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MAXIMUM METABOLISM AND THE AEROBIC FACTORIAL SCOPE OF ENDOTHERMS

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Summary

Minimum and maximum metabolism in response to cold were measured in 30 species of Australian monotremes, marsupials, eutherians and birds. In marsupials and the echidna, maximum metabolism was also determined during treadmill locomotion. These data were used to determine, for the first time, the relationships between maximum metabolism and body mass in the four endothermic groups and to compare aerobic factorial scopes (the ratio of maximum to minimum metabolism) elicited by cold and locomotion. The effect of body mass on maximum metabolism is the same in marsupials and eutherians (the therians) but is significantly less in birds. At the same body mass, there is no difference between the two therian groups for either minimum or maximum metabolism induced by either cold or locomotion. Aerobic scope during cold is significantly higher in marsupials (8.3) than in eutherians (5.1), birds (5.4) and monotremes (5.4). Aerobic scope during locomotion in all groups is almost twice that observed in cold conditions.

Introduction

Minimal or basal levels of metabolism in vertebrates are highly predictable and are determined principally by mass, ambient temperature and phylogeny. Among endothermic vertebrates, these levels are reduced in order from passerine birds to non-passerines, eutherians, marsupials and monotremes (Bartholomew, 1982). A similar mass-dependence of metabolism is found throughout these taxa and the theoretical basis for this scaling regularity has attracted vigorous debate (see Heusner, 1982, 1991).

Comparisons of higher metabolic rates induced by activity or exposure to low temperatures are more limited. Among interspecific comparisons, Lechner (1978) pooled exercise- and cold-induced metabolic maxima to derive scaling relationships for eutherians, and Taylor *et al.* (1981) reported maximum metabolism during treadmill

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locomotion for 21 eutherian and one marsupial species. More recently, Bozinovic and Rosenmann (1989) determined a relationship between cold-induced maximum metabolic rate and body mass in 25 species of rodents and suggested a correlation between energetic capability and habitat range. Measurements of flight metabolism have been conducted on several bird species but, unfortunately, in none of these studies is there a clear measurement of maximum metabolism. However, within this limited data set it seems reasonable to suggest that flight results in increases of around eight times the standard rate of oxygen consumption (see Marsh and Dawson, 1989). Marden (1987) examined load-lifting capabilities in 10 species of flying birds and concluded that the maximum mass-specific power was independent of body mass because all birds could lift about six times their muscle mass. What this analysis failed to provide for the present study was the relationship between power output and lifting ability (see also Ellington, 1991). Maximal rates of cold-induced thermogenesis in birds are better defined and show an increase of up to six times the comparable resting rate (Marsh and Dawson, 1989).

Comparisons have also been made within species. Hayes (1989) used residual analysis to demonstrate a significant correlation between resting and thermogenic maximal metabolic rates in the mouse *Peromyscus maniculatus*. Using the same species, Hayes and Chappell (1990) have shown that a significant correlation between thermogenic and exercise maximal metabolic rates within individuals is maintained following acclimation of the animals to low temperatures or altitude. In contrast, dogs show a lower maximum metabolism in the cold than when exercising (Lucas *et al.* 1980), a finding consistent with those from rodents (Hinds and Rice-Warner, 1992) and birds (Marsh and Dawson, 1989).

Despite this range of studies, the quantitative relationship between resting and maximum metabolism and the relative effects of cold and exercise on the latter are poorly understood. In eutherians, allometric analyses have shown that the effect of body mass on minimum metabolism and maximum metabolism during locomotion is similar, but the latter is elevated by a factor of around 10 (Taylor *et al.* 1981). This factor, the ratio of maximum to minimum metabolism, is referred to as factorial aerobic scope (shortened hereafter to scope), and it has been suggested that within and between taxa it is 'fixed' in value by various physiological constraints (Dawson, 1973; Bennett and Rubin, 1979; Hinds and MacMillen, 1984). The relationship between resting and maximal resting metabolic rates has been questioned (Koteja, 1987; Taigen, 1983), in part because scope may differ between species of the same body mass (Weibel *et al.* 1987) and among individuals of the same species under varying conditions (Wickler, 1980). Support for the model comes from Hinds and Rice-Warner (1992) and Bozinovic (1992), who demonstrated that mass-independent maximum and minimum metabolic levels in rodents are positively and significantly correlated.

If scope is the same for each endothermic taxon, then maximal and minimal levels of metabolism should correspond; i.e. passerine birds should have the highest maxima and monotremes the lowest since they have the highest and lowest minima, respectively. The present investigation was initiated to determine whether this is the case. It reports measurements of scope in individuals of various vertebrate taxa and determines for the first time the relationships between body mass and maximum metabolism in the cold for endotherms other than eutherians. In addition, we compare marsupials and eutherians

with respect to the relative effects of locomotion and cold on maximum metabolism and scope.

Materials and methods

Rates of minimum and maximum oxygen consumption were measured in 30 species of Australian endotherms; nine birds, two monotremes, seven eutherians and 12 marsupials (see Table 1). The species were selected using the criterion of relatively small body size, a prerequisite for eliciting rates of maximum metabolism in cold conditions. We also trained a random selection of individuals from seven marsupial species to run on a motor-driven treadmill in order to measure maximum metabolism during locomotion.

