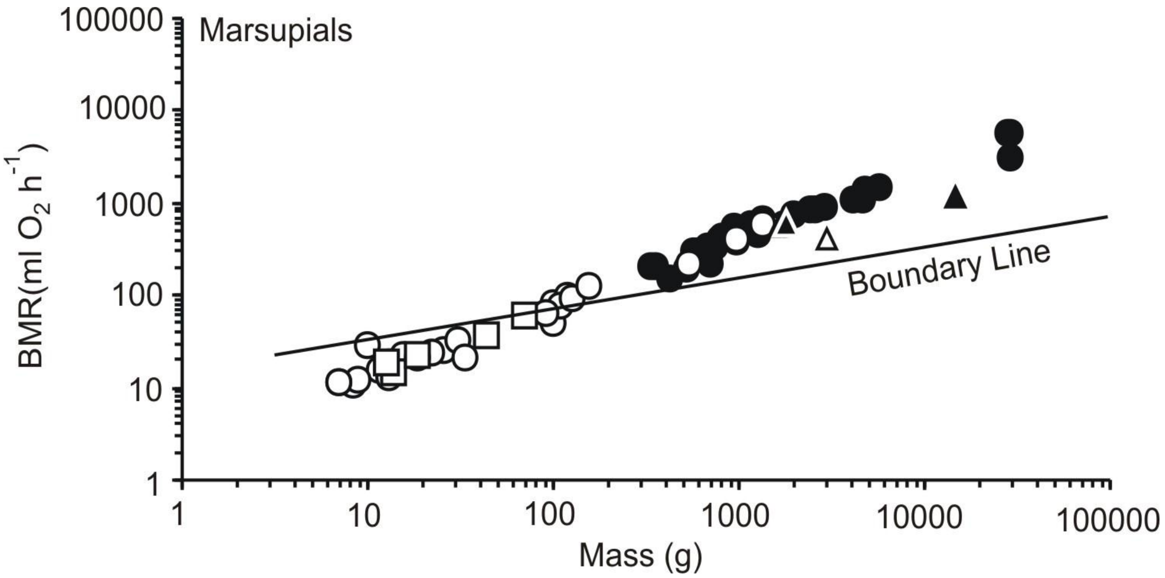

Figure 1:

Relationship between mass and basal metabolic rate (BMR) for monotremes (n = 3; data from Dawson 1983) and marsupials (n = 64; data from Withers *et al*. 2006) relative to the boundary line. Homeothermic species are represented by dark symbols, heterothermic species by light symbols. Species that use daily heterothermy are represented by circles and those that use hibernation by squares. Triangles represent monotremes.

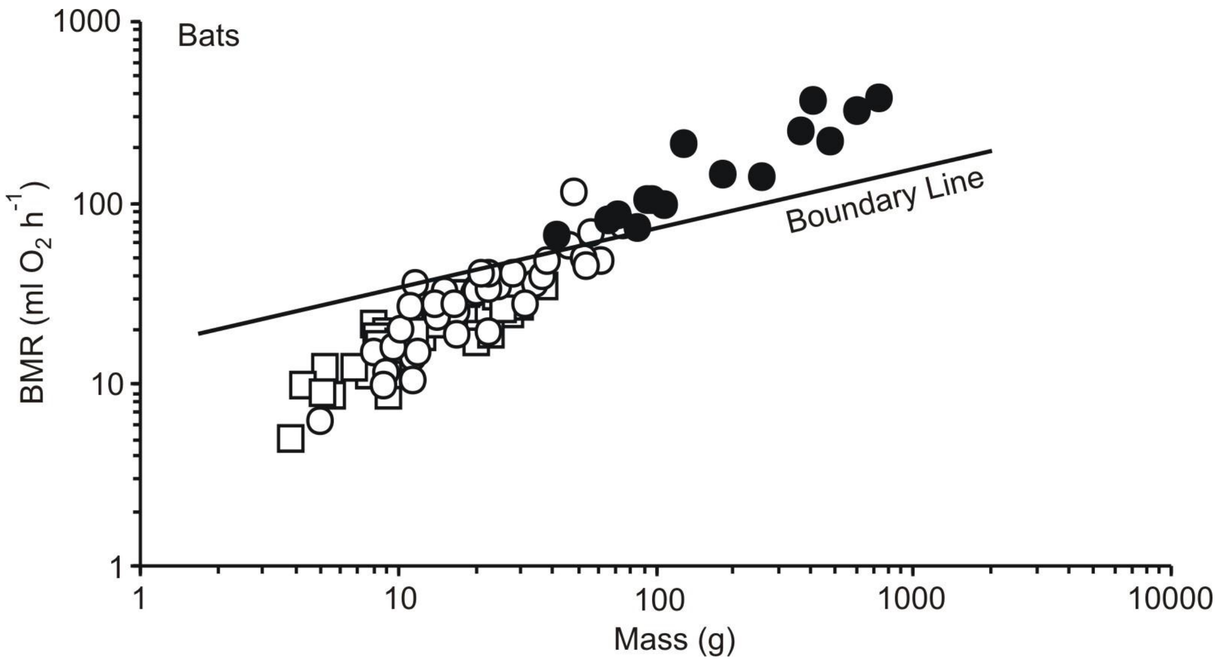

Figure 2:

Relationship between mass and basal metabolic rate for bats (n = 85; data from Cruz-Neto and Jones 2006) relative to the boundary line. Homeothermic species are represented by dark symbols, heterothermic species by light symbols. Species that use daily heterothermy are represented by circles and those that use hibernation by squares.

