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Causes and significance of variation in mammalian basal metabolism

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Abstract Mammalian basal metabolic rates (BMR) increase with body mass, whichs explains approximately 95% of the variation in BMR. However, at a given mass, there remains a large amount of variation in BMR. While many researchers suggest that the overall scaling of BMR with body mass is due to physiological constraints, variation at a given body mass may provide clues as to how selection acts on BMR. Here, we examine this variation in BMR in a broad sample of mammals and we test the hypothesis that, across mammals, body composition explains differences in BMR at a given body mass. Variation in BMR is strongly correlated with variation in muscle mass, and both of these variables are correlated with latitude and ambient temperature. These results suggest that selection alters BMR in response to thermoregulatory pressures, and that selection uses muscle mass as a means to generate this variation.

Keywords Energetics · Allometric scaling · Basal metabolic rate · Body mass

Introduction

Energy metabolism is one of the fundamental currencies of life. All organisms use energy to power behavior, reproduction, and survival. However, the rates at which mammals expend energy at rest and in a thermoneutral state [basal metabolic rate (BMR)] vary considerably. Since BMR constitutes a major portion of total energy expenditures (approximately 30% of total energy expenditure; Ricklefs et al. 1996), variation in BMR may have significant implications for mammalian evolution. For example, energy use may act as a constraint on group dynamics, life history, habitat use, mortality, and reproductive output (see Jackson et al. 2001; McNab 2002; Brown et al. 2004; Blackmer et al. 2005; Artacho and Nespolo 2009). Therefore, the evolution of mammalian energetics must have played a major role in the evolution of mammalian behavioral ecology. In this study, we examine the interactions between habitat, morphology, and energetics in a wide range of mammals to better understand how variation in energy expenditures evolved.

Body size accounts for much of the variation in mammalian BMR (Kleiber 1932; Savage et al. 2004; White and Seymour 2003). However, after body mass is taken into account, there remains a sixfold range of variation in BMR that must be explained (Mueller and Diamond 2001). Understanding this variation is essential to determining how selection acts on BMR across mammals. Although several models propose explanations for how body mass

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constrains BMR (see West et al. 1997, 1999; Darveau et al. 2002; Kozłowski et al. 2003), selection acts within these constraints to generate variation in BMR at a given body mass (e.g., there may be adaptive reasons for relatively high or low BMR at a given body mass; see Artacho and Nespolo 2009).

At its most fundamental level, BMR is the sum of tissue metabolic rates (Schmidt-Nielsen 1984; Wang et al. 2001). Thus, it is possible that variation in organ size with differing mass-specific metabolic rates at a given body mass will account for variation in whole organism metabolism at a given body mass. For example, across a small sample of birds ($n = 22$ species), variation in heart and kidney masses explains much of the variation in BMR (Daan et al. 1990). Konarzewski and Diamond (1995) showed that heart and kidney masses also explain some of the intraspecific variation in BMR in laboratory mice. Selman et al. (2001) found that liver mass was also a significant predictor of BMR variation in mice. Isler and Van Schaik (2006) showed that variation in brain mass explains a small proportion of variation in BMR in a large sample of mammals (i.e., ~5% of the variation in BMR). Finally, McNab (2007) suggested that muscle mass may explain BMR variation in mammals, drawing on studies showing relatively low muscle masses were associated with relatively low BMRs in sloths (McNab 1978, 2007), and possibly some arboreal felids (McNab 2000). Muscle mass appears to influence BMR in birds as well, with taxa having relatively low pectoral muscle mass (i.e., flightless birds) also having relatively low BMRs (McNab 1994; McNab and Ellis 2006). In this study, we examine the relationship between variation in organ mass and variation in mammalian BMR.

Although organ size represents a possible mechanism for altering BMR at a given body mass, we must also address the underlying reasons for the variation. Is this variation a product of selection and, if so, what are the advantages of relatively high or low BMRs? Recent attention has focused on the role of climate in determining variation in BMR at a given body mass, suggesting there is a selective advantage to relatively high or low BMRs. In this context, variation in BMR may be a response to thermoregulatory selection pressures (McNab 2002). For example, residual variation in BMR of small mammals is correlated with both latitude and mean annual temperature, such that animals living in high latitudes and cold climates generally have relatively higher BMRs than those living in the tropics, after controlling for body size (Lovegrove 2003). Others have found a similar relationship between climate and BMR in humans (Leonard et al. 2002; Roberts 1978), larger bodied mammals (Lovegrove 2000), rodents (Mueller and Diamond 2001; Rezende et al. 2004), and canids (Careau et al. 2007).

Here, we tested the hypothesis that variation in organ mass explains variation in BMR across mammals by examining muscle mass in a taxonomically diverse sample ($n = 50$; see Table 1). We focused on muscle mass, since it is typically the largest single component of body mass, accounting for 24–61% of total body mass in mammals (Calder 1984; Grand 1977; Holliday 1986; Muchlinski et al. 2003). Although muscle has a relatively low mass-specific metabolic rate at rest, since it is the largest organ in the body, it makes up a large percentage of basal metabolic rate (Schmidt-Nielsen 1984). For example, in humans, muscle generates as much, or more, metabolic heat than all other organs except the splanchnic organs (Schmidt-Nielsen 1984), and accounts for 20% of oxygen consumption at rest (greater than any other organ except for the brain; Rolfe and Brown 1997). Additionally, in rats, muscle tissue metabolism accounts for nearly 50% of total tissue metabolism (see Field et al. 1939). We also examine the relationship between muscle mass, BMR and climate to test the hypothesis that selection due to climatic pressures acts on muscle mass to alter BMRs. Although we focus mainly on muscle mass, it is possible that other organs will also influence BMR [e.g., Daan et al. (1990) and Konarzewski and Diamond (1995)] Therefore, we also examined the relationships between other metabolically expensive organs and BMR in a smaller sample.