Data were collected at Flinders University, except those for the platypus, in which measurements were taken near their collecting site 180km southeast of Melbourne. This enabled us to decrease their time in captivity. All other animals were housed at the animal facility at Flinders University for at least 2 weeks before measurements were made. A majority (52%) of the species was caught specifically for this investigation; however, many were born in captivity (35%) and a few had been in captivity for at least 4 months prior to measurements (13%). Small animals were typically caged in thermally controlled laboratory conditions with 12h:12h light:dark cycles, while larger animals were housed in outdoor pens under natural temperature (15–23˚C) and photoperiod conditions. All animals were fed and watered *ad libitum* and appeared healthy and maintained body weight throughout the study period.

Measurements were made on all animals during daytime from August to March, 1990, using the same general procedures. Oxygen consumption ($\dot{V}_{O_2}$) was measured in an open-circuit system using an oxygen analyzer to compare inlet and outlet oxygen concentrations of air flowing through chambers or masks. Volumes of all sample lines, including drying columns, were kept to a minimum to maximize the ratio of flow to volume and to conform to the principles of a single-chamber system (Frappell *et al.* 1989). Continuous subsamples of air from the chambers and masks were dried and then passed through the oxygen analyzer without removing CO_2. Servomex paramagnetic O_2 analyzers (model OA 184), calibrated daily with gases of known concentrations, were used for all species except the platypus, for which an Applied Electrochemistry oxygen analyzer (model S3A) was used. Airflows through the chambers and masks were sufficient to maintain O_2 concentrations above 20.2% in the excurrent gas. Flow rates were calibrated volumetrically (Brooks, vol-u-meter: Brooks, Pennsylvania), allowing correction for back-pressure in the system. All $\dot{V}_{O_2}$ values were corrected to STPD, and for respiratory quotient (RQ) values of 0.8 for minimal and 1.0 for maximal metabolic levels. Equation 6 of Depocas and Hart (1956), modified for use with RQs, was used to calculate minimum and cold-induced maximum $\dot{V}_{O_2}$. Exercise-induced maximum metabolism was calculated using either equation 3a of Withers (1977; see also Baudinette *et al.* 1976) or equation 11a of Fedak *et al.* (1981), modified for use with dried air flowing through the flowmeter and analyzer.

For measurements of minimum and cold-induced maximum metabolism, animals were placed in metabolic chambers of appropriate sizes inside temperature-controlled cabinets.

For the smaller species, the chambers had volumes of 0.5 and 2l; for the two largest species the chamber volume was 50l. To determine minimum $\dot{V}_{O_2}$, animals were thermally equilibrated at 28–33˚C for 1–2h before initiation of measurements. Published measurements in the same or closely related species indicated that these temperatures were within thermoneutrality. Air was dried and metered through the chamber at flow rates varying from 0.3 to 3.8l$\,min^{-1}$ depending on the body mass of the animal. Minimum $\dot{V}_{O_2}$ was determined to be the lowest steady-state measurement obtained over a continuous 15-min interval during a test period of at least 2h. Typically, the 15-min interval was within a longer period of low and stable $\dot{V}_{O_2}$. Observation *via* closed-circuit television indicated that the animals were at rest during the measurement period. A fine thermocouple was used to take rectal/cloacal temperatures immediately after the animals had been removed from the chambers. Maximum $\dot{V}_{O_2}$ in response to cold was measured by using a gas mixture of 79% helium with 21% oxygen (Helox). Since helium conducts heat four times faster than nitrogen, heat loss in Helox is considerably increased relative to air, and maximum $\dot{V}_{O_2}$ can be elicited at relatively high temperatures (Rosenmann and Morrison, 1974). Animals were placed in a metabolism chamber within a controlled-temperature cabinet and, while the temperature was reduced, the dried Helox mixture was introduced at rates varying from 0.5 to 11.1 l$\,min^{-1}$ depending on the size of the animal. The exposure time required before our criteria of maximum $\dot{V}_{O_2}$ were reached was dependent upon the body mass of the animal, but did not exceed 5h for any one animal, and more typically took less than 2h. Animals were removed from the chamber as soon as a decline in $\dot{V}_{O_2}$ was observed, and rectal/cloaca temperatures were taken immediately. Maximum $\dot{V}_{O_2}$ was defined as the highest rate of oxygen consumption measured continuously for 5min before the decline. Typically $\dot{V}_{O_2}$ plateaued at the highest level before declining, and the 5min period was taken from this plateau. In all cases, the maximum level of $\dot{V}_{O_2}$ was followed by a decline in both metabolism and body temperature, with the latter falling at least 2˚C relative to its value at thermoneutrality. Several measurements were discarded because body temperature was not lowered by the required 2˚C. In all cases except the black duck (*Anas castanea*) maximum levels of $\dot{V}_{O_2}$ were obtained in subsequent determinations.

Exercise-induced maximum $\dot{V}_{O_2}$ was measured during treadmill locomotion using similar systems and calibration procedures to those of Baudinette *et al.* (1976, 1987). Maximum values for *A. flavipes* and *D. viverrinus* were taken from Baudinette *et al.* (1976), who used similar techniques of data collection. Individuals of the two small *Sminthopsis* species were run on an inclined treadmill enclosed in a Perspex chamber of 840ml with an airflow of 2l$\,min^{-1}$. The rest of the animals wore lightweight masks, made from acetate sheeting or light latex, through which air was metered at 7.5–130l$\,min^{-1}$. These animals were run on a treadmill 1.6m long and 0.6m wide whose speed could be varied by a hydraulically driven assembly and the incline of which could be varied (Baudinette *et al.* 1987). Over the training period of the animals, appropriate combinations of speeds and inclines were selected to provide reproducible, maximal metabolic levels. For the smaller animals, the training period was typically 5 days; for the larger animals, 2 weeks. Both chamber and mask systems were calibrated by bleeding in nitrogen and were found to have 95% response times of less than 30s at the lower flows.

