LETTER

The broad-scale ecology of energy expenditure of endotherms

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Abstract

Energy expenditure in animals scales allometrically with body mass, but residual variation is not well understood. We examine the existing data on field metabolic rates (FMR) in endotherms for the potential role of environmental conditions. Across latitude, mass-corrected FMR of 248 bird and mammal populations fall between two constraint lines: a lower bound that increases towards the poles and is driven by environmental factors and an upper bound that is invariant with latitude and may represent physiological limitations. This triangular pattern can be explained statistically with a multipredictor model that combines environmental conditions and species biology (including phylogeny). Lower environmental temperature and longer day length increase FMR, while taxonomy and diet explain much of the remaining variation. Combined, these effects appear to form a diversity of 'metabolic niches' that overall decreases from the tropics to the poles. The potential of factors related to latitude acting as constraints on the ecology and evolution of metabolic strategies in endotherms is discussed.

INTRODUCTION

Field metabolic rate (FMR), or an animal's rate of energy expenditure in natural conditions, is one of the most important variables in ecology (Brown *et al.* 2004). An animal's metabolic rate determines its resource (e.g. food) requirements (Nagy 2001) and various life-history parameters (e.g. growth rate, lifespan, r_{max}; Brown *et al.* 2004 and references therein). On larger geographical and temporal scales, FMR is a crucial component for understanding processes such as the partitioning of energy across individuals and species (Damuth 1981; Allen *et al.* 2002; Jetz *et al.* 2004), the movement of energy through food webs (e.g. Lindeman 1942; Brown & Gillooly 2003), and even molecular evolution rates (Gillooly *et al.* 2005).

FMR, along with other measures of metabolic rate, scales with mass (*M*) according to the relation:

$$\text{FMR} = B_0 M^b \tag{1}$$

where *b* is the allometric scaling exponent (typically, $b \approx 0.75$, although this is sensitive to the composition of the data set) and B_0 is a mass-independent normalization constant (e.g. Kleiber 1932; Peters 1983; Calder 1984).

Mass-corrected FMR (mcFMR) can be obtained by dividing FMR by M^b (mcFMR = FMR/M^b).

Across mammals and birds, both intrinsic (biological) and extrinsic (environmental) characteristics have been suggested to contribute to variation in mcFMR. Proposed biological characteristics include diet (Nagy 1987; Nagy & Obst 1991; Speakman 1997; Nagy *et al.* 1999; Speakman 2000; but see Harvey *et al.* 1991), life-stage (e.g. Tatner & Bryant 1993; Bryant 1997), activity level (Tatner & Bryant 1993; Bryant 1997), and phylogeny (Nagy 1987; Nagy & Obst 1991; Speakman 1997; Nagy *et al.* 1999). Relevant external factors include latitude (Speakman 1997, 2000; Piersma *et al.* 2003), temperature (Tatner & Bryant 1993; Bryant 1997; Speakman 1997, 2000), day length (Bryant 1997), season (e.g. Nagy 1987; Weathers & Sullivan 1993; Corp *et al.* 1997; Speakman 1997), habitat (i.e. desert, marine; Nagy 1987; Nagy & Obst 1991; Nagy 1994; Nagy *et al.* 1999), and ecosystem productivity (Mueller & Diamond 2001). While these studies implicate an array of potential determinants of FMR, a unified approach to examine their combined effects on the broad-scale variation in endotherm FMR is still lacking (but see Speakman 2000 for small mammals).

Here, we present a synthetic analysis of extrinsic and intrinsic effects on FMR of endotherms. Our goal is to understand how broad-scale climate variation and functional diversity combine to influence the observed macroecological pattern in energy expenditure. Based upon findings of ecological physiology, we make the following predictions. First, because endotherms rely on metabolic heat production in order to maintain a constant body temperature (Scholander *et al.* 1950; Calder 1984), we predict that mass-corrected FMR will increase with decreasing environmental temperature (Tatner & Bryant 1993; Bryant 1997; Speakman 1997, 2000). Secondly, as longer day lengths represent longer potential activity periods for diurnal species (Aschoff 1969; Daan & Aschoff 1975) and (above 12 h) correspond to increasingly short summers, when many organisms are expending energy at high rates for reproduction and preparation for winter, they should result in increased FMR (Bryant 1997). Accounting for phylogeny and for the finding that high metabolic rates tend to correlate with diets rich in extractable energy and nutrients (e.g. McNab 1986; Speakman 2000), we test these predictions using the available data for mammals and birds. In addition, we test the idea that FMR is positively correlated with net primary productivity (NPP) of the animal's ecosystem (Mueller & Diamond 2001). Finally, we consider how broad-scale environmental variation may place ecological and evolutionary constraints on the occurrence of endotherm energetic strategies across large geographical scales.