Methods

Data for BMR were taken from published sources ($n = 50$; see Table 1 for references). If data from multiple individuals of the same species were available, data were pooled and mean BMRs were included for study. The goal of this study was to amass the largest number of taxa for which both muscle mass and BMR were available. Thus, if data were available for both sexes, means were taken. Muscle masses were either compiled from the literature, or collected from cadavers for this study (see Table 1). Cadavers for this study were obtained from the Duke University Primate Center (DUPC). All animals used in this study were adult, and all had died of natural causes. All cadavers ($n = 11$) were dissected by two of the authors (MNM and JJS) according to techniques and standards described by Grand (1977). Muscle masses were weighed to the nearest 0.1 g using an Ohaus N1D110-2A1 balance (Pine Brook, NJ). Body masses at death were available for all but three species sampled (*Perodicticus potto*, *Hapalemur griseus*, and *Tarsius syrichta*). For these species, a body mass was derived by compiling weights during their last year of life (based on DUPC records) and calculating an average. The calculated mass was then compared to published averages (Terranova and Coffman 1998). All derived masses fall within known ranges. For each species sampled, we calculated a single unweighted body mass and muscle mass

Table 1 Metabolic and climatic data for taxa included in this study

Higher clade	Species	*N*	Body mass (g)	Muscle mass (g)	Ref	Body mass (g)	BMR (ml O_2 h^{-1})	Ref	Weather station code	Weather station name	Lat	*T*	Ref
Artiodactyla	*Madoqua kirki*	6	4,400	1,980	Pitts and Bullard (1968)	4,290	500	Lovegrove (2000)					
Carnivora	*Felis rufus*	3	6,152	3,600.3	Grand (1977)	9,400	4,220	White and Seymour (2003)					
Carnivora	*Mustela erminea*	3	183.3	104.7	Grand (1977)	75	165	White and Seymour (2003)	7002600	Barrow	71.3N	12.38	Lovegrove (2000)
Carnivora	*Mustela vison*	2	1,032	581.5	Grand (1977)	660	488	White and Seymour (2003)					
Carnivora	*Procyon lotor*	3	6,040	2,920.7	Grand (1977)	5,075	1,599	White and Seymour (2003)	74794000	Cape Kennedy	28.47N	21.69	This study
Chiroptera	*Artibeus jamaicensis*	14	40.5	18	Grand (1977)	45.2	78	White and Seymour (2003)	83967000	Porto Alegre	30S	19.52	This study
Chiroptera	*Artibeus lituratus*	5	63.7	29.1	Grand (1977)	70.1	37.3	White and Seymour (2003)					
Chiroptera	*Glossophaga soricina*	3	7.2	3.9	Grand (1977)	9.6	17.7	White and Seymour (2003)					
Chiroptera	*Phyllostomus discolor*	7	34.4	16.5	Grand (1977)	33.5	11.1	White and Seymour (2003)					
Chiroptera	*Phyllostomus hastatus*	2	92.3	47	Grand (1977)	84.2	38.8	White and Seymour (2003)					
Chiroptera	*Eptesicus fuscus*	2	17.9	7.4	Grand (1977)	10.4	25.2	White and Seymour (2003)	72306004	Chapel Hill, NC	35.92N	15.1	This study
Chiroptera	*Sturnira lilium*	2	15.4	6.3	Grand (1977)	21.9	39.9	White and Seymour (2003)					
Insectivora	*Scalopus aquaticus*	1	44.6	21.9	Grand (1977)	48	67.7	White and Seymour (2003)	72212002	Gainesville/ Muni Arpt	29.68N	20.48	This study
Rodentia	*Clethrionomys gapperi*	1	18.3	9.3	Grand (1977)	22.3	49.3	White and Seymour (2003)	72604003	Bethlehem Vermont	44.28N	5.51	This study
Rodentia	*Clethrionomys rutilus*	20	25.3	11.3	Grand (1977)	28	77	White and Seymour (2003)	7025103T/ 7026106R	Fairbanks	64.9N	3.37	Lovegrove (2000)
Rodentia	*Mus musculus*	4	15.9	7.1	Grand (1977)	13.2	65.34	Lovegrove (2000)	1237500	Warsaw	52.17N	7.53	Lovegrove (2000)
Rodentia	*Peromyscus leucopus*	9	17	8	Grand (1977)	20	33.2	White and Seymour (2003)	7251900T/ 7251901R	Ithaca	42.5N	8.73	Lovegrove (2000)
Rodentia	*Marmota monax*	2	2194	817.1	Grand (1977)	2,650	662.5	White and Seymour (2003)					
Rodentia	*Ondatra zibethicus*	8	1,180	679.4	Grand (1977)	1,004.6	642.9	White and Seymour (2003)					
Rodentia	*Microtus pennsylvanicus*	7	31.4	14.5	Grand (1977)	38.9	75.1	White and Seymour (2003)	7251900T/ 7251901R	Ithaca	42.5N	8.73	Lovegrove (2000)
Rodentia	*Microtus pinetorum*	7	19.4	9.5	Grand (1977)	25.5	58.4	White and Seymour (2003)	7251900T/ 7251901R	Ithaca	42.5N	8.73	Lovegrove (2000)
Rodentia	*Microtus oeconomus*	9	24.8	11.1	Grand (1977)	33.7	100.9	White and Seymour (2003)	7002600	Barrow	71.3N	12.38	Lovegrove (2000)
Rodentia	*Sciurus carolinensis*	1	499	306.5	Grand (1977)	440	369.6	White and Seymour (2003)	7242800	Columbus	40N	11.33	Lovegrove (2000)
Rodentia	*Spermophilus undulatus*	4	479	257.9	Grand (1977)	680	667.1	White and Seymour (2003)	7002600	Barrow	71.3N	12.38	Lovegrove (2000)
Rodentia	*Tamiasciurus hudsonicus*	11	192.8	114.2	Grand (1977)	228.3	254.6	White and Seymour (2003)	7185200	Winnipeg	49.9N	2.1	Lovegrove (2000)
Lagomorpha	*Lepus californicus*	1	1,867	868	Pitts and Bullard (1968)	2,300	1,311	White and Seymour (2003)					
Primates	*Pan troglodytes*	1	31,500	11,025	Zihlman (1984)	18,300	5,772.81746	Snodgrass et al. (2007)					
Primates	*Macaca mulatta*	3	6,043.3	2,498.3	Pitts and Bullard (1968)	5,380	2,388.6	Snodgrass et al. (2007)					
Primates	*Callithrix jacchus*	4	186	87.9	Grand (1977)	190	152	White and Seymour (2003)					