No reduction in measured oxygen consumption, or simulated oxygen consumption using metered nitrogen, was detected when flow rates were reduced by 30%; thus, we assume that no leakage of respiratory gases occurred from the chamber or masks. Maximum metabolic rates are based on the highest steady-state values (±5%) of $\dot{V}_{O_2}$ measured continuously for at least 2min. These plateaus were almost always followed by an immediate cessation of running by the animal. Maximum metabolism was calculated as the average of three such measurements taken on different days. Following runs that were at maximal levels, lactate levels were measured in venous blood from some individuals of all of the seven marsupial species. Samples were deproteinised with $HClO_4$ and, following centrifugation, were analysed using an assay kit (Sigma Chemicals). The absorbance changes were compared with those of standard concentrations of lactate in $HClO_4$. In all cases, blood lactate levels increased by at least 6mmoll^{-1} during the running period.

Relationships of $\dot{V}_{O_2}$ to body mass were determined by transforming the data to logarithms to the base 10 and calculating regression equations by the method of least squares. Deviations of observed $\dot{V}_{O_2}$ values from predicted values based on body mass, and use of appropriate allometric equations, were considered statistically significant if they exceeded two standardized residuals (Sokal and Rohlf, 1981). Differences between regression equations were determined using analysis of covariance and SNK (Snedecor, 1956; Zar, 1984). We tested the assumption that the slopes were not heterogeneous and only compared elevations if this condition was met. The 0.05 level was used for all statistical tests of significance.

Results

Minimum metabolic rates

The measurements of minimum metabolism in the 30 species of endotherms made in this study (Table 1, Figs 1–3) are generally similar to those predicted from body mass using equations in the literature. Of the 12 marsupial species measured, both the high value for *Sminthopsis crassicaudata* and the lower value for the bandicoot, *Isodon obesulus*, differ significantly from the values predicted by the equation of Thompson (1988). Previous measurements from *S. crassicaudata* are lower than those given here (MacMillen and Nelson, 1969), but these are the first measurements reported for *I. obesulus*. These also are the first measurements reported, as indicated in Table 1, for three additional species of marsupials, five species of eutherians and three species of birds. For eutherians, the minimum metabolic rates of the six species measured here are not significantly different from those predicted from the equations of McNab (1988) for rodents and lagomorphs. Similarly, the minimum metabolic levels for the nine birds reported in this study are all within 2% of the predicted values of Aschoff and Pohl (1970).

In order to restrict our comparisons of metabolic scope to the mass range of the animals used in this study, equations relating minimum metabolism with body mass were derived only for the animals considered here (Table 2). Those for marsupials and eutherians were not significantly different in their slopes or intercepts and are grouped as ‘Theria’ in Table 2. The Tammar wallaby (*Macropus eugenii*, Table 3) is included in the minimum

Table 1. *Minimum and maximum oxygen consumption ($\dot{V}_{O_2}$, ml O_2 min^{-1}) in response to cold, and factorial scope in 30 species of endotherms*

Species	*N*	T_b	Minimum *m*	Minimum $\dot{V}_{O_2}$	%P	Maximum *m*	Maximum $\dot{V}_{O_2}$	Factorial scope
Monotremes								
Ornithorhynchus anatinus	3[b]	30.8	1112.5	10.87	69	1316.7	49.86	4.6
Tachyglossus aculeatus	5	30.8	3293.0	7.76	−20	3111.4	47.05	6.1
Marsupials								
Order Dasyuromorphia	Family Dasyuridae							
Sminthopsis crassicaudata	3	35	15.6	0.48	54	15.3	2.38	5.0
Sminthopsis macroura[a]	3	32.7	16.7	0.35	7	16.7	2.38	6.8
Dasyuroides byrnei	7	35.3	119.5	1.52	8	122.7	19.36	12.7
Dasyurus hallucatus	4	33.7	532.3	3.20	−25	537.2	29.85	9.3
Dasyurus viverrinus	3	35.1	1054.0	6.28	−11	1021.7	68.60	10.9
Order Peramelemorphia	Family Peramelidae							
Isodon obesulus[a]	2	33.9	717.2	3.71	−30	717.7	43.43	11.7
Perameles gunni[a]	3	35.2	837.3	7.01	18	847.0	48.76	7.0
Order Diprotodonta	Family Petauridae							
Petaurus breviceps	3	34.9	122.0	1.40	−2	122.0	8.24	5.9
	Family Potoroidae							
Bettongia penicillata[a]	3	37.2	965.7	9.39	42	957.6	70.07	7.5
Potorous tridactylus	2	35.8	1027.8	8.72	26	1039.3	65.9	7.6
Bettongia gaimardi[a]	1	35.6	1385.0	10.69	24	1420.0	100.1	9.4
	Family Phalangeridae							
Trichosurus vulpecula	3	35.8	2026.5	13.85	21	2031.7	74.65	5.4
Eutherians								
Order Rodentia	Family Muridae							
Notomys alexis	3	36.2	38.8	0.83	−1	38.8	3.48	4.2
Rattus colletti[a]	3	36.2	165.7	2.05	−9	165.6	11.51	5.6
Rattus norvegicus	1	−	−	−	−	181.2	20.26	−
Conilurus penicillatus[a]	2	35.9	212.3	2.71	1	214.1	14.85	5.5
Rattus villosissimus[a]	3	36	247.8	2.43	−18	253.4	14.48	6.0
Uromys caudimaculatus[a]	3	34.6	819.0	9.51	42	803.1	44.27	4.7
Order Lagomorpha	Family Leporidae							
Oryctolagus cuniculus[a]	2	38.3	1242.0	14.56	8	1231.8	63.58	4.4
Aves								
Order Psittaciformes	Family Psittacidae							
Melopsittacus undulatus	2[b]	39.7	36.0	1.28	10	37.9	7.91	6.2
Platycercus eximius[a]	1	−	−	−	−	89.4	12.79	−
Order Galliformes	Family Phasianidae							
Coturnix chinensis	2[b]	40.5	42.1	1.20	−8	43.2	6.57	5.5
Coturnix coturnix japonica	2	41.3	161.0	4.41	27	148.0	20.48	4.6
Order Gruiformes	Family Gruidae							
Gallinula porphyrio[a]	1	37.4	850.3	9.19	−21	856.8	52.08	5.7
Order Anseriformes	Family Anatidae							
Anas castanea[a]	1	39.7	944.1	12.23	−3	969.0	61.51	5.0
Order Columbiformes	Family Columbidae							
Columba livia	2[b]	41.7	302.0	4.34	−21	361.5	28.24	6.5
Order Sphenisciformes	Family Spheniscidae							
Eudyptula minor	3	38.5	1080.0	13.31	−4	982.7	57.42	4.3
Order Passeriformes	Family Estrildidae							
Poephila guttata	2	−	11.3	0.68	−22	11.8	4.03	5.9

