

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

BY FRITZ GEISER

*Department of Zoology, University of New England, Armidale,
New South Wales 2351, Australia*

AND R. V. BAUDINETTE

*School of Biological Sciences, Flinders University, Bedford Park,
South Australia 5042, Australia*

Accepted 7 March 1990

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 endotherms 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

Key words: arousal, body mass, endotherm, temperature, hibernation, placentals, marsupials.

(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 (1985*a,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 $0.1^\circ\text{C min}^{-1}$ or less.

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

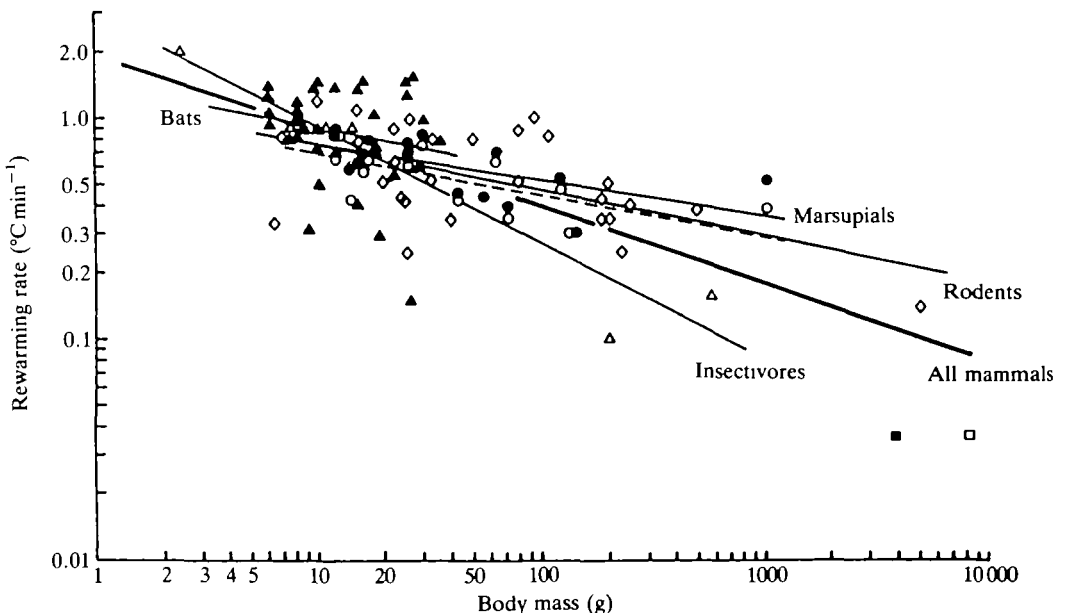


Fig. 1. Logarithmic plot of rewarming rates from torpor and body mass in heterothermic mammals. The symbols indicate: (■) echidna, *Tachyglossus aculeatus*; (—●—) marsupials, maximum rewarming rate over 10 min; (---○---) marsupials, fastest overall rewarming rate; (Δ) insectivores; ($\blacktriangle$) bats; ($\diamond$) rodents; and ($\square$) 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			
<i>Tachyglossus aculeatus</i>	5000	0.037	Augee and Ealey, 1968
Marsupials			
<i>Marmosa</i> sp.	15	0.63 (0.63)	Morrison and McNab, 1962
<i>Dasyurus geoffroii</i>	approx. 1000	0.53 (0.40)	Arnold, 1976
<i>Dasyuroides byrnei</i>	120	0.55 (0.48)	Present study
<i>Dasyercus cristicauda</i>	62	0.6 (0.54)	Morrison, 1965
<i>Sminthopsis crassicaudata</i>	16	0.69 (0.57)	Present study
<i>Sminthopsis macroura</i>	25	0.70 (0.60)	Present study
<i>Antechinomys laniger</i>	28	0.84 (0.75)	Geiser, 1986
<i>Ningau i yvonneae</i>	12	0.82 (0.64)	Geiser and Baudinette, 1988
<i>Planigale gilesi</i>	8	0.95 (0.93)	Geiser and Baudinette, 1988
<i>Antechinus stuartii</i>	25	0.78 (0.66)	Present study
<i>Antechinus flavipes</i>	42	0.45 (0.44)	Present study
<i>Cercartetus nanus</i>	approx. 70	0.40 (0.35)	Bartholomew and Hudson, 1962