MATERIALS AND METHODS

We compiled data (Appendix S1) on body mass (M; g) and FMR (kJ day^{-1}) measured using the doubly labelled water method (Lifson & McClintock 1966; reviewed in Butler *et al.* 2004) for 112 mammal and 136 bird populations representing 86 and 96 species, respectively. Some species had been measured in multiple seasons and/or study locations, and we represented these with multiple points (four species had 5–10 data points, nine species 3–4 points, 21 species 2 points, and 148 had only a single point). Study locations ($n = 147$) and the corresponding latitude–longitude coordinates were obtained from the original papers and maps. When not given in the original paper, average temperatures for the months during which each study was conducted were obtained from a global model with 0.5° spatial resolution (Legates & Wilmott 1990). Day length for the time of study was calculated based upon the latitude and time of year according to the formula given by Campbell & Norman (1998). We used day length as a variable to capture (i) season (< 12 h is winter, > 12 h is summer), (ii) seasonality (the magnitude of deviation from 12 h indicates the extremity of seasonality), and (iii) the potential time for activity available to diurnal species (birds: $n = 133$ of 134;

mammals, $n = 58$ of 112). We calculated NPP as an 18-year average of annual values from the DOLY global model (original spatial resolution 0.5°; Woodward 1995). Study site NPP values range from 0.01 to 14.53 t C ha^{-1} year^{-1}. We grouped species into dietary classes according to the approximate energy content of their food (see Karasov 1990); species were classified as nectarivores, carnivores (including insectivores), herbivores (including granivores and frugivores), or omnivores. The data set included some migrant bird populations ($n = 44$ of 134), but their exclusion did not qualitatively affect the results. Phylogenetic trees (Appendix S2) were modified from those of Nagy *et al.* (1999) according to more recent phylogenies (mammals: Kirsch *et al.* 1995; Bininda-Emonds *et al.* 1999; Speakman 2000; Wroe *et al.* 2000; Murphy *et al.* 2001; Jones *et al.* 2002; DeBry 2003; Horovitz & Sanchez-Villagra 2003; Herron *et al.* 2004; birds: Lauk 2002).

In studies examining variation in mass-corrected FMR, assumptions regarding the value of b (eqn 1) have the potential to influence results. Traditionally, b has been estimated through regression analysis with body size as a covariate (FMR $\propto M^x$). This approach 'mass-corrects' metabolic rate by using the value for b that is characteristic for, but also sensitive to, the particular data set. In the case of FMR, the parameter estimates may be affected by the data bias towards small-sized species and uneven distribution of studies among phylogenetic lineages. An alternative that overcomes these data biases is to correct metabolic rate for mass using a value of b that is typical for larger data sets or theoretically predicted. Although the exact scaling of metabolic rate has been subject to debate – regarding both its measurement and supporting biological mechanisms – both theoretical (West *et al.* 1997, 1999) and empirical (Savage *et al.* 2004) basis for a 3/4 power scaling (FMR $\propto M^{0.75}$) are strong. Thus, in this study we use $b = 3/4$ to estimate a mass-corrected value, although we also present some results from an M^x model.

We first examine the importance of individual variables on the broad-scale variation in energy expenditure using (log-transformed) mcFMR (assuming $M^{0.75}$) as the response variable. The results for the same analyses after statistical correction for body size (M^x) are qualitatively similar and we do not present them. As log[mcFMR] displays a distinctly triangular pattern with both latitude and environmental temperature, we used quantile regression (Koenker & Bassett 1978; Cade *et al.* 1999) to quantify the upper and lower boundaries of these patterns and thereby to test for constraints that may operate at the high or low end of data values. We used the quantreg package version 3.31 implemented for R (for further information see http://www.econ.uiuc.edu/~roger/research/rq/rq.html) and tested the slopes of focal quantiles in steps of 0.05 from $tau = 0.05$ to $tau = 0.95$. The slopes showed a consistent trend

across quantiles, and we chose the extreme values of *tau* to illustrate the bounds of the examined relationships.