All values are means where *N* is greater than 1.

Source of minima prediction equations: monotremes, Hayssen and Lacy (1985); marsupials, Thompson (1988); rodents and lagomorphs, McNab (1988); birds in active period, Aschoff and Pohl (1970).

N, number of individuals; T_b, body temperature in ˚C; *m*, body mass in grams; %P, percentage difference of measured value from predicted $\dot{V}_{O_2}$ [100(M−P)/P]; [a]species for which minimum metabolism has not previously been measured; [b]*N*−1 for minimum.

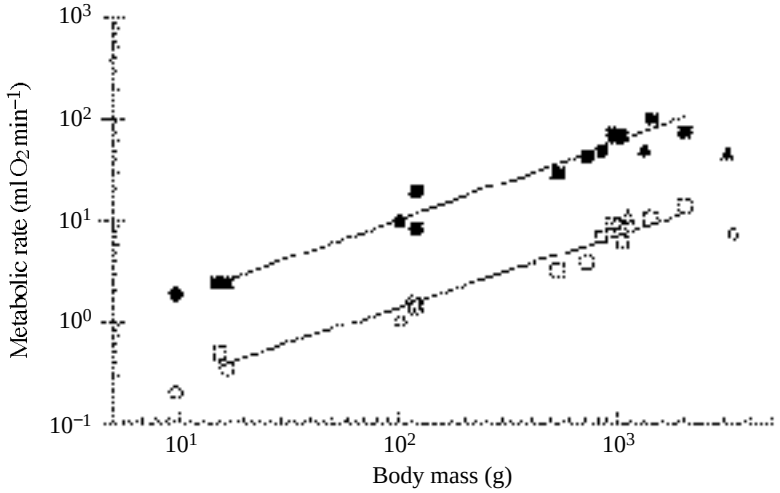

Fig. 1. The relationship of body mass to minimum (open symbols) and maximum (filled symbols) metabolism in response to cold in two species of monotreme (triangles) and 12 species of Australian marsupials (squares; species listed in Table 1). Equations for the lines are given in Table 2; data for an Australian and a South American marsupial (circles) were not used in generating the equations: *Planigale gilesi*, 9.8g, 0.20ml O_2 min^{-1} (min) and 1.85ml O_2 min^{-1} (max) (Dawson and Dawson, 1982*a*,*b*); *Monodelphis domesticus*, 102.5g, 1.0ml O_2 min^{-1} (min) and 9.9ml O_2 min^{-1} (max) (Dawson and Olson, 1988).

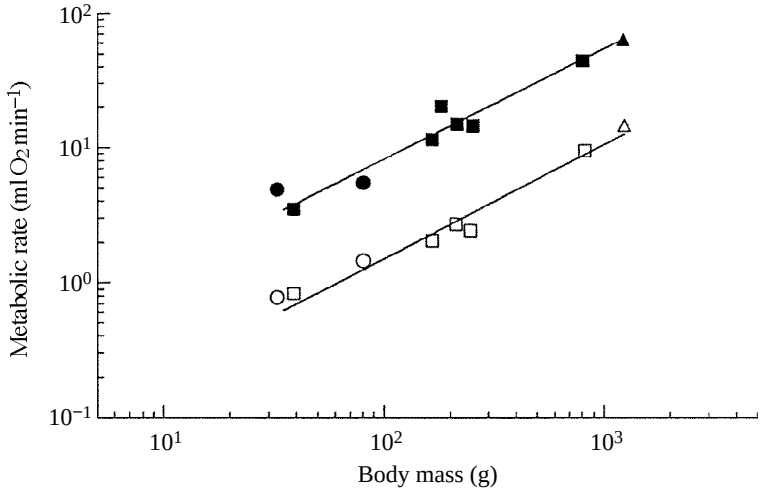

Fig. 2. The relationship of body mass to minimum (open symbols) and maximum (filled symbols) metabolism in response to cold in seven species of Australian eutherians (squares; species listed in Table 1). Equations for the lines are given in Table 2; data for two additional Australian eutherians (circles) were not used in generating the equations: *Notomys cervinus*, 32.8g, 0.78ml O_2 min^{-1} (min) and 4.88ml O_2 min^{-1} (max); *Pseudomys gracilicuadatus*, 80.5g, 1.46ml O_2 min^{-1} and 5.45ml O_2 min^{-1} (Dawson and Dawson, 1982*a*,*b*).