<i>Cercartetus concinnus</i>	17	0.79 (0.65)	Geiser, 1987
<i>Cercartetus lepidus</i>	12	0.90 (0.81)	Geiser, 1987
<i>Burramys parvus</i>	54	0.44	Fleming, 1985a
<i>Acrobates pygmaeus</i>	14	0.58 (0.43)	Fleming, 1985b
<i>Petaurus breviceps</i>	132	0.3 (0.3)	Fleming, 1980
Insectivores			
<i>Crocidura russula</i>	13.7	0.9	Nagel, 1977
<i>Crocidura leucodon</i>	12	0.9	Nagel, 1977
<i>Crocidura suaveolens</i>	7.5	0.9	Nagel, 1977
<i>Suncus etruscus</i>	2.4	2.0	Nagel, 1977
<i>Erinaceus europaeus</i>	560	0.17	Pembrey, 1903
<i>Echinops telfairi</i>	approx. 200	0.10	Scholl, 1974
Bats			
<i>Rhinopoma microphyllum</i>	19	0.3	Kulzer <i>et al.</i> 1970
<i>Rhinopoma hardwickei</i>	10	0.5	Kulzer <i>et al.</i> 1970
<i>Taphozous melanopogon</i>	26	0.15	Kulzer <i>et al.</i> 1970
<i>Taphozous australis</i>	22	0.57	Kulzer <i>et al.</i> 1970
<i>Rhinolophus megaphyllus</i>	8	0.84	Kulzer <i>et al.</i> 1970
<i>Rhinolophus ferrumequinum</i>	18	0.75	Kulzer <i>et al.</i> 1970
<i>Rhinolophus hipposideros</i>	6	1.05	Kulzer <i>et al.</i> 1970
<i>Hipposideros speoris</i>	9	0.32	Kulzer <i>et al.</i> 1970
<i>Asellia tridens</i>	15	0.42	Kulzer <i>et al.</i> 1970
<i>Myotis myotis</i>	25	1.5	Kulzer <i>et al.</i> 1970
<i>Myotis nattereri</i>	8	1.05	Kulzer <i>et al.</i> 1970
<i>Myotis lucifugus</i>	7.6	0.8	Stones and Wiebers, 1967
<i>Myotis californicus</i>	approx. 6	1.29	Hirschfeld and O'Farrell, 1976
<i>Myotis thysanodes</i>	approx. 10	0.91	Hirschfeld and O'Farrell, 1976
<i>Myotis adversus</i>	8	1.2	Kulzer <i>et al.</i> 1970
<i>Miniopterus schreibersii</i>	15	1.4	Kulzer <i>et al.</i> 1970
<i>Chalinolobus picatus</i>	6	1.4	Kulzer <i>et al.</i> 1970
<i>Chalinolobus gouldii</i>	12	1.4	Kulzer <i>et al.</i> 1970
<i>Pipistrellus hesperus</i>	4	1.2	Bartholomew <i>et al.</i> 1957
<i>Pipistrellus pipistrellus</i>	6	0.95	Kulzer <i>et al.</i> 1970
<i>Nyctalus noctula</i>	27	1.58	Kulzer <i>et al.</i> 1970
<i>Plecotus auritus</i>	12	0.7	Kulzer <i>et al.</i> 1970