In order to examine joint effects of more than one variable, we employed multipredictor linear models. Before detailing these, we discuss the role of phylogeny in this analysis. Mass-corrected FMR of two populations may be similar for two main reasons: (i) they face similar environmental demands and expend energy at the rate required to meet these, or (ii) they are closely related and expend energy at rates influenced by phylogenetic inertia, in which case they should not be considered statistically independent (Felsenstein 1985; Harvey & Pagel 1991). Without knowing the rate at which FMR is adjusted to the environment relative to that at which phylogenetic divergence occurs, there is no *a priori* reason to assume that the effects of either environment or phylogeny should be given precedence in statistical analysis. The order in which these factors are accounted for can be important, as any variation correlated with both environment and phylogeny would be attributed to the factor that is accounted for first (McNab 2002).

Considering this, we performed two types of analysis: cross-species and phylogenetic. First, we developed two conventional cross-species multipredictor models: one in which log[mcFMR] is the response variable and one in which we use log[FMR] as the response variable and include log[*M*] as a covariate. The final model included temperature, day length and diet. We also tested the effect of NPP (both linear and quadratic terms) on mcFMR, but because this was not significant and because NPP is highly collinear with temperature, we did not include it. In order to ensure that the most parsimonious model was selected, we confirmed our final minimum set of model parameters by checking that attempted stepwise variable exclusion using the Akaike Information Criterion was unsuccessful. We tested the residuals of both models for a phylogenetic signal by using a χ-statistic to compare variance in the contrasts calculated for the real tree to that of 100 randomized trees – a method simplified from that described by Blomberg *et al.* (2003).

Second, we used Felsenstein's (1985) method of independent contrasts to test for effects of diet, temperature, and day length after accounting for phylogeny. Contrasts for log[mcFMR], log[*M*], log[FMR] and diet (classified as herbivore/omnivore or carnivore/nectarivore) were calculated for a tree with branch lengths arbitrarily set at 1, and a 'star phylogeny' (internal branch lengths set to 0) was used to compute contrasts for the environmental variables (following Lovegrove 2003). Again, we ran two multipredictor models, one in which log[mcFMR] is the response variable and one in which we use log[FMR] as the response variable and include log[*M*] as a covariate. All phylogenetic analyses were performed using the PDAP package (Midford *et al.* 2003) implemented in Mesquite version 1.01 (Maddison & Maddison 2004).

RESULTS

The FMR of both mammals and birds was strongly correlated with body size, M (birds: FMR = 1.02 $M^{0.68}$, $t_{(b=0)} = 46.00$, $P < 0.001$, $n = 132$; mammals: FMR = 0.68 $M^{0.72}$, $t_{(b=0)} = 42.61$, $P < 0.001$, $n = 111$). The scaling exponents were not significantly different (interaction between class membership and body size: $F_{1,241} = 2.53$, $P = 0.11$). The independent contrasts analysis gave similar results: (birds: FMR = 1.02 $M^{0.67}$, $t_{(b=0)} = 25.61$, $P < 0.001$, $n = 131$; mammals: FMR = 0.68 $M^{0.73}$, $t_{(b=0)} = 26.21$, $P < 0.001$, $n = 110$).

Examining the variation of mcFMR in relation to latitude, we found a distinctly triangular pattern (Fig. 1) with uniformly high mcFMR values at high latitudes and much greater variation near the equator. This was supported by results from quantile regression. The 0.95th quantile (*tau* = 0.95) of mcFMR (i.e. the line that separates the highest 5% of mcFMR values from the rest) showed no significant latitudinal gradient for either birds or mammals (birds: $t = 0.64$, $P = 0.52$; mammals: $t = 1.25$, $P = 0.21$). In contrast, the 0.05th quantile (*tau* = 0.05) had a significantly positive slope (birds: $t = 3.15$, $P < 0.01$, mammals: $t = 3.48$, $P < 0.001$). Across all latitudes, birds reached higher mcFMR values than mammals (intercept for *tau* = 0.95: birds: 1.05, mammals: 0.82; difference: $t = 3.40$, $P < 0.001$).

