THE RELATIONSHIP BETWEEN BODY MASS AND RATE OF REWARMING FROM HIBERNATION AND DAILY TORPOR IN MAMMALS

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Summary

1. Rewarming rate from torpor and body mass were inversely related in. 86 mammals ranging in body mass between 2 and 8500 g.

2. Most of the mammalian taxa investigated showed a similar change of rewarming rate with body mass. Only the insectivores showed a more pronounced increase in rewarming with a decrease in body mass than did the other taxa. The rates of rewarming of marsupials were similar to those of placentals.

3. At low air temperature (T_a), the rate of rewarming of marsupials was not related to body mass, although a strong relationship between the two variables was observed in the same species at high T_a.

4. The slopes relating rewarming rates and body mass of the mammalian groups and taxa analysed here were similar to those obtained earlier for mass-specific basal metabolic rate (BMR) and body mass in mammals, suggesting that the rate of rewarming and BMR are physiologically linked.

Introduction

One of the major differences between hibernation in ectotherms and endo-therms is that endotherms actively terminate the torpor episode by internal heat production. All heterothermic endotherms actively raise their body temperature (T_b) from low levels during torpor. However, not all rewarm at the same rate. Slow rewarming rates have been observed in large species, with small species showing rapid rewarming, and Heinrich and Bartholomew (1971) demonstrated that body mass and rewarming rates in heterothermic vertebrates show an inverse allometric relationship.

Although body mass appears to have a strong impact on rewarming rates, it is not the only factor that influences the process. For example, low air temperatures

(T_a) considerably slow the rate of rewarming in marsupials (Geiser and Baudinette, 1987). It also has been shown that acclimation to high temperatures reduces the rewarming rates in bats (Stones and Wiebers, 1967). Furthermore, the rate of rewarming is not uniform throughout the arousal process. Slow rates are observed at the beginning of the arousal process when T_b values are low; fastest rewarming rates are observed at T_b values that are several degrees below the normothermic T_b (Lyman, 1948; Hammel, 1986). It also has been suggested that rewarming rates may differ between mammalian groups (Heldmaier, 1978). In particular, Wallis (1982) and Fleming (1985a,b) claimed from data on a small number of species ($N=5$) that marsupials rewarm significantly more slowly than do placental mammals.

We compared rewarming rates from torpor as a function of body mass in 86 species, ranging in body mass between 2 and 8500 g, from the three mammalian subclasses. We re-examined the previously suggested differences between mammalian taxa and studied the influence of T_a on the rewarming rate.

Materials and methods

Body masses and rewarming rates of 17 marsupial species were collected from data in the literature or measured in the present study (Table 1). Rates of rewarming in the present study were measured by 2- to 3-cm rectal insertion of a thermocouple probe and readings were taken at intervals of several minutes. The thermocouple wire was taped to the tail of the animals. The rewarming rates of marsupials were compared with values from the literature from one monotreme, six insectivores, 33 bats, 28 rodents and one carnivore (Table 1). The fastest rewarming rate that could be obtained for each species was used in the comparison because in most studies this was the only value reported. These rewarming rates were usually measured at 'room temperature', i.e. a T_a of about 20°C. In marsupials, arousal rates at a T_a of 9–11°C were compared with those at a T_a of 18–24°C from species ranging in body mass between 8 and 120 g to determine whether the inverse relationship between body mass and rewarming rate observed at high T_a (Heinrich and Bartholomew, 1971) is maintained at low T_a. In many of the accounts in the literature, it was not clear whether the authors determined maximum arousal rates over a short time or the fastest overall rewarming rates from the beginning of the arousal until normothermic T_b values were reached. We therefore investigated whether maximum arousal rates (over a 10-min interval) and fastest overall arousal rates (from beginning to end of the arousal process) differ significantly in marsupials for which reliable data on both rates were available. Both the maximum arousal rate and the fastest overall arousal rate of marsupials were compared with values from the other mammalian taxa. Large placental mammals show distinct temperature differences during rewarming between the anterior and posterior part of the body (Lyman, 1948; Lyman et al. 1982). For those placental mammals in which head or oesophageal rewarming rates were available these measurements were used, because maximum rectal rewarming rates in these animals reflect redistribution of heat with blood flow

from the warmer anterior part to the cooler posterior part of the body rather than a direct rate of heat production.