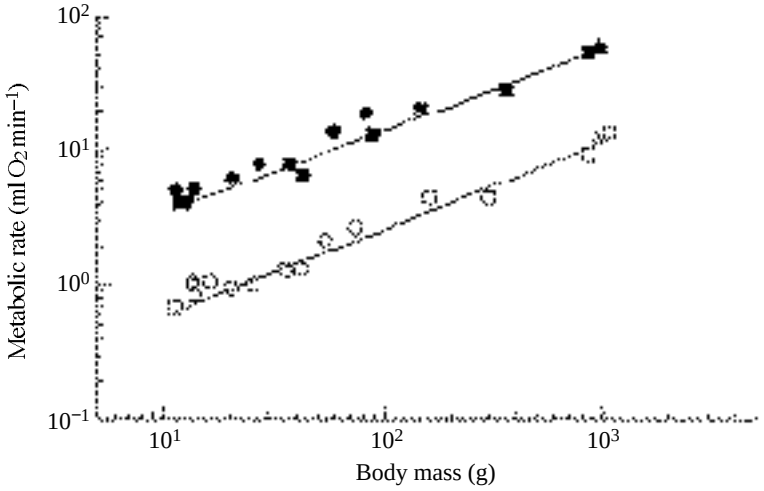

Fig. 3. The relationship of body mass to minimum (open symbols) and maximum (filled symbols) metabolism in response to cold in eight species of Aves (squares; species listed in Table 1). Equations for the lines are given in Table 2; data for the teal (triangles; Table 1) and passerine birds reported in the literature (circles) were not used in generating the equations. For data from the literature, minimum metabolism was taken from Bennett and Harvey (1987) and maximum metabolism was obtained as averages from the original sources cited in Table 2, Marsh and Dawson (1989): *Carduelis tristis*, 13.6g, 1.00ml O_2 min^{-1} (min), 11.4 g and 4.89ml O_2 min^{-1} (max); *Carduelis carduelis*, 16.5g and 1.04ml O_2 min^{-1} (min), 13.0 g and 4.00ml O_2 min^{-1} (max); *Carduelis pinus*, 13.8g and 1.04ml O_2 min^{-1} (min), 13.8g and 4.94ml O_2 min^{-1} (max); *Carduelis flammea*, 14.0g and 0.85ml O_2 min^{-1} (min), 4.0g and 5.09ml O_2 min^{-1} (max); *Carpodacus mexicanus*, 20.4g and 0.93ml O_2 min^{-1} (min), 20.6 g and 6.16ml O_2 min^{-1} (max); *Passer domesticus*, 25.5g and 1.00ml O_2 min^{-1} (min), 27.4 g and 8.00ml O_2 min^{-1} (max); *Coccothraustes vespertinus*, 54.5g and 2.16ml O_2 min^{-1} (min), 60.1g and 13.55ml O_2 min^{-1} (max); *Sturnus vulgaris*, 75.0g and 2.68ml O_2 min^{-1} (min), 83.2g and 18.80ml O_2 min^{-1} (max).

equations for both marsupials and therians. For this species, we were unable to elicit cold-induced maxima that met our criteria. Measured metabolism of the larger monotreme (echidna) is significantly lower than predicted by the therian equation, whereas that for the platypus is only slightly higher (Fig. 1). Allometric relationships were not determined for these animals because of the limitation of two species. The equation for birds is significantly elevated above the therian equation (Table 2).

Maximum metabolism in the cold

The relationships of maximum metabolism in the cold to body mass do not differ significantly between marsupials and eutherians (Table 1, Figs 1 and 2), and the data from these infra-classes have been combined to produce an equation for therians (equation 7, Table 2). The kowari (*Dasyuroides byrnei*) exhibits a metabolism significantly elevated by 75% above the value predicted by the therian equation. Again, the larger monotreme (echidna) has a significantly lower maximum than the therians, while the value for the smaller platypus falls below the predicted value but not

Table 2. *Comparison of the relationships between body mass (*m, *grams) and minimal and maximal metabolism (ml O_2 min^{-1}) in the cold and during locomotion in endotherms (species are listed in Tables 1 and 3)*

Taxon	*N*	Equation: metabolism=	%r^2	s_{yx}	s_b	s_a	Mean mass (g)	Predicted for750 g
Minimum								
1 Marsupials	13	$0.047(m^{0.734})$	96.6	0.110	0.041	0.113	1046	6.06
2 Eutherians	6	$0.031(m^{0.843})$	97.0	0.088	0.074	0.182	454	8.22
3 Theria	19	$0.048(m^{0.739})$	95.9	0.109	0.037	0.098	854	6.40
4 Aves	7	$0.129(m^{0.646})$	97.9	0.078	0.043	0.095	355	9.29
Maximum – cold								
5 Marsupials	12	$0.289(m^{0.772})$	96.6	0.111	0.046	0.121	737	47.91
6 Eutherians	7	$0.187(m^{0.821})$	95.8	0.092	0.077	0.187	413	42.88
7 Theria	19	$0.248(m^{0.789})$	96.0	0.106	0.039	0.100	618	46.01
8 Aves	8	$0.812(m^{0.615})$	98.7	0.053	0.029	0.065	316	47.61
Maximum – locomotion								
9 Marsupials	9	$0.298(m^{0.882})$	99.5	0.055	0.024	0.065	1138	102.33