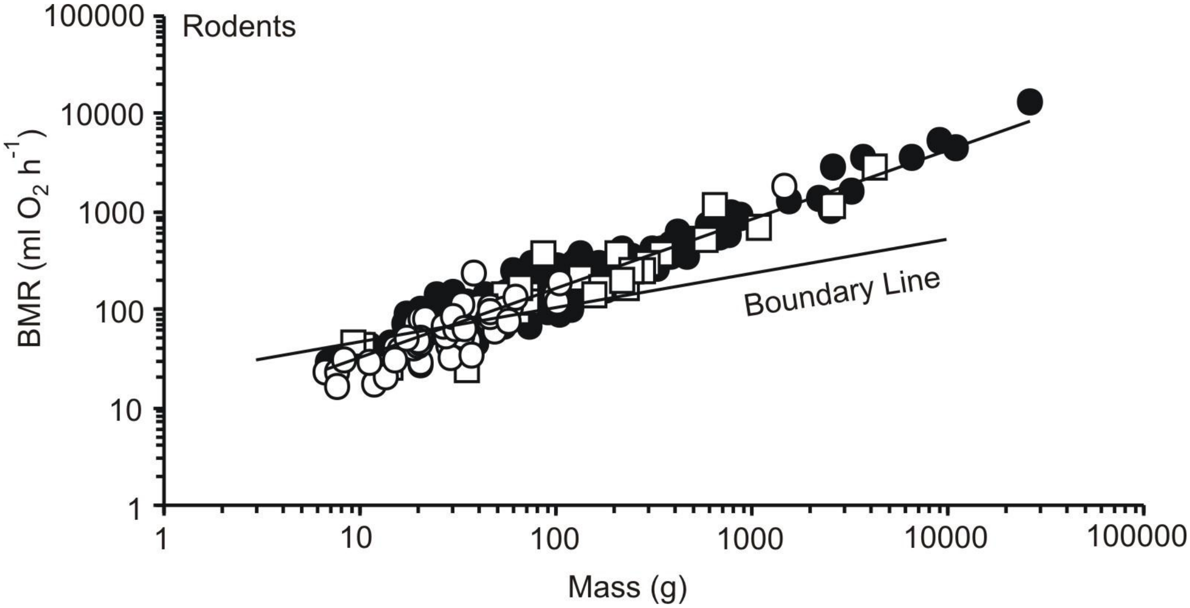

Figure 3: Relationship between mass and basal metabolic rate for rodents (n = 157; data from Lovegrove 2000a) relative to the boundary line. Homeothermic species are represented by dark symbols, heterothermic species by light symbols. Species that use daily heterothermy are represented by circles and those that use hibernation by squares.

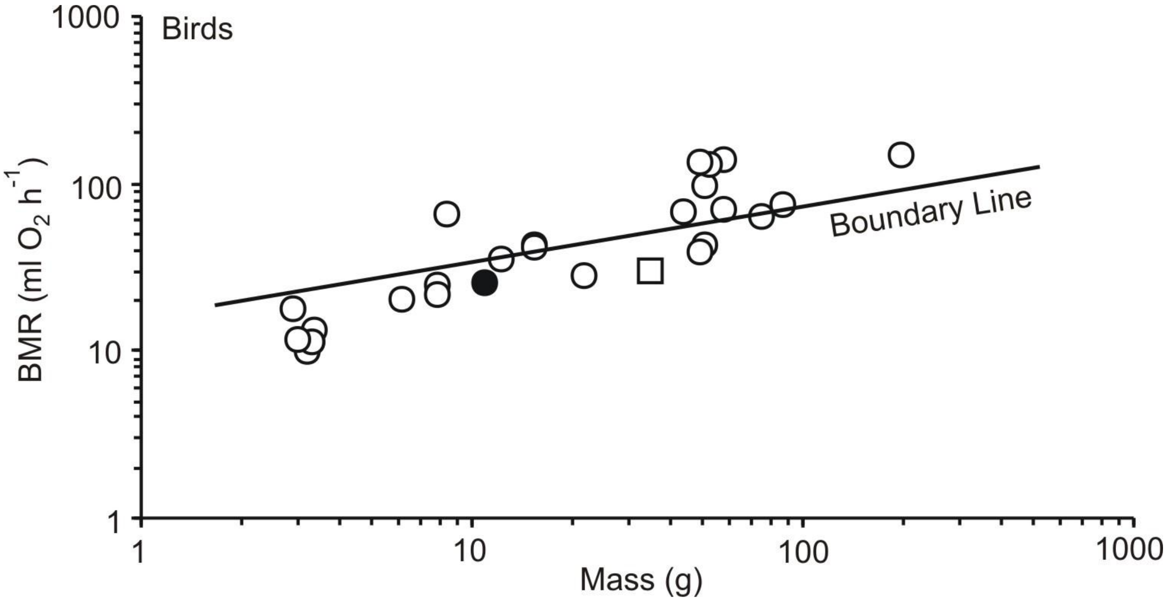

Figure 4:

Relationship between mass and basal metabolic rate for birds with known thermoregulatory strategies (n = 28, data from Aschoff and Pohl 1970; McKechnie and Lovegrove 2002) relative to the boundary line. The homeothermic silvereye (*Zosterops australis*) is represented with a dark symbol, heterothermic species by light symbols. Daily heterotherms are represented with circles, the hibernating poorwill (*Phalaenoptilus nuttallii*) with a square.