Body masses and arousal rates were transformed to logarithmic values. Least-squares linear regressions were performed on the transformed data for all heterothermic mammals and on the different mammalian taxa. The curves relating body mass and rewarming rates of the various groups were compared for differences in elevation and slope using an *F*-test. We also investigated whether rewarming rates of daily heterotherms (torpor duration several hours) and hibernators (torpor duration several days or weeks) (see Geiser, 1988) were different; bats were excluded from this comparison because in many species it is not known whether they show daily or prolonged torpor. Statistical differences were assumed significant at the 95 % level (*P*<0.05).

Results

Rewarming rates of heterothermic mammals were inversely related to body mass (Tables 1, 2; Fig. 1). Most small mammals of body mass less than 10 g rewarmed at rates of about $1 °C min^{-1}$ or more, whereas larger species of body mass greater than 1000 g rewarmed at rates of about $0.1 °C min^{-1}$ or less.

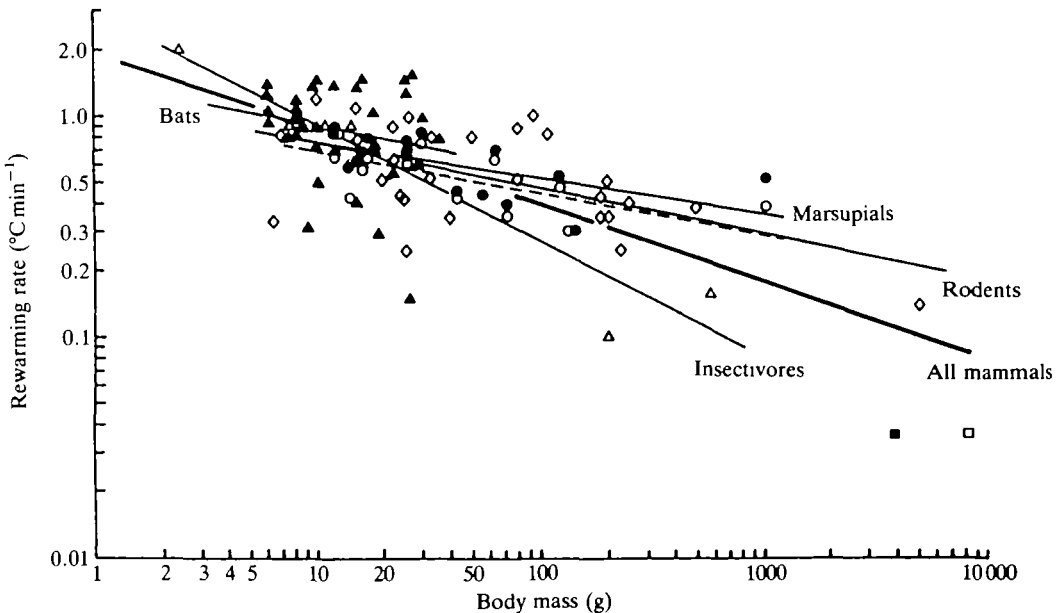Marsupials and placentals rewarmed at similar rates. When the rewarming rates

Fig. 1. Logarithmic plot of rewarming rates from torpor and body mass in heterothermic mammals. The symbols indicate: (■) echidna, *Tachyglossus aculeatus*; (———●———) marsupials, maximum rewarming rate over 10 min; (---○---) marsupials, fastest overall rewarming rate; (△) insectivores; (▲) bats; (◇) rodents; and (□) badger, *Taxidea taxus*. The regression lines were fitted to log-transformed data from Table 1 and the equations are shown in Table 2.