Table 1 continued

Higher clade	Species	N	Body mass (g)	Muscle mass (g)	Ref	Body mass (g)	BMR (ml O_2 h^{-1})	Ref	Weather station code	Weather station name	Lat	T	Ref
Primates	*Aotus trivirgatus*	4	628.8	193	Pitts and Bullard (1968)	820	442	White and Seymour (2003)	78767000	Puerto Limon	10N	25.49	This study
Primates	*Tarsius syrichta*	1	125	27.2	Muchlinski et al. (2003)	173	149	White and Seymour (2003)	98550000	Tacloban	11.25N	27.17	This study
Primates	*Microcebus murinus*	2	61.2	17.5	Muchlinski et al. (2003)	54	48.61	Snodgrass et al. (2007)					
Primates	*Galago crassicaudatus*	3	994.1	377.9	Pitts and Bullard (1968); Muchlinski et al. (2003)	950	412	White and Seymour (2003)	6374000	Nairobi	1.32S	19.08	Lovegrove (2000)
Primates	*Galago moholi*	2	134.5	45	Muchlinski et al. (2003)	170	51	White and Seymour (2003)	6817400T/ 6817602R	Louis Trichardt	23S	17.43	Lovegrove (2000)
Primates	*Galago senegalensis*	2	245.5	90	Pitts and Bullard (1968)	171.5	137	White and Seymour (2003)					
Primates	*Perodicticus potto*	4	989.3	214.25	Pitts and Bullard (1968)	964	327	White and Seymour (2003)	64556000	Makokou Weather Station	0.57N	23.71	Lovegrove (2000)
Primates	*Loris tardigradus*	1	144	40	Muchlinski et al. (2003)	284	35.5	White and Seymour (2003)	4218200	New Delhi	28.58N	25.08	Lovegrove (2000)
Primates	*Nycticebus coucang*	5	1,157.4	298.2	Pitts and Bullard (1968)	1,160	273	White and Seymour (2003)	4864700	Kuala Lumpur	3.12N	26.54	Lovegrove (2000)
Scandentia	*Tupaia glis*	4	151.3	49.8	Pitts and Bullard (1968)	123	93.5	White and Seymour (2003)					
Xenarthra	*Choloepus hoffmanni*	2	4,595	1,232	Pitts and Bullard (1968)	3,770	603	White and Seymour (2003)					
Xenarthra	*Euphractos sexcinctus*	2	2,459	864.1	Grand (1977)	8,190	1,237	White and Seymour (2003)					
Marsupial	*Dendrolagus matschiei*	2	6,110	2,077.4	Grand (1990)	6,960	1,426.8	White and Seymour (2003)					
Marsupial	*Macropus rufus*	2	23,900	11,233	Grand (1990)	34,490	5,848.2	White and Seymour (2003)	94719001	Trangie Post Office	32.03S	18.25	This study
Marsupial	*Phascolarctos cinereus*	10	5,974.5	1,818.3	Grand and Barboza (2001)	4,765	1,034	White and Seymour (2003)	95935001	Montague Island Lighthouse	36.25S	16.58	This study
Marsupial	*Potorous tridactylus*	2	1,026.5	451.7	Grand (1990)	976	416.4	White and Seymour (2003)					
Marsupial	*Pseudocheirus peregrinus*	5	939.6	300.7	Grand (1990)	860	37.4	White and Seymour (2003)					
Marsupial	*Didelphis marsupialis*	2	1,441	682	Grand (1977)	1,165	571	White and Seymour (2003)					
Marsupial	*Metachirus nudicaudatus*	1	391	179	Grand (1983)	336	205	White and Seymour (2003)	7880601T/ 7880601R	Cristobal	9.4N	26.53	Lovegrove (2000)
Marsupial	*Monodelphis brevicaudata*	1	73.1	29	Grand (1983)	75.5	57	White and Seymour (2003)	8045000	San Fernando de Apure	7.9N	27.09	Lovegrove (2000)
Marsupial	*Philander opossum*	5	364.8	141.4	Grand (1983)	751	338	White and Seymour (2003)	7880601T/ 7880601R	Cristobal	9.4N	26.53	Lovegrove (2000)

average. We also compiled masses for other metabolically expensive organs (liver [$n = 28$], kidney [$n = 26$], heart [$n = 28$]; see supplementary materials) from Crile and Quiring (1940). All data from Crile and Quiring (1940) include individual body masses for each specimen.