The increase of mcFMR with latitude was reflected in its relationship with environmental temperature (Fig. 2). High temperatures allowed the full range of mcFMR values (at least in birds), whereas only relatively high mcFMRs occurred at low temperatures. The 0.95th quantile of birds
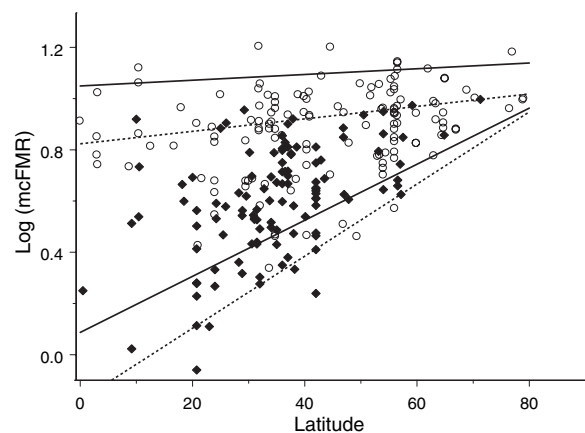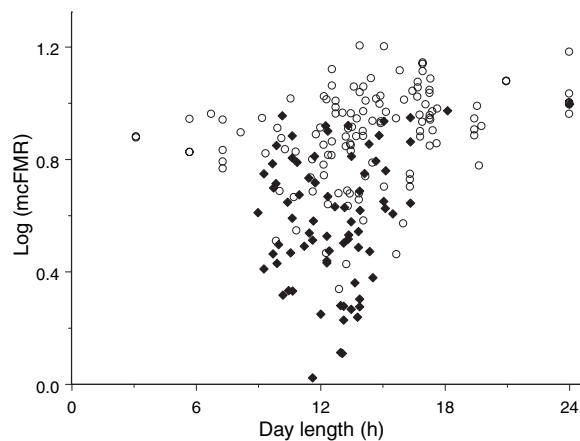

Figure 1 The latitudinal gradient in (log) mass corrected field metabolic rate (mcFMR = FMR/$M^{3/4}$) for birds (open circles) and mammals (solid diamonds). Data from northern and southern hemisphere are combined. The lines indicate the 0.95th and 0.05th quantile regression estimates of the slope of the relationship (solid: birds, dashed: mammals).
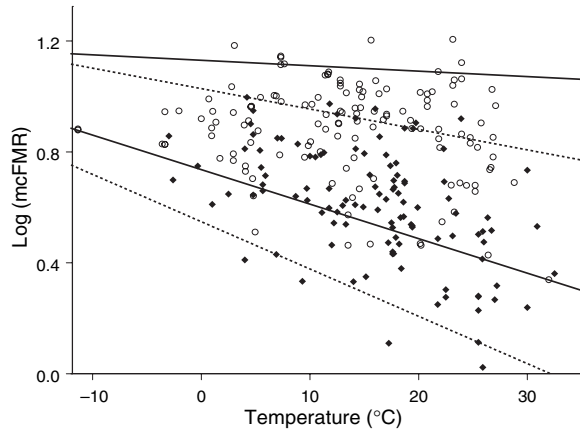
Figure 2 The effect of mean environmental temperature on (log) mass corrected field metabolic rate (mcFMR = FMR/$M^{3/4}$) for birds (open circles) and mammals (solid diamonds). The lines indicate the 0.95th and 0.05th quantile regression estimates of the slope of the relationship (solid: birds, dashed: mammals).

did not vary with temperature ($t = -0.70$, $P = 0.49$), while the same quantile for mammals had a negative slope ($t = -3.08$, $P < 0.01$). The slopes of the 0.05th quantiles were negative in both groups (birds: $t = -2.66$, $P < 0.01$; mammals: $t = -2.64$, $P < 0.01$). The relationship between mcFMR and day length was more complex; maximum variation in mcFMR occurred at day lengths of approximately 12 h, and mcFMR increased with the deviation of day length from this value (Fig. 3).