Table 1. *Rewarming rates in mammals*

Group Species	Body mass (g)	Rewarming rate (°C min^{-1})		References
Monotremes				
Tachyglossus aculeatus	5000	0.037		Augee and Ealey, 1968
Marsupials				
Marmosa sp.	15	0.63	(0.63)	Morrison and McNab, 1962
Dasyurus geoffroii	approx. 1000	0.53	(0.40)	Arnold, 1976
Dasyuroides byrnei	120	0.55	(0.48)	Present study
Dasycercus cristicauda	62	0.6	(0.54)	Morrison, 1965
Sminthopsis crassicaudata	16	0.69	(0.57)	Present study
Sminthopsis macroura	25	0.70	(0.60)	Present study
Antechinomys laniger	28	0.84	(0.75)	Geiser, 1986
Ningaui yvonneae	12	0.82	(0.64)	Geiser and Baudinette, 1988
Planigale gilesi	8	0.95	(0.93)	Geiser and Baudinette, 1988
Antechinus stuartii	25	0.78	(0.66)	Present study
Antechinus flavipes	42	0.45	(0.44)	Present study
Cercartetus nanus	approx. 70	0.40	(0.35)	Bartholomew and Hudson, 1962
Cercartetus concinnus	17	0.79	(0.65)	Geiser, 1987
Cercartetus lepidus	12	0.90	(0.81)	Geiser, 1987
Burramys parvus	54	0.44		Fleming, 1985a
Acrobates pygmaeus	14	0.58	(0.43)	Fleming, 1985b
Petaurus breviceps	132	0.3	(0.3)	Fleming, 1980
Insectivores				
Crocidura russula	13.7	0.9		Nagel, 1977
Crocidura leucodon	12	0.9		Nagel, 1977
Crocidura suaveolens	7.5	0.9		Nagel, 1977
Suncus etruscus	2.4	2.0		Nagel, 1977
Erinaceus europaeus	560	0.17		Pembrey, 1903
Echinops telfairi	approx. 200	0.10		Scholl, 1974
Bats				
Rhinopoma microphyllum	19	0.3		Kulzer *et al.* 1970
Rhinopoma hardwickei	10	0.5		Kulzer *et al.* 1970
Taphozous melanopogon	26	0.15		Kulzer *et al.* 1970
Taphozous australis	22	0.57		Kulzer *et al.* 1970
Rhinolophus megaphyllus	8	0.84		Kulzer *et al.* 1970
Rhinolophus ferrumequinum	18	0.75		Kulzer *et al.* 1970
Rhinolophus hipposideros	6	1.05		Kulzer *et al.* 1970
Hipposideros speoris	9	0.32		Kulzer *et al.* 1970
Asellia tridens	15	0.42		Kulzer *et al.* 1970
Myotis myotis	25	1.5		Kulzer *et al.* 1970
Myotis nattereri	8	1.05		Kulzer *et al.* 1970
Myotis lucifugus	7.6	0.8		Stones and Wiebers, 1967
Myotis californicus	approx. 6	1.29		Hirschfeld and O'Farrell, 1976
Myotis thysanodes	approx. 10	0.91		Hirschfeld and O'Farrell, 1976
Myotis adversus	8	1.2		Kulzer *et al.* 1970
Miniopterus schreibersii	15	1.4		Kulzer *et al.* 1970
Chalinolobus picatus	6	1.4		Kulzer *et al.* 1970
Chalinolobus gouldii	12	1.4		Kulzer *et al.* 1970
Pipistrellus hesperus	4	1.2		Bartholomew *et al.* 1957
Pipistrellus pipistrellus	6	0.95		Kulzer *et al.* 1970
Nyctalus noctula	27	1.58		Kulzer *et al.* 1970
Plecotus auritus	12	0.7		Kulzer *et al.* 1970