When capture sites were given for a BMR study, mean annual temperature and latitude were taken from the nearest weather station to that capture site from the National Climatic Data Center (NCDC) in Asheville, NC (http://ingrid.ldgo.columbia.edu/SOURCES/.NOAA/.NCDC) or from Lovegrove (2003) who used similar methods. If capture sites were not reported, but the taxon uses a restricted geographic range, a weather station was chosen in the center of the species distribution (Lovegrove 2003). Because of these limitations, the data used to examine correlations between physiology and climate are a subset of the overall sample ($n = 27$).

Relationships between organ mass and BMR were investigated using a residual analysis. Although multiple regression might be preferred over residuals to investigate the relationship between organ mass and BMR at a given body size, two sets of body mass values were used for each species because organ mass and BMR data were collected on different samples within each species (see Table 1) and thus all three variables (body mass, organ mass, and BMR) could not be included in a single multiple regression analysis. Instead, residuals from least squares regression lines against body mass were calculated for organ mass and BMR individually, and correlations calculated between these residuals. All data were $\log_{10}$-transformed prior to analysis and statistics were calculated using *R* (Ihaka and Gentleman 1996).

For the phylogenetic analysis, when standard relationships were significant, phylogenetically independent contrasts were calculated for BMR, organ mass, body mass from the BMR data set, and body mass from the organ mass data set using the PDAP module in Mesquite version 2.6 (Maddison and Maddison 2009; Midford et al. 2003). The phylogenetic branching sequence is provided in Fig. 1. Branch lengths were assigned using Grafen's method based on number of descendant observed taxonomic units, followed by Grafen's rho transform using $\rho = 0.25$ (Grafen 1989); absolute values of the resulting contrasts are uncorrelated with contrasts standard deviations as suggested by Garland et al. (1992). Contrasts residuals were calculated from least squares regressions against body mass contrasts where the intercept was constrained to equal zero.

Results

Consistent with earlier work, the scaling relationship between log BMR and log body mass has a 95% confidence interval which includes 2/3, 3/4, or both, depending on regression model and whether or not phylogeny is considered; the scaling of muscle mass and body mass does not differ significantly from isometry (Table 2). Residual variation in muscle mass is positively correlated with residual variation in BMR (Table 3). The 95% confidence intervals for the slope and intercept of the regression lines relating muscle mass residuals and BMR residuals include the line of identity ($y = x$; slope [95% CI] = 1.13 [±0.67]; y-intercept [95% CI] = 0.00 [±0.07]) (Fig. 2a). These relationships remain significant once phylogeny is taken into account using independent contrasts and also include the line of identity (slope [95% CI] = 0.973 [±0.854]; y-intercept [95% CI] = 0.002 [±0.013]) (Fig. 2b; Table 3). Additionally, a sign test shows that muscle mass residuals and BMR residuals are significantly more likely to be of the same sign (i.e., both positive or both negative) than expected by chance ($p < 0.001$). Therefore, not only are residuals positively correlated, but also hypermetabolism is consistently associated with larger than expected muscle mass and hypometabolism is consistently associated with lower than expected muscle mass. We did not find any significant correlations between residual organ mass and residual BMR for other metabolically expensive organs in a smaller sample of mammals (kidney, $p = 0.36$; heart, $p = 0.062$; liver, $p = 0.39$; see supporting materials).

Similar to the findings of Lovegrove (2003), residual BMR was positively correlated with latitude and negatively correlated with mean annual temperature (Fig. 3a, b; Table 3). Residual variation in muscle mass was also positively correlated with latitude and negatively correlated with mean annual temperature (Fig. 3c, d; Table 3). Intriguingly, the majority of BMR and muscle mass residuals within the tropics (latitudes less than 23.4) are negative, and residuals outside of the tropics are positive (Fig. 3a, c).

Discussion

Variation in mammalian BMR is highly correlated with variation in muscle mass. This relationship appears to be linked to climate, as variation in both BMR and muscle mass is correlated with temperature and latitude. Contrary to within-species studies in mice (Konarzewski and Diamond 1995) and inter-specific studies of birds (Daan et al. 1990), we found no significant correlation between residual organ mass and residual BMR for other metabolically expensive organs in mammals. In a similar study of relative brain size and BMR in mammals, Isler and Van Schaik (2006) showed a slight, but significant, positive relationship between residuals of BMR from body mass and residuals of brain mass from body mass. However, residuals of muscle mass explain four times the amount of