We present two multipredictor models, one in which we used mcFMR as the independent variable (assuming a $M^{0.75}$ relationship) and one in which we modelled the effect of body size statistically (M^x) (Table 1). As there was no

indication that mcFMR was positively correlated with NPP in either mammals ($t = -1.96$, $P > 0.05$, $n = 80$) or birds ($t = -0.07$, $P = 0.95$, $n = 70$), we did not include NPP as a variable in our multiple regression model. All variables examined – that is, class, mass (M^x model only), diet, temperature, and day length – but none of their interactions, had a significant effect on FMR (Table 1). Both models were highly significant (M^x: $F_{7,195} = 733.5$, $P < 0.001$, $r^2 = 0.96$; $M^{0.75}$: $F_{6,195} = 43.18$, $P < 0.001$, $r^2 = 0.57$). In the M^x model, body size had the highest predictive power of all variables and had a strongly positive effect (Fig. 4a; $P < 0.001$). Birds had higher FMR than mammals (Fig. 4b; $P < 0.001$). Controlled for all other variables, nectarivores had higher FMR than all other trophic groups (Tukey *post hoc* comparisons; all $P < 0.001$), and carnivores were statistically higher than herbivores ($P < 0.01$). Omnivores did not differ significantly from herbivores or carnivores. Both temperature and day length had significant effects on FMR (Table 1, Fig. 4d,e; all $P < 0.001$). In the multi-predictor model these relationships appeared more linear than in the single-predictor analysis (compare Figs 2 and 4d, Figs 3 and 4e), yet a slight tendency for higher variance in some data ranges remained, notably at higher temperatures. The residual variation failed to show any relationship with the originally evaluated latitude (Fig. 5); adding latitude to the multipredictor model did not explain any additional variation ($F_{1,194} = 0..45$, $P = 0.51$). The residuals displayed a phylogenetic signal (mammals: M^x: $z = -2.61$, $P < 0.01$; $M^{0.75}$: $z = -2.56$, $P < 0.01$; birds: M^x: $z = -5.61$, $P < 0.01$; $M^{0.75}$: $z = -5.82$, $P < 0.01$).

When phylogeny was given primacy (i.e. multipredictor models using independent contrasts), the effects of diet were significant only in the mammal M^x and bird $M^{0.75}$ models (mammals: M^x: $t = 2.41$, $P = 0.02$, d.f. = 67; $M^{0.75}$: $t = 1.23$, $P = 0.22$, d.f. = 69; birds: M^x: $t = 1.49$, $P = 0.13$, d.f. = 120; $M^{0.75}$: $t = -2.30$, $P = 0.02$, d.f. = 122), and the significance of environmental factors was also reduced. Temperature was significant for mammals (M^x: $t = -4.34$, $P < 0.01$, d.f. = 67; $M^{0.75}$: $t = -4.07$, $P < 0.01$, d.f. = 69) but not for birds (M^x: $t = -0.69$, $P = 0.49$, d.f. = 120; $M^{0.75}$ $t = -1.30$, $P = 0.20$, d.f. =122). Likewise, day length was significant for mammals (M^x: $t = 2.59$, $P < 0.01$, d.f. = 67; $M^{0.75}$: $t = 2.72$, $P = 0.01$, d.f. = 69) but not for birds (M^x: $t = 1.26$, $P = 0.21$, d.f. = 120; $M^{0.75}$: $t = 1.17$, $P = 0.25$ d.f. = 122).

DISCUSSION

Mass-corrected FMRs of endotherms fall into a triangular space consisting of an upper bound that is invariant with latitude and a lower bound that increases with increasing latitude (Fig. 1). While there is a paucity of FMR data from the tropics that results in a poorly defined lower bound

Figure 3 The effect of day length on (log) mass-corrected field metabolic rate (mcFMR = FMR/$M^{3/4}$) for birds (open circles) and mammals (solid diamonds).

Predictor	M^x				$M^{0.75}$			
	b	SE	F	P-value	b	SE	F	P-value
Intercept	0.7582	0.0482			0.6946	0.0493		
Group								
Birds	0.0763	0.0137	31.14	***	0.0902	0.0142	40.35	***
Mammals	−0.0763	0.0137			−0.0902	0.0142		
log (Mass) (g)	0.6979	0.0107	4266.23	***	0.7500			
Diet								
nectarivores	0.1862	0.0375	12.28	***	0.2333	0.0389	15.41	***
carnivores	0.0017	0.0200			0.1865	0.0231		
omnivores	−0.0482	0.0283			−0.2520	0.0207		
herbivores	−0.1397	0.0269			−0.1678	0.0281		
Temperature (°C)	−0.0075	0.0013	33.96	***	−0.0079	0.0014	33.55	***
Day length (h)	0.0180	0.0031	34.35	***	0.0156	0.0032	23.08	***

Table 1 Multi-predictor model of log-FMR and log-mcFMR

***Statistically significant at $P < 0.001$.

Estimates of coefficients b and results of t-test for H$_0$: $b = 0$ are given.