Table 1. *Continued*

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

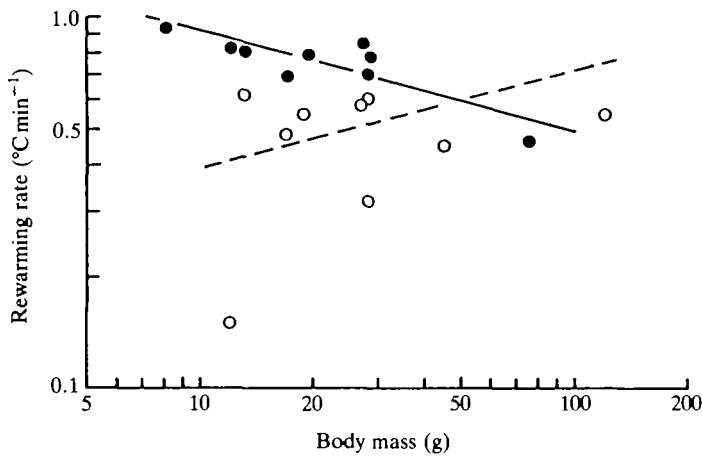


Fig. 2. Logarithmic plot of rewarming rates and body mass in heterothermic marsupials at high (●, 18–24°C) and low (○, 9–11°C) T_a values. Data are shown in Table 3. Linear regression for $T_a=18-24^{\circ}\text{C}$, $\log_{10}y=0.23-0.27\log_{10}x$, $r^2=0.72$, $P<0.002$, $N=9$; for $T_a=9-11^{\circ}\text{C}$, $\log_{10}y=-0.66+0.22\log_{10}x$, $r^2=0.11$, $P>0.40$, $N=9$.

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

Species	$T_a=9-11^{\circ}\text{C}$ ($^{\circ}\text{C min}^{-1}$)	$T_a=18-24^{\circ}\text{C}$ ($^{\circ}\text{C min}^{-1}$)	Body mass (g)
<i>Sminthopsis crassicaudata</i>	0.48	0.69	17
<i>Sminthopsis macroura</i>	0.32	0.70	28
<i>Dasyuroides byrnei</i>	0.55		120
<i>Dasyuroides byrnei</i>		0.46	75
<i>Antechinus stuartii</i>	0.60	0.78	28
<i>Antechinus flavipes</i>	0.45		42
<i>Antechinomys laniger</i>	0.58	0.84	27
<i>Ningau yvonneae</i>	0.15	0.82	12
<i>Planigale gilesi</i>		0.95	8
<i>Cercartetus concinnus</i>	0.55	0.79	19
<i>Cercartetus lepidus</i>	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, 1985*b*). 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

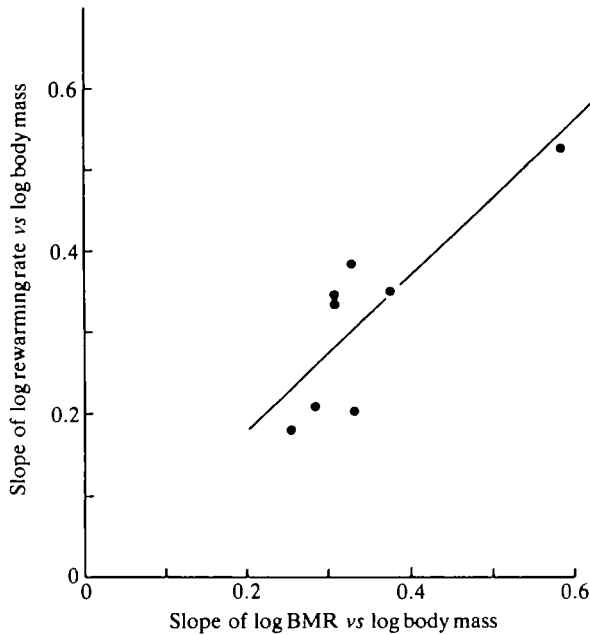


Fig. 3. The slope of $\log_{10}$ rewarming rate ($^{\circ}\text{C min}^{-1}$) vs $\log_{10}$ body mass (g) as a function of the slope of $\log_{10}$ basal metabolic rate (BMR, $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) vs $\log_{10}$ body mass (g) in mammals. Slopes for rewarming rate vs body mass 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.

This research was supported by a Flinders University Research Scholarship and by a grant from the Australian Research Council.

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