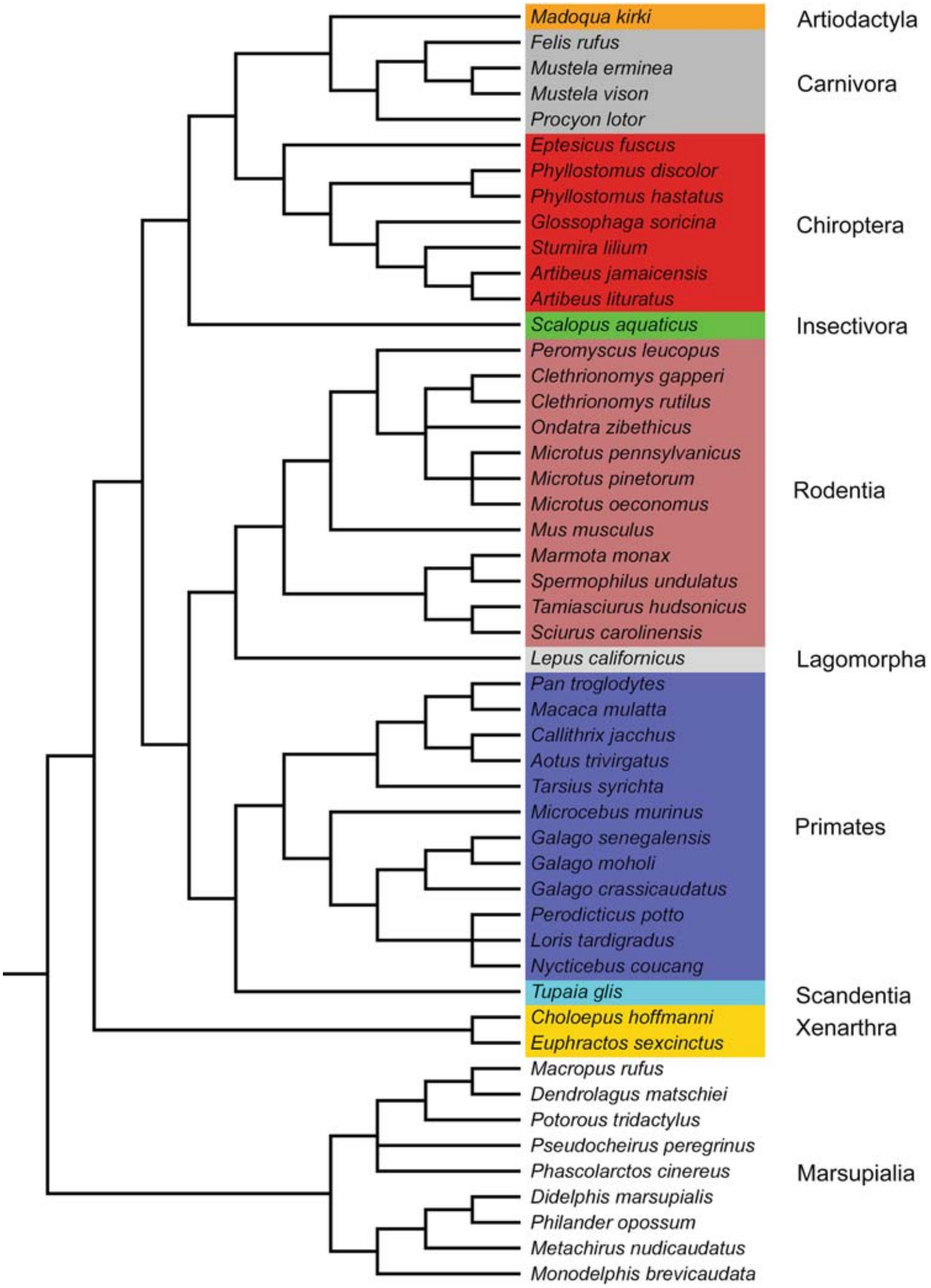

Fig. 1 Phylogenetic branching sequence used for the taxa in this study. See *text* for how branch lengths were assigned

Table 2 Reduced major axis (RMA) and ordinary least squares (OLS) regression parameters calculated for logged data (standard) or phylogenetically independent contrasts of logged data (phylogenetic)

Regression variables	RMA slope	RMA 95% confidence interval	OLS slope	OLS 95% confidence interval	r^2
Muscle mass versus body mass (standard)	0.986	0.952–1.02	0.978	0.945–1.01	0.986
Muscle mass versus body mass (phylogenetic)	1.00	0.973–1.04	0.999	0.966–1.03	0.988
BMR versus body mass (standard)	0.716	0.635–0.807	0.651	0.565–0.737	0.828
BMR versus body mass (phylogenetic)	0.765	0.674–0.869	0.688	0.591–0.785	0.808

Table 3 Correlation statistics for residual analyses

Correlation variables	r	r^2	p
BMR residuals versus muscle mass residuals (standard)	0.440	0.194	0.001
BMR residuals versus muscle mass residuals (phylogenetic)	0.317	0.100	0.027
Muscle mass residuals versus latitude (standard)	0.604	0.364	<0.001
Muscle mass residuals versus mean annual temperature (standard)	−0.592	0.350	0.001
BMR residuals versus latitude (standard)	0.597	0.357	0.001
BMR residuals versus mean annual temperature (standard)	−0.574	0.330	0.002