Parameters were estimated for two separate models: in the M^x model, the coefficient of log[Mass] was estimated statistically (response variable: log[FMR]), in the $M^{0.75}$ model, the response data were mass-corrected by division by $M^{0.75}$ (response variable: log[mcFMR]) M^x: $F_{7,186} = 574.4$, $P < 0.001$, $R^2 = 0.96$; $M^{0.75}$: $F_{6,186} = 40.34$, $P < 0.001$, $R^2 = 0.57$.
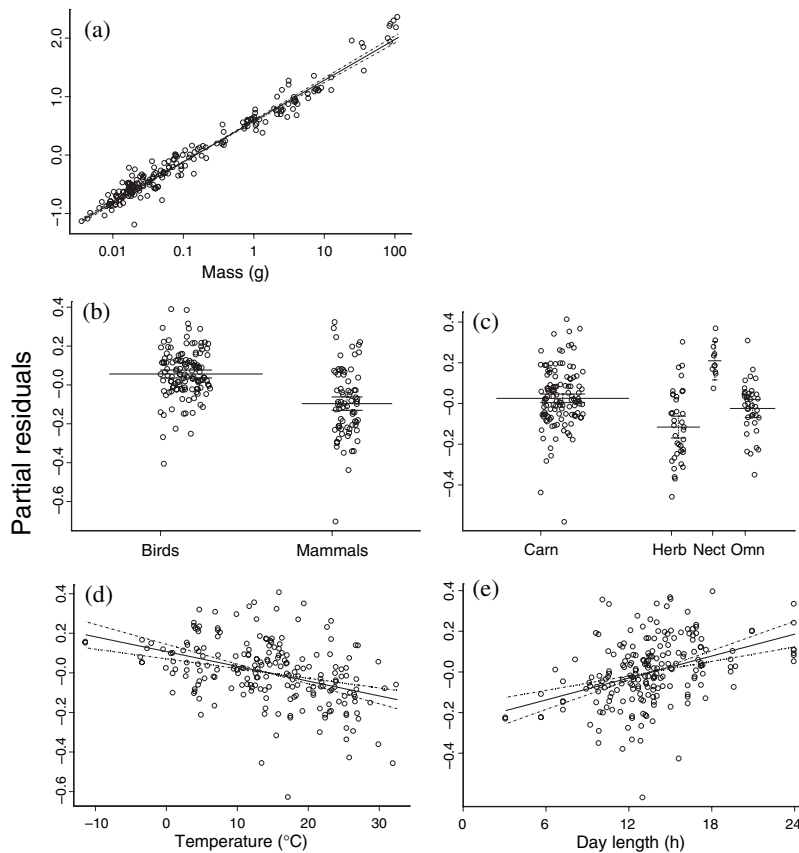
Figure 4 Partial residual plots for the M^x model presented in Table 1, including the partial fit (solid line) and its 95% confidence interval (dashed line). Plotted are $r_i + b_k x_{ik}$ vs. x_{ik}, where r_i is the ordinary residual for observation i, x_{ik} is corresponding observation of variable k, and b_k is the regression coefficient estimate for variable k. Partial residuals are plotted for (a) log-mass, (b) taxonomic class (x-axis spacing is arbitrary), (c) diet (x-axis spacing is arbitrary), (d) environmental temperature, and (e) day length.