			Slope		Elevation	
			F	*P*	*F*	*P*
Analyses of covariance						
Comparisons						
Minima						
		Marsupials (1) *vs* Eutherians (2)	1.291	0.273	2.636	0.121
		Theria (3) *vs* Aves (4)	2.132	0.155	19.806	<0.001
Minimum *vs* maximum						
Cold		Marsupials (5 *vs* 1)	1.014	0.548	413.054	<0.001
		Eutherians (6 *vs* 2)	0.043	0.834	232.352	<0.001
		Theria (7 *vs* 3)	0.666	0.575	568.430	<0.001
		Aves (8 *vs* 4)	0.370	0.561	495.940	<0.001
Locomotion		Marsupials (9 vs 1)	3.923	0.061	45.889	<0.001
Maxima						
Cold		Marsupial (5) *vs* Eutherian (6)	0.247	0.631	2.068	0.167
		Theria (7) *vs* Aves (8)	7.564	0.011	–	–
Locomotion[a]		Marsupial (9) *vs* Eutherian	1.199	0.280	0.484	0.501
Locomotion *vs* cold		Marsupials (9 *vs* 5)	3.923	0.061	45.889	<0.001

Analysis of covariance was used to compare the relationships.

Maximum during locomotion was determined only for marsupials; [a]comparison with eutherian equation based on data from Taylor *et al.* (1981) (=$0.432m^{0.809}$).

N, number of species.

%r^2 denotes the coefficient of variation and *s* denotes the standard deviation of the subscripted variable: b (slope), a (intercept) and yx (the unexplained error in y).

significantly so. In birds, the effect of body mass (i.e. slope) on maximum metabolism in the cold is significantly less than that for therians. At 316g, the average body mass of the birds examined here, the maximum metabolism of birds is elevated by 20% above that of the therians.

Table 3. *Relationship of minimum and maximum metabolism during locomotion to body mass and factorial scope in the echidna and nine marsupial species*

		Minimum			Maximum			
Species	*N*	Mass	$\dot{V}_{O_2}$	%P	Mass	$\dot{V}_{O_2}$	%P	Factorial scope
Monotreme								
Tachyglossus aculeatus	3	3150.0	6.82	−57	3053.0	65.93	−77	9.7
Marsupials								
Order Dasyuromorphia	Family Dasyuridae							
Sminthopsis crassicaudata	2	15.5	0.32	3	16.1	3.29	−19	10.3
Antechinus flavipes	2	−	−	−	39.4	7.17	−15	−
Dasyuroides byrnei	1	119.5	1.52	8	120.2	23.92	15	15.7
OrderPeramelemorphia	Family Permeliadae							
Isodon obesulus	1	761.3	3.58	−35	649.3	95.53	18	26.7
OrderDiprotodonta	Family Potoroidae							
Potorous tridactylus	5	908.6	8.78	39	956.5	122.40	10	13.9
Bettongia pencillata	2	922.5	9.96	56	913.9	129.50	21	13.0
Dasyurus viverrinus	3	1054.0	6.28	−11	1082.6	112.60	−8	17.9
Bettongia gaimardi	3	1606.3	12.96	34	1622.9	230.89	+5	17.8
	Family Macropodidae							
Macropus eugenii	2	4675.0	26.22	23	4843.4	505.70	23	19.3

Maximum metabolism was determined for *A. flavipes* and *D. viverrinus* by Baudinette *et al.* (1976).

N, number of individual animals; $\dot{V}_{O_2}$, is measured in ml O_2 min^{-1}; mass is measured in grams; %P, measured $\dot{V}_{O_2}$ as a percentage of predicted $\dot{V}_{O_2}$, where the predicted value is based for minimum on the marsupial equation from Thompson (1988) and for maximum on the equation for both wild and domestic species of Taylor *et al.* (1981); factorial scope, maximum $\dot{V}_{O_2}$/minimum $\dot{V}_{O_2}$; M, measured; P, predicted.

The average aerobic factorial scope in response to cold of the marsupials is significantly elevated above the scopes of the other three groups (Table 4; $F_{3,24}$=6.247, P=0.003). There were no differences between the scopes of the birds, monotremes and eutherians.

Metabolism during locomotion in marsupials

Maximum aerobic metabolism during locomotion in marsupials (Table 3, Fig. 4) and associated aerobic factorial scopes are significantly higher than during cold-induced thermogenesis (Table 4). The metabolic rate at a mass of 750g for an exercising marsupial is just over double that in response to cold (see Table 2). However, the effect of body mass on cold-induced and exercise-induced metabolic ceilings is statistically similar. Furthermore, the slopes and elevations of the regression equations relating body mass and maximum metabolism during locomotion for marsupials do not differ significantly from those previously reported for eutherians by Taylor *et al.* (1981).

Discussion

From our experience, eliciting maximal metabolism by exposure to low temperatures

Table 4. *Aerobic factorial scopes of endotherms in the cold and during locomotion*

Taxa	Aerobic factorial scope	
	Cold	Locomotion
Reptilia	–	5.6
Aves	5.4	16.3
Mammalia		
Monotremata	5.4	9.7
Marsupialia	8.3	16.8
Eutheria	5.1	13.6

Average scopes are computed from species listed in Tables 1 and 3.