Residuals are calculated from OLS regressions

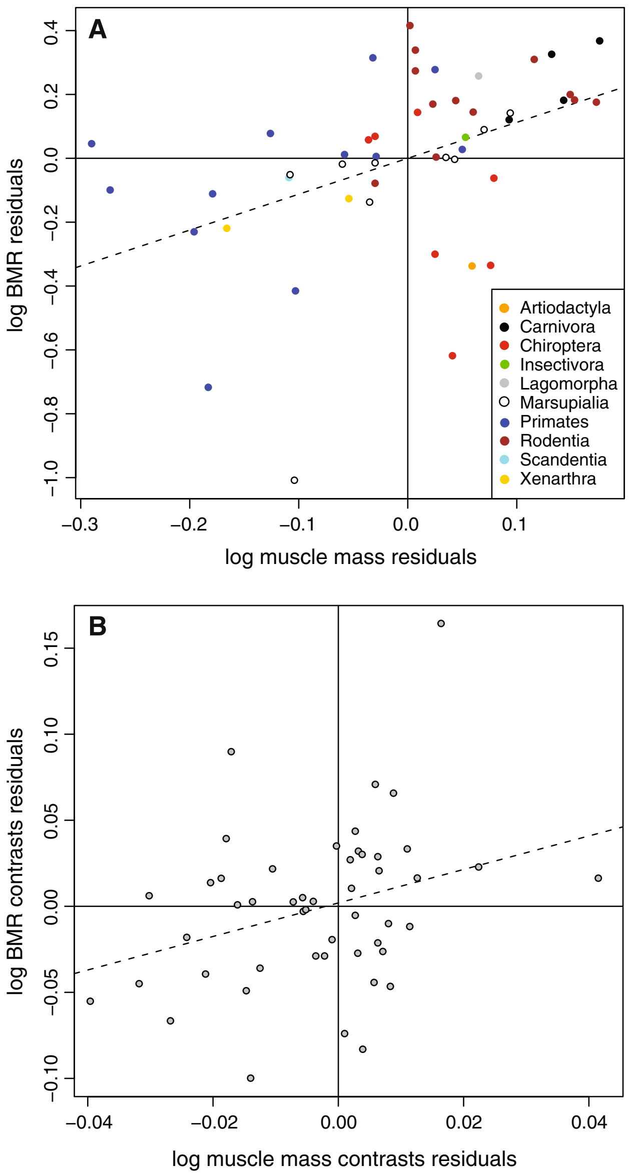

Fig. 2 Relationship between residual variation in log BMR and residual variation in log muscle mass, where residuals are calculated from OLS regressions against log body mass. *Dashed lines* are fitted OLS lines to illustrate the bivariate relationships, although analyses are based on correlations alone (see *text*). **a** Bivariate plot of residuals of BMR from body mass versus residuals of muscle mass from body mass. **b** Bivariate plot of phylogenetically independent contrast residuals for BMR and muscle mass. Independent contrasts calculated using phylogeny in Fig. 1

inter-specific variation in BMR residuals compared to residuals of brain mass (compare the values in Table 3 to $r^2 = 0.053$ for residual brain mass vs. residual BMR; Isler and Van Schaik 2006). In addition, the statistically significant association of hypometabolism with relatively low muscle mass and hypermetabolism with relatively high muscle mass argues for a strong relationship between differences in relative muscle mass and relative BMR. Thus, we believe that variation in muscle mass plays a major role in determining inter-specific variation in BMR among mammals. The strong correlation between residual muscle mass and residual BMR, and our limited data for other organs, suggests that taxa with relatively low muscle masses do not significantly increase the mass of other metabolically expensive organs, which would lead to an increase in BMR. It is more likely that those taxa with relatively low muscle masses have relatively large bone or fat mass, two tissues with lower metabolic rates than muscle (Daan et al. 1990).

Contribution of muscle metabolism to BMR

Muscle has a low metabolic rate per gram, however, it also makes up the largest portion of body mass in organisms, and thus, total muscle metabolic rate (the product of total muscle mass and metabolic rate per gram) makes up a substantial portion of BMR (see Schmidt-Nielsen 1984). The contribution of muscle metabolism to total metabolism is available for a small number of taxa, and the data suggest that changes in muscle mass can have an important impact on BMR. For example, in mice, the total organ metabolic rate of muscle is 8.63 ml O_2 h^{-1} while BMR for these subjects is 24.38 ml O_2 h^{-1} (Martin and Fuhrman 1955). Thus, muscle metabolic rate accounts for ~35% of total BMR. If muscle mass were increased by 10%, these subjects would have BMRs of 25.26 ml O_2 h^{-1}, which is a 3.5% increase due to altered muscle mass (calculated based on a per gram muscle metabolic rate of 1.26 ml O_2 h^{-1} and a change in muscle mass from 6.85 to 7.54 g). In dogs, the increase in BMR due to an increase in muscle mass is even greater. The total metabolic rate of muscle in dogs is 4,642 ml O_2 h^{-1}, which is ~61% of BMR (BMR is 7,597 ml O_2 h^{-1}; Martin and Fuhrman 1955). A 10% increase in muscle mass for these subjects would lead to a ~6% increase in BMR (calculated using a per gram muscle