below 20° latitude, we argue that the proposed constraint space can be expected to hold there for two reasons. First, data for temperatures and day lengths typical of tropical regions (c. 20–30 °C and 12 h respectively) are plentiful and suggest that the greatest variations in mcFMR occur at these values (Figs 2 and 3). Second, tropical mammals (Lovegrove
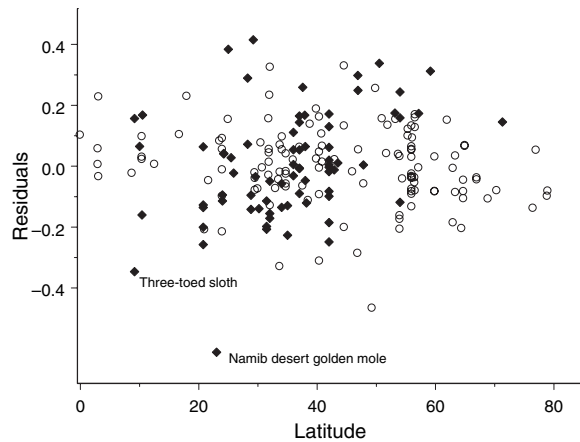
Figure 5 The residual (response minus fitted) variation in log-FMR after accounting for body size, temperature, day length, taxonomic class, and diet (see full M^x model; Table 1) across latitude for birds (open circles) and mammals (solid diamonds). Data from northern and southern hemisphere are combined. When the labelled points are excluded, latitude fails to explain any additional variation in FMR.

2000, 2003) and birds (Weathers 1979) tend to have low basal metabolic rates (BMR), and because BMR tends to be correlated with FMR (e.g. Speakman 2000), this should result in low mcFMRs. Similarly, on the basis of circumstantial evidence, the tropics are home to a number of sedentary, slow-paced mammals (e.g. sloths, armadillos, echidnas, pangolins, anteaters) and birds (e.g. flightless rails, megapods) that most likely have low mcFMRs. Thus, we expect that inclusion of more tropical species would fill in the data-poor region at low mcFMRs and low latitudes. Nevertheless, we caution that the described relationships are poorly supported for tropical species and suggest that more FMR measurements on tropical species would be of particular value for understanding global patterns of endotherm energetics.

Across the latitudinal gradient, birds tend to have higher FMR than mammals (Table 1, Fig. 4a; Bartholomew 1982; Nagy *et al.* 1999). The relationships between latitude or other environmental predictors and mcFMR take similar shapes in both taxa, with the pattern in birds simply shifted upwards (Figs 1–3), suggesting that similar mechanisms control the observed patterns for both taxa.

Our analysis suggests that environmental temperature and day length, but not annual NPP, drive the increase of the lower bound of mcFMR with latitude (Figs 2–4; Table 1). The increase in minimum mcFMR with temperature (Figs 2 and 4d) is consistent with previous analyses of FMR in birds (Tatner & Bryant 1993; Bryant 1997; Piersma *et al.* 2003) and small mammals (Speakman 1997, 2000), and is to be expected based on the mechanics of heat production and

loss in an endotherm that is maintaining a stable body temperature. Specifically, as environmental temperature decreases, endotherms may (i) have elevated BMRs (Weathers 1979; Lovegrove 2003), which decreases their lower critical temperature (i.e. the environmental temperature at which metabolism must increase to compensate for heat loss) and/or (ii) increase energy expenditure when environmental temperature falls below their lower critical temperature (Scholander *et al.* 1950; Calder & King 1974; McNab 2002). Both options require the observed increase in FMR with decreasing temperature. Conversely, at high environmental temperatures, endotherms must decrease their rate of metabolic heat production and/or increase their rate of heat loss in order to prevent their body temperature from increasing above critical limits. Thus, endotherms adapted to hot environments (specifically deserts) may have reduced FMRs and BMRs (e.g. Lovegrove 2000; Tieleman & Williams 2000; Lovegrove 2003; Tieleman *et al.* 2003), possibly in order to minimize the need for evaporative cooling (Tieleman & Williams 2000; Tieleman *et al.* 2003); however, our analysis shows that, although the lowest observed mcFMRs do occur in hot environments, high environmental temperatures do not necessarily result in low mcFMRs. In addition to its response to temperature, mcFMR increases with day length (Fig. 4e, Table 1), which explains why mcFMRs of the long days of summer are equal to (or even higher than) those of the short days of winter (Fig. 3). This may result from increased intensity of activity and/or increased time spent in activity. First, the energetic demands of activity are generally greater during the long days of summer, when endotherms are typically breeding and preparing for winter, than during the winter. This effect may be magnified at high latitudes, where short summers force endotherms to concentrate these energetically costly activities into a few months. Second, for diurnal species, day length is closely correlated with time spent in activity (Aschoff 1969; Daan & Aschoff 1975). This also should result in high FMR at long day lengths, as has been suggested before (Bryant 1997). Finally, we note that the lack of positive correlation between annual regional NPP and FMR suggests that total food availability may have only minor effects on broad-scale patterns of energy expenditure. This appears contrary to the idea that the food limitation caused by low primary productivity results in low metabolic rates (extrinsic limitation hypothesis; e.g. Schoener 1971; Mueller & Diamond 2001), but may warrant further investigation given the strong inverse correlation between seasonality and time over which net productivity actually occurs. Thus, the lower limit of mcFMR is high at high latitudes where winters are cold and summer days are long, and more variation in FMR occurs at low latitudes, where day lengths are nearly constant and environmental temperatures are warm. The finding that environmental conditions dictate minimum