Table 1. *Continued*

Group Species	Body mass (g)	Rewarming rate (°C min^{-1})	References
Plecotus townsendii	approx. 10	1.52	Hirschfeld and O'Farrell, 1976
Antrozous pallidus	approx. 30	1.0	Hirschfeld and O'Farrell, 1976
Eptesicus serotinus	approx. 25	1.3	Eisentraut, 1934
Eptesicus fuscus	16	1.5	Hayward and Lyman, 1967
Tadarida teniotis	30	0.78	Kulzer *et al.* 1970
Tadarida hindei	18	1.05	Kulzer *et al.* 1970
Tadarida condylura	36	0.8	Kulzer *et al.* 1970
Tadarida loriae	8.5	0.9	Kulzer *et al.* 1970
Tadarida planiceps	9.5	1.4	Kulzer *et al.* 1970
Tadarida brasiliensis	approx. 10	0.73	Hirschfeld and O'Farrell, 1976
Nyctimene albiventer	28	0.6	Bartholomew *et al.* 1970
Rodents			
Tamias striatus	92	1.0	Wang and Hudson, 1971
Eutamias amoenus	50	0.8	Cade, 1963
Spermophilus mohavensis	250	0.4	Bartholomew and Hudson, 1960
Spermophilus lateralis	approx. 190	0.35	Twente and Twente, 1965; cited in Heinrich and Bartholomew, 1971
Spermophilus tridecemlineatus	approx. 190	0.45	Johnson, 1929
Spermophilus mexicanus	190	0.35	Neumann and Cade, 1965
Spermophilus undulatus	approx. 500	0.4	Mayer, 1960
Spermophilus tereticaudus	230	0.25	Hudson, 1964
Spermophilus citellus	approx. 250	0.4	Kayser, 1961
Marmota marmota	5000	0.14	Pembrey, 1901
Cricetus cricetus	approx. 200	0.5	Eisentraut, 1928
Mesocricetus auratus	approx. 80	0.43	Lyman, 1948
Muscardinus avellanarius	approx. 15	1.1	Eisentraut, 1929
Glis glis	110	0.85	Hayward and Lyman, 1967
Eliomys quercinus	80	0.9	Ambid, 1971; cited in Raths and Kulzer, 1976
Zapus princeps	26	1.0	Cranford, 1983
Sicista betulina	approx. 10	1.2	Johansen and Krog, 1959
Perognathus californicus	22	0.91	Tucker, 1965
Perognathus longimembris	8	0.8	Bartholomew and Cade, 1957
Perognathus hispidus	40	0.35	Hudson, 1973
Peromyscus crinitus	20	0.51	Morhardt, 1970
Peromyscus maniculatus	22	0.64	Morhardt, 1970
Peromyscus eremicus	24	0.43	Morhardt, 1970
Peromyscus leucopus	24	0.42	Morhardt, 1970
Peromyscus boylii	33	0.54	Morhardt, 1970
Microdipodops pallidus	15.2	0.8	Bartholomew and MacMillen, 1961
Baiomys taylori	6.4	0.34	Hudson, 1965
Mus musculus	25	0.25	Hudson and Scott, 1979
Carnivores			
Taxidea taxus	8500	0.037	Harlow, 1981

The fastest rewarming rate which could be obtained for each species is listed. For marsupials both the maximum rewarming rate (measured over at least 10 min) and the fastest overall warming rate (in parenthesis) are given.

Table 2. *Allometric relationships between body mass and rates of rewarming in heterothermic mammals*

Group	N	a	b	r^2	P
All mammals	86	0.295±0.056	−0.345±0.034	0.55	<0.0001
All placentals	68	0.294±0.065	−0.334±0.041	0.50	<0.0001
Marsupials, maximum	17	0.052±0.085	−0.169±0.053	0.41	<0.002
Marsupials, overall	16	0.006±0.078	−0.174±0.048	0.48	<0.001
Insectivores	6	0.479±0.142	−0.526±0.086	0.90	<0.005
Bats	33	0.164±0.183	−0.206±0.161	0.05	>0.20
Rodents	28	0.073±0.108	−0.200±0.057	0.32	<0.0005
Hibernators*	26	0.409±0.129	−0.382±0.064	0.63	<0.0001
Daily heterotherms*	27	0.237±0.083	−0.349±0.051	0.65	<0.0001

Linear regression analyses were performed on log-transformed data and are described by the equation: $\log_{10}$ rewarming rate $(°C \, min^{-1}) = a + b \log_{10}$ body mass (g); a, intercept±s.e.; b, slope±s.e.

The elevations of the rewarming rates of the groups were indistinguishable ($P>0.05$; F-test).

Differences in slope were observed between insectivores and the other mammalian taxa ($P<0.01$; F-test).

The other mammalian taxa were indistinguishable ($P>0.05$; F-test).

* Bats were excluded from the comparison of hibernators and daily heterotherms because not enough reliable information is available about the pattern of torpor in many species.

and body masses of all placentals and those of marsupials were fitted with two parallel regressions rather than a single regression, we could detect no statistical differences between slope and elevation of the two regression lines, nor was the relationship improved by the two-line fit (Table 2). Within the marsupials, overall and maximum rates of rewarming were also indistinguishable. In a comparison with the different mammalian taxa, both overall and maximum rewarming rates of marsupials did not differ in slope and elevation from those in bats and rodents. However, a difference in the slope relating rewarming rate and body mass could be detected between insectivores and the other mammalian taxa. Bats were the only mammalian group in which no significant relationship between body mass and rewarming rate could be detected (Table 2; Fig. 1). The echidna *Tachyglossus aculeatus* (Monotremata) and the badger *Taxidea taxus* (Carnivora) were similar to insectivores in their rates of rewarming (Fig. 1). When the hibernators of all mammalian taxa (excluding bats) were compared with the daily heterotherms no significant difference could be detected in slope or elevation of the lines relating body mass and rewarming rate.