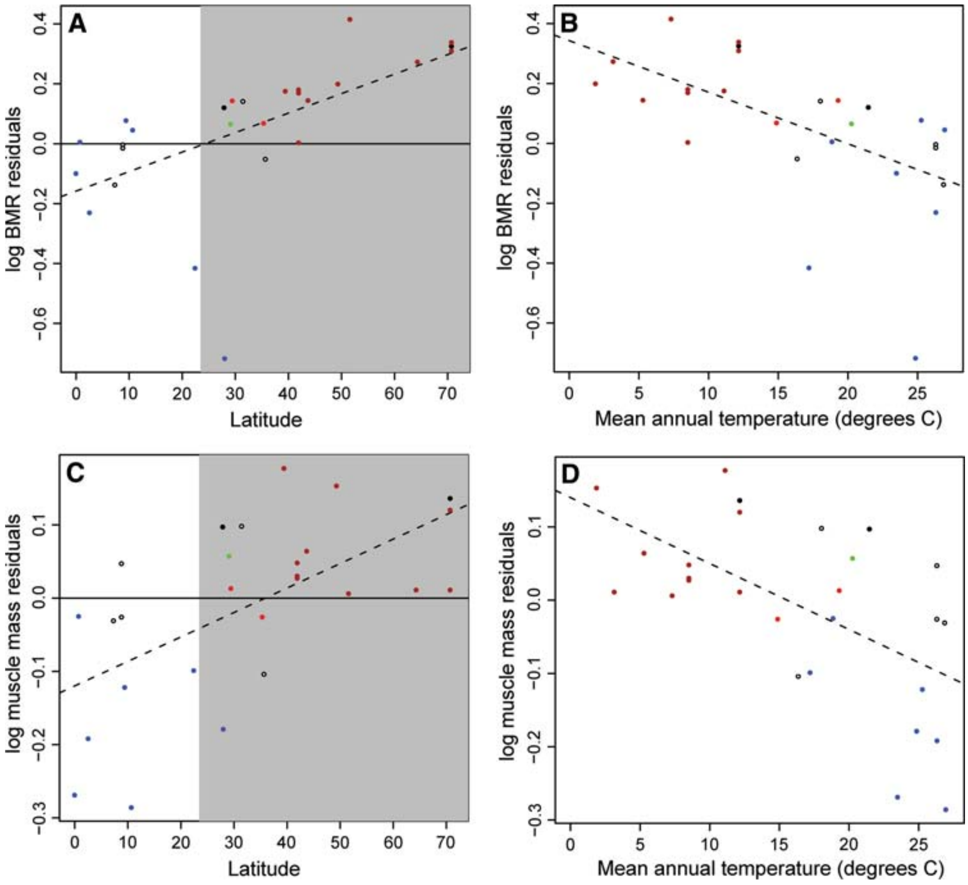

Fig. 3 Effects of the environment on BMR and muscle mass. *Symbols* and *lines* are as in Fig. 2a; *shaded areas* indicate latitudes outside of the tropics. **a** Relationship between residual variation in BMR and latitude. **b** Relationship between residual variation in BMR and mean annual temperature. **c** Relationship between residual variation in muscle mass and latitude. **d** Relationship between residual variation in muscle mass and mean annual temperature

metabolic rate of 0.57 ml O_2 h^{-1} and a change in muscle mass from 8,144 to 8,958.4 g). Field et al. (1939) provide similar data for rats, and changes in muscle mass result in similar estimated changes in total BMR. Rat muscles consume 53.72 ml O_2 h^{-1}, which is ~50% of their total BMR (110.08 ml O_2 h^{-1}; Field et al. 1939). Increasing muscle mass by 10% would result in a ~5% increase in total BMR (calculated based on a per gram muscle metabolic rate of 0.875 ml O_2 h^{-1} and a change in muscle mass from 61.4 to 67.54 g). Although there are not enough data to quantify the effects of changes in muscle mass on BMR across a wide range of taxa and body masses, changes in muscle mass can clearly have a major impact on total BMR. So, if alterations in muscle mass help generate relatively high or low BMRs, why would variation in BMR evolve in the first place?

BMR and thermoregulation

Climate might play a strong role as a selection pressure for energy expenditures since BMR acts as a set point for body temperature regulation (McNab 2002; Schmidt-Nielsen 1997). The set point is significant because endotherms generally maintain a constant body temperature, regardless of ambient air temperature (Schmidt-Nielsen 1997), which means that heat production (e.g., metabolic rate) must be equal to heat loss in both hot and cold climates. This balance of heat production and heat loss is easily achieved within the thermoneutral zone, which is the ambient air temperature range within which metabolic rate does not change to maintain a constant body temperature (Schmidt-Nielsen 1997). In a hot climate, a relatively low BMR provides a higher critical temperature and allows taxa to reduce chances of hyperthermia and dehydration (Careau et al. 2007). In a cold climate, having a higher BMR results in a lower critical temperature (the lower limit, or set point of the thermoneutral zone) (Schmidt-Nielsen 1997) and may increase thermogenic capacity, which is highly correlated with cold tolerance and will help compensate for heat loss (Swanson and Liknes 2006; Careau et al. 2007). Thus, a relatively high BMR may be a thermoregulatory adaptation that increases the ability to withstand colder climates, while a relatively low BMR reduces the chances of overheating and dehydration in hotter or drier climates (Careau et al. 2007).

It is important to note that latitude and mean annual temperature are coarse indicators of local thermoregulatory needs. Because exact capture locations are rarely noted in studies of BMR, the thermoregulatory challenges suggested by our climate data are necessarily vague. Indeed, recent discussions have focused on the validity of examining large-scale correlations of climatic variables and physiology (see Hodkinson 2003; Chown et al. 2003). Although it is certainly true that large-scale variables such as latitude and mean annual temperature fail to account for the different microhabitats that taxa live within (Hodkinson 2003), Chown et al. (2003) effectively argue that when a signal is found in these large-scale analyses, it is likely physiologically significant. However, the strength of these relationships would likely increase if metabolic data were linked more closely to the microhabitats of the individuals studied. Given the gross level of climate analysis, it is noteworthy that a substantial amount of variation (~35%; see Table 3) in both BMR and muscle mass is explained by latitude and mean annual temperature. Future studies should focus on obtaining more detailed indicators of thermoregulatory needs of individuals with associated metabolic measurements.