feasible mcFMR implies that range boundaries may occur where the combined costs of thermoregulation (driven by temperature) and other necessary activities (partially driven by day length) become too great (Root 1988; Bozinovic & Rosenmann 1989; Repasky 1991; Canterbury 2002).

The upper data boundary for FMR in mammals and birds behaves differently from the lower boundary in that it is independent of latitude for both mammals and birds (Fig. 1). This suggests that there is some maximal physiological limit to the average daily energy expenditure of a free-living endotherm of a given body size. Endotherms can increase their ability to meet metabolic demands by increasing the size or capacity of their energy-supplying organs (e.g. heart, lungs, stomach, intestines, liver), thereby increasing their maximum FMR (e.g. Toloza *et al.* 1991; Hammond & Diamond 1994). While it is not clear whether FMR will first be limited by these organs (central limitation) or by other factors (peripheral limitation) (e.g. Hammond & Diamond 1997; Speakman 2000; Bacigalupe & Bozinovic 2002), inherent limits to the relative size of these organs imply that a ceiling on FMR must exist. We propose that this limit represents the upper bound of the observed pattern in mcFMR.

While environmental conditions and physiological limits shape the limits to mcFMR, variation within this playing field occurs on both ecological and evolutionary time scales. On an ecological scale, the position of endotherm within the constraint space is controlled by factors such as life-stage (e.g. Tatner & Bryant 1993; Bryant 1997), breeding status (e.g. Scantlebury *et al.* 2002) and geographical position (for migrants). Such factors may cause significant seasonal movements within the constraint space – in keeping with the idea that animals do not always operate at their maximum rate ('increased demand hypothesis'; Herbers 1981), yet endotherms may face pressure to time activities and allocate energy so as to expend energy at a rate within the constraint space ('reallocation hypothesis'; King & Murphy 1985; Weathers & Sullivan 1993). On an evolutionary level, the existence of a phylogenetic signal in the data confirms that metabolic rate is at least partially inherited (Wikelski *et al.* 2003), either directly or because phylogenetically inherited characteristics influence a population's position within the constraint space. An example of such a characteristic is diet, which has a significant influence on mcFMR (Fig. 4c, Table 1), with mcFMR tending to be correlated with metabolizable energy content of the diet (nectarivores > carnivores > herbivores). Likewise, inherited characteristics such as life-history strategies, degrees of ecological specialization and predator avoidance tactics may influence metabolic rate (e.g. Lovegrove 2000). Thus, the strategy of an endotherm within a community exposed to certain environmental conditions – *i.e.* its ecological niche – determines its position within the constraint space, which

we refer to as a 'metabolic niche' in order to emphasize the intimate connection between an animal's metabolic rate and its intrinsic characteristics. The range of metabolic niches decreases with increasing latitude (Fig. 1), suggesting that low latitudes may allow a greater variety of feasible ecological strategies than high latitudes. This, along with the principle of competitive exclusion (Gause 1934), may contribute to the well-recognized decrease in species specialization and diversity associated with increasing latitude.

In summary, our findings suggest that a metabolic constraint space across the latitudinal gradient – consisting of a lower bound that increases with decreasing environmental temperature and with increasing day length and an upper bound representing a fundamental physiological limit to the rate at which endotherms can process energy – may limit the realized ecological niches and geographical distributions of endotherms. These findings link environmental effects on physiology and behaviour of endotherms at the level of the individual to their ecology and biogeography at the scale of the globe.

SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE723/ELE723sm.htm

Appendix S1 Data on mass, FMR, diet and environmental conditions for free-living bird and mammal populations.
Appendix S2 Phylogenetic trees (i) birds, and (ii) mammals.

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