The relationship between body mass and rate of rewarming in marsupials at high T_a differed significantly ($P<0.001$, t-test; slope and intercept) from that at low T_a (Fig. 2; Table 3). At high T_a (18–24°C), a negative relationship was observed between the two variables, although data were available only for a narrow range of body masses. At low T_a (9–11°C) no significant relationship between body mass and rate of rewarming could be detected and the slope of the regression line was
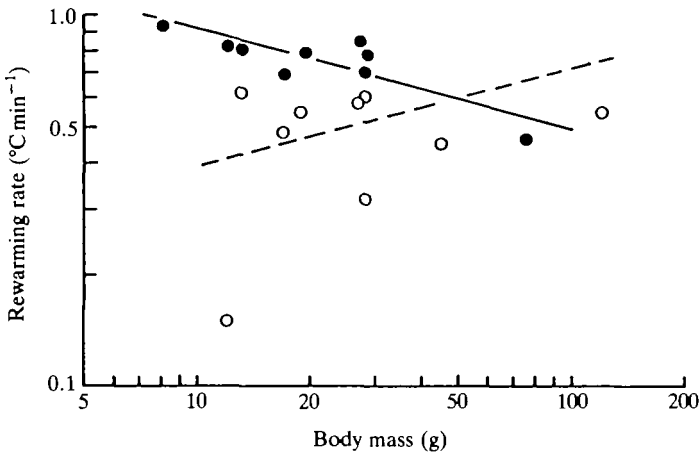
Fig. 2. Logarithmic plot of rewarming rates and body mass in heterothermic mar-supials at high (●, 18–24 °C) and low (○, 9–11 °C) T_a values. Data are shown in Table 3. Linear regression for $T_a=18$–24 °C, $\log_{10}y=0.23-0.27\log_{10}x$, $r^2=0.72$, $P<0.002$, $N=9$; for $T_a=9$–11 °C, $\log_{10}y=-0.66+0.22\log_{10}x$, $r^2=0.11$, $P>0.40$, $N=9$.

Table 3. *Rates of rewarming of marsupials at different air temperatures*

Species	$T_a=9$–11 °C ($^{\circ}C\,min^{-1}$)	$T_a=18$–24 °C ($^{\circ}C\,min^{-1}$)	Body mass (g)
Sminthopsis crassicaudata	0.48	0.69	17
Sminthopsis macroura	0.32	0.70	28
Dasyuroides byrnei	0.55		120
Dasyuroides byrnei		0.46	75
Antechinus stuartii	0.60	0.78	28
Antechinus flavipes	0.45		42
Antechinomys laniger	0.58	0.84	27
Ningaui yvonneae	0.15	0.82	12
Planigale gilesi		0.95	8
Cercartetus concinnus	0.55	0.79	19
Cercartetus lepidus	0.62	0.80	13

T_a, ambient temperature.

reversed in comparison to measurements at high T_a (i.e. the larger species rewarmed at a rate similar to or faster than that of the smaller species).

Discussion

The present study shows that body mass and rate of rewarming in heterothermic mammals are inversely related, as has been suggested previously (Heinrich and Bartholomew, 1971). However, at low environmental temperatures this relation-

ship may no longer hold. Differences in the rate of rewarming between the different mammalian taxa were not very distinct.

Air temperature had a profound effect on the rate of rewarming in marsupials. The inverse relationship of rewarming rate and body mass at high T_a was abolished at low T_a. The relatively large surface area of small animals results in a much greater heat loss to the environment than in large species and therefore a large proportion of the internal heat produced during arousal is immediately lost. It has been previously documented that the time required for rewarming from torpor to normothermia in large marsupials is much less affected by a lowering of T_a than in small marsupials (Geiser and Baudinette, 1987).