Locomotion scopes are predicted for an animal weighing 750g, the average body mass of the species presented herein, using the equations for reptilesat 35˚C (Bennett, 1982), non-passerine birds in flight (Rayner, 1982) and eutherians during treadmill locomotion (rest, McNab, 1988; locomotion, Taylor *etal*. 1981).

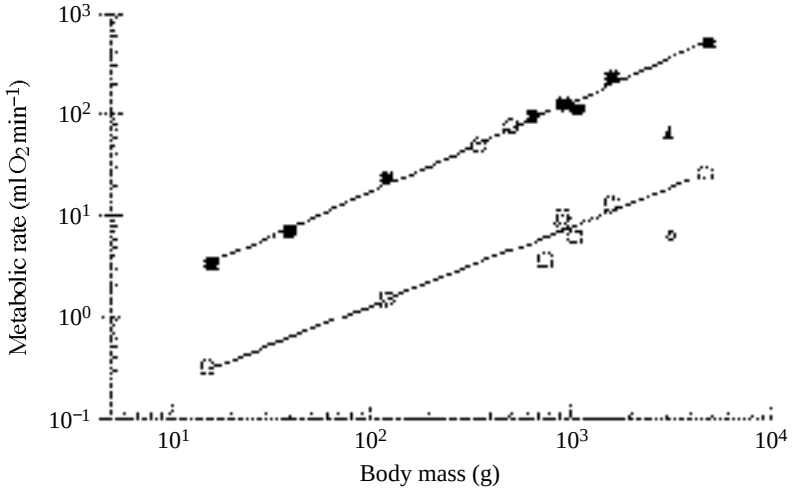

Fig. 4. The relationship of body mass to minimum (open symbols) and maximum (filled symbols) metabolism during locomotion in nine species of marsupials (squares) and the echidna (triangle, see Table 1 for species). Data for juvenile *Potorous tridactylus* (circles) were not included in generating the equation for the line, which is given in Table 2.

and helium is logistically constrained to using animals no greater than 2kg in mass, with the result that allometric analysis is limited to a mass range of two orders of magnitude. However, even within this limitation, differences in factorial aerobic scope are apparent between taxa and treatments (Fig. 5). The data show that the magnitudes of cold-induced aerobic scopes are similar in birds, monotremes and eutherians and are somewhat higher in marsupials. In contrast, exercise-induced scope in all the groups is approximately double that of cold-induced scope. Allometric cancellation techniques are not useful in deriving comparative values for scope because of the differing relationships of body mass to both minimum and maximum metabolism within a taxon and between taxa. Thus, we

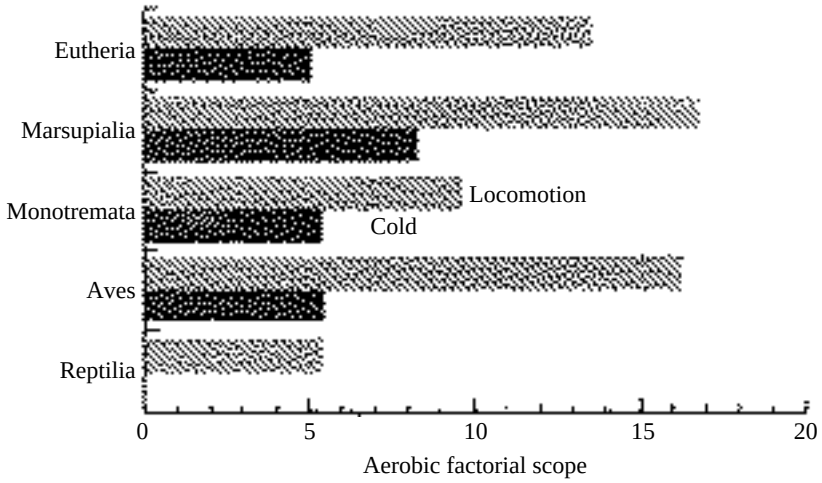

Fig. 5. Aerobic factorial scopes of endotherms in the cold and during locomotion. Average scopes were computed from values for the species listed in Tables 1 and 3. Locomotion scopes were predicted for an animal weighing 750g, the average body mass of the species described in this paper, using the equations for reptiles at 35˚C (Bennet, 1982), non-passerine birds in flight (Rayner, 1982) and eutherians during treadmill locomotion (rest, McNab, 1988; locomotion, Taylor *et al.* 1981).

used the averages of the measured factorial scopes we obtained (Tables 1 and 4) and added allometric values from the literature using the mean body mass of the animals measured in our analysis (750g) as an arbitrary reference point. The data in Fig. 5 make the clear point that locomotion induces a greater metabolic response than cold, ranging from an approximately threefold difference for birds to an approximately twofold difference for monotremes.