Despite the coarse nature of the climate data, the relationships between BMR, muscle mass, and thermoregulatory needs are clear. Several other studies have found similar relationships between climatic variables and BMR. For example, Lovegrove (2003) found that variation in the BMRs of small mammals follows a latitudinal gradient. Small mammals living in low latitudes with high mean annual temperatures generally have low BMRs relative to body mass (Lovegrove 2003). In addition, Lovegrove (2000, 2003) found that rainfall (and therefore, possibly ecosystem productivity and energy availability) can have an effect on BMR (see also Bozinovic et al. 2007, 2009; Mueller and Diamond 2001; Withers et al. 2006). It is possible that the effects of rainfall are tied to water availability for thermoregulation in relatively hot environments. Canids also show this pattern of climate-related BMR variation (Careau et al. 2007). Careau et al. (2007) found that canids living in arctic climates have significantly higher BMRs than canids living in hot desert climates, matching the trend found for more distantly related taxa.

Other studies with more restricted phylogenetic groups make the case for a relationship between climate and BMR more compelling. Species of *Peromyscus* that live in deserts have lower BMRs than con-generics living in cooler climates (McNab and Morrison 1963; Mueller and Diamond 2001). Desert hedgehogs also have lower BMRs than species living in wetter, more temperate climates (Schkolnik and Schmidt-Nielsen 1976). Finally, human groups that are native to circumpolar regions have relatively higher BMRs than human groups native to low latitudes (Leonard et al. 2002; Snodgrass et al. 2005). These relatively high BMRs do not appear to be due to acclimatization, since recently arriving populations have relatively lower BMRs than populations native to these regions (see Leonard et al. 2002). Thus, the results of this study are consistent with a great deal of previous research linking variation in BMR to climate. However, here, we show that this variation is tied to the climate-related variation in muscle mass.

Natural selection and BMR

Considerable work has focused on the overall scaling relationship between BMR and body mass. In addition to debates over the exact exponent that best describes this relationship (see Kleiber 1932; West et al. 1997; White and Seymour 2003), several researchers have attempted to explain how these relationships evolved. West et al. (1997, 1999) suggest that BMR scales with body mass raised to the ¾ power because of constraints imposed by the nutrient delivery system (e.g., the vascular system of mammals). Researchers have questioned the validity of their hypothesis, both based on the scaling exponent (White and Seymour 2003), as well as on the assumptions and mathematics that form the basis of their model (e.g., Kozłowski and Konarzewski 2004). Others suggest that BMR scales with body mass to the 2/3 power (see White and Seymour 2003), and that this scaling relationship may be due to the simple loss of heat through the surface area of the body (see Nevill et al. 2004), allometric cascade (Darveau et al. 2002), or as a byproduct of the evolutionary diversification of genome size (Kozłowski et al. 2003). Regardless of why these scaling laws exist, it is important to note that there remains a large amount of variation about any regression line used to describe the relationship between BMR and body mass (see Mueller and Diamond 2001). If there are constraints that determine overall scaling patterns of BMR with body mass, either from the vascular network or from the surface area of the body, then the variation about this line likely represents the action of selection.

In this study, the evolution of variation in mammalian BMRs is related to variation in muscle mass and both are correlated with climatic variables. These results suggest the possibility that selection has acted on mammalian muscle mass to alter BMRs in response to climatic selection pressures. Previous explanations of residual variation in BMR have focused on dietary adaptations (Kurland and Pearson 1986; McNab 1969, 1986, 2007, arboreality (Kurland and Pearson 1986; McNab 1978), and phylogenetic inertia (Eisentraut 1961). However, none of these hypotheses adequately explain residual variation in BMR across large samples of mammals (Snodgrass et al. 2007) and none of the ecological hypotheses detail a mechanism for either reducing or increasing BMR in certain taxa. The organ mass hypothesis tested here provides a proximate mechanism for BMR variation at a given body mass.

The evolution of large muscle mass in response to climate selection pressures may have implications beyond BMR. Muscle does not simply function to generate heat, but it also produces motion and thus, increased muscle mass may have implications for the evolution of locomotor behaviors. For example, maximum aerobic capacity has been linked to locomotor muscle mass (see Weibel and Hoppeler 2005). Additionally, larger muscle mass, mostly concentrated in limb extensors, is linked to higher maximum running speeds (Blanco and Gambini 2007). Interestingly, Lovegrove (2004) found a positive correlation between BMR and maximum running speed, and this correlation may be explained by our results. If relatively low muscle mass is correlated with relatively low BMR, then both should be correlated with relatively low maximum running speeds. These relationships might also suggest that maximum running speed should be tied to latitude, given the results of our study linking variation in muscle mass to geography.

Conclusions

The relationship between variation in muscle mass and variation in BMR suggests that selection has acted on muscle mass to alter BMR at a given body mass. The best evidence suggests that thermoregulation is the selection pressure, and that selection is targeting BMR through its action on muscle mass. These results support previous studies linking variation in BMR to variation in both organ mass and to climatic variables. Here, we show that organ mass and climate are also linked, and that selection appears to alter organ mass to achieve variation in BMR. In addition, because muscle mass produces as much or more heat than all other organs except the splanchnic organs (Schmidt-Nielsen 1997), alterations in muscle mass may produce large gains in heat production without altering visceral organ functions.

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