When the slope of rewarming rate and body mass was compared among different mammalian taxa only the insectivores differed significantly from the other groups. The steeper slope of the line relating these variables in insectivores seems to result from the relatively slow rewarming rates of the poorly insulated, rather large hedgehog and *Echinops*, and the fast rewarming rates in the very small shrews. The lack of a significant relationship between rewarming rate and body mass in bats could either be because of the small range of body mass available from this order or because other factors, such as climate or state of acclimation, are more important than body mass in determining their rate of rewarming. Unlike the slope relating rate of rewarming and body mass, the elevations of linear regressions from any of the mammalian taxa were statistically indistinguishable.

Rewarming rates of marsupials did not differ substantially from the values for any of the other mammalian groups. This observation does not support earlier suggestions that marsupials show slower rewarming rates than placentals and that this may be due to a lower thermogenic capacity in marsupials (Fleming, 1985b). The apparent lack of brown fat in adult marsupials does not appear to slow their rate of rewarming, thus supporting the findings of Lyman and O'Brien (1986) that the direct contribution of brown fat to heat production during rewarming from torpor may have been overestimated in the past.

Interestingly, the slopes relating basal metabolic rate (BMR) and body mass of the mammalian groups and taxa show a similar pattern to that observed for the rewarming rates in the present study. When the slopes for rewarming rate as a function of body mass (Table 2) were plotted against the slope of mass-specific BMR as a function of body mass (Hayssen and Lacy, 1985, for the mammalian taxa and Geiser, 1988, for the hibernators and daily heterotherms), a significant linear relationship was observed between the two (Fig. 3). When the same analysis was performed on mammalian orders only, the relationship was also significant ($r^2=0.97$, $P<0.01$). The slope relating the two variables was close to 1.0, suggesting that maximum heat production during rewarming from torpor is related to the BMR of the animal. Both BMR and rewarming rate are related to the thermogenic capacity of the combined animal tissues and therefore the correlation between the two is not surprising. However, the strong impact of the value for the insectivores on the regression line necessitates cautious interpretation of this relationship. Because the slopes of BMR *versus* body mass are, apart from the
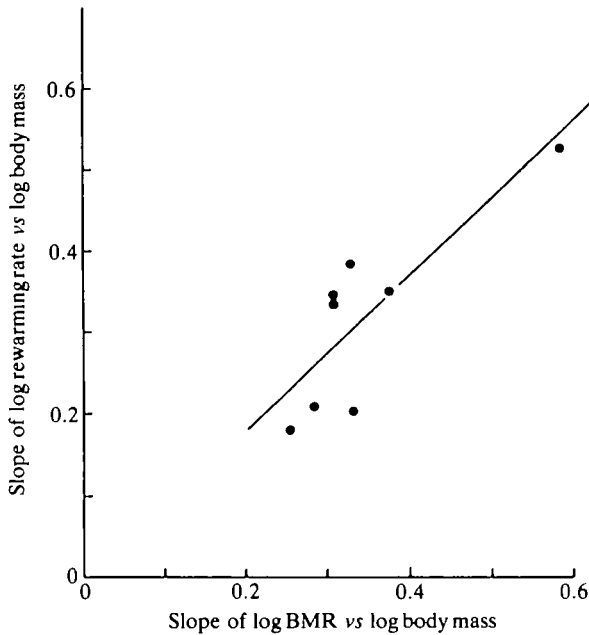
Fig. 3. The slope of $\log_{10}$ rewarming rate ($°C\,min^{-1}$) *vs* $\log_{10}$ body mass (g) as a function of the slope of $\log_{10}$ basal metabolic rate (BMR, $ml\,O_2\,g^{-1}\,h^{-1}$) *vs* $\log_{10}$ body mass (g) in mammals. Slopes for rewarming rate *vs* body mass were taken from Table 2, those for BMR *vs* body mass from Hayssen and Lacey (1985) and Geiser (1988). When all groups from Table 2 were included in the regression the equation was: $y=-0.013+0.95x$, $r^2=0.68$, $P<0.01$, $N=8$. When only the four mammalian orders from Table 2 were included in the regression the equation was: $y=-0.12+1.10x$, $r^2=0.97$, $P<0.01$, $N=4$.

insectivores, very similar among the mammalian orders (Hayssen and Lacy, 1985) more data on other orders may not further clarify whether BMR and rate of rewarming are related in mammals.

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