Why are factorial scopes during locomotion routinely greater than those observed during cold-induced metabolism? In the laboratory rat, the former is elevated by endurance training while the cold-induced maximum is not (Conley *et al.* 1985). However, in other species, cold acclimation significantly increases both thermogenic and locomotory aerobic capacity, but the increase is greater for thermogenic capacity (Hayes and Chappell, 1986). Such studies suggest that the mitochondrial populations that adapt to cold acclimation and endurance training do not overlap. There have been claims that the uncoupling effects of free fatty acids on muscle mitochondria are enhanced following cold acclimation in ducklings (Barre, 1986); however, the importance of this in thermogenesis has been challenged (Marsh and Dawson, 1989). In the case of acute exposure to cold, as used in this study, in which animals were held at moderate temperatures around 20˚C, the situation would appear to be simplified. Non-shivering thermogenesis in mammals is largely an acclimatory response involving the development of brown fat and, perhaps, responsiveness in other tissues to catecholamines (see Feist and White, 1989). The possible exception to this is the role of glucagon in thermogenesis; however, this may be secondary to its role in resynthesising glycogen and triacylglycerols (see Marsh and Dawson, 1989). In birds, the demonstration of non-shivering

thermogenesis has been controversial and has recently been reviewed by Marsh and Dawson (1989). Acute treatment with catecholamines elicits no thermogenic response in non-acclimated animals and intensive attempts to identify brown adipose tissue in birds have failed. We are left with the conclusion that shivering is the main source of thermogenesis in birds and mammals exposed to acute cold stress, and that this dominates the responses measured in this study.

Given that muscle is probably the only tissue recruited under cold-induced and exercise-induced thermogenesis, we are still left with the question of the quantitative difference between the two conditions. Lucas *et al.* (1980) have examined a series of hypotheses bearing on this problem. In dogs, they found that maximum metabolism during exposure to cold water was only 65% of that induced during treadmill exercise. Plasma catecholamine levels measured under both conditions were not significantly different, an indication that the treatments provided comparable levels of stress. Differences in the roles of the sympathetic neurohumoral system in the cold and during exercise therefore appear unlikely. However, two other hypotheses proposed in the study do have supporting evidence. When under cold stress, dogs show increases in $\dot{V}_{O_2}$ and shivering intensity after the injection of insulin (Therminarius *et al.* 1979), suggesting that shivering may compromise glucose uptake. Alternatively, the reduction in blood flow caused by isometric contraction of muscle during shivering may have the same effect.

A final hypothesis to explain enhanced $\dot{V}_{O_2}$ in exercise invokes the type of muscle fibres used. Lucas *et al.* (1980) claim that shivering in dogs involves most of the locomotory muscles. Many of these muscles are of mixed fibre types, slow twitch oxidative fibres and fast twitch fibres, which have higher glycogen, and therefore higher anaerobic, capacity. Running at maximum metabolic levels may involve both fibre types; however, shivering probably only involves the former type. The evidence for this is the low rate of lactate produced during shivering. Lucas *et al.* (1980) conclude that the lower maximum metabolism elicited by shivering may be due to the differences in fibre type recruitment. A corollary to this view is the finding that maximal exercise in the cold can be sustained for longer periods than during exercise, a finding consistent with low rates of lactate production.

In birds, the peculiar anatomy of the wing musculature may result in a limitation for shivering thermogenesis (Marsh and Dawson, 1989). The cross-sectional area of the supracoracoideus muscle is much less than that of the pectoralis, resulting in uneven forces if both were to produce maximal forces. Given the large size of the pectoral musculature, this potential compromise may be manifested in a lower $\dot{V}_{O_2}$ during shivering than during flight.

Can the differences in aerobic scope between cold exposure and exercise be due to a Q_{10} effect on metabolism? Our experimental design does not allow us to answer this question directly, since simultaneous measurements of maximum metabolism and body temperature were not taken. The criteria we used for maximum metabolism were (1) a drop in oxygen consumption from the steady-state maximal value, and (2) a drop in body temperature when the animal was removed from the chamber. However, indirect calculations show that a Q_{10} effect is of insufficient magnitude to account for the difference. A model eutherian at the midpoint of our mass range (750g) would have a

maximum rate of oxygen consumption in the cold of 46mlmin^{-1} and let us assume that this level of metabolism is sufficient to maintain body temperature at the resting level of 38°C. Animals of this mass show a typical increase in body temperature of around 2°C during locomotion and, assuming a Q_{10} value of 2, this correction predicts a maximum $\dot{V}_{O_2}$ for exercise of 52mlmin^{-1}. This is only 57% of the value expected from our allometric equation (Table 2). Similarly, the echidna has a maximum $\dot{V}_{O_2}$ in the cold of 47mlmin^{-1} and a maximum during locomotion of 65.9ml O_2 min^{-1}. Our unpublished measurements suggest that an increase of about 2°C in body temperature is also maximal during locomotion for this species. Using this temperature increase for a Q_{10} value of 2 gives a derived maximum $\dot{V}_{O_2}$ of 54mlmin^{-1}, 82% of the measured value. It seems likely that, even after correcting for a Q_{10} effect, the differences between cold-induced and exercise-induced maxima will remain.

In a recent analysis Peterson *et al.* (1990) examined the available data on 'sustained metabolic rates', integrated metabolic rates in free-ranging animals measured by the washout constants of hydrogen and oxygen isotopes. Although the resting metabolic rates in their analysis varied 150-fold among the species used, values of sustained metabolic scope were mostly between 1.5 and 5, but all less than 7. The study asked whether metabolic ceilings varied with different modes of energy expenditure, such as heat production, exercise and lactation. The present study has shown this to be the case, and the suggestion that some general limitation is in force, such as the rate of intestinal absorption, appears unlikely. Rather, the limit is a property of the process itself; the heat production from muscle during thermogenesis is different from that produced as a consequence of locomotory work. Maximal sustained levels of energy production for thermogenesis, at least, are therefore lower than the ceiling theoretically imposed by intestinal absorption. The question of the ultimate evolutionary responses to a common sustained metabolic ceiling is fascinating (see Hammond and Diamond, 1992). The resolution of differences between sustainable limits in exercise and thermogenesis may assist its resolution.

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