

LETTER

Expenditure freeze: the metabolic response of small mammals to cold environments

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Abstract

There is renewed focus on the ecological determinants of animal metabolism and recent comparative analyses support the physiological expectation that the field metabolic rate (FMR) of homeotherms should increase with declining ambient temperature. However, sustained elevation of FMR during prolonged, seasonal cold could be prevented by intrinsic limits constraining FMR to some multiple of basal metabolic rate (BMR) or extrinsic limits on resource abundance. We analysed previous measures of mammalian FMR and BMR to establish the effect of ambient temperature on both traits and found no support for intrinsic limitation. We also measured the FMR of a northern population of red squirrels (*Tamiasciurus hudsonicus*) exposed to ambient temperatures much colder than all but one previous study of mammal FMR. These measurements revealed levels of energy expenditure that are, unexpectedly, among the lowest ever recorded in homeotherms and that actually decrease as it gets colder. Collectively, these results suggest the metabolic niche space of cold climate endotherms may be much larger than previously recognized.

Keywords

Boreal forest, cost of living, doubly labelled water, energetics, nests, Sciuridae, thermoregulation, winter, Yukon.

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INTRODUCTION

As a measure of the energy expenditure of free-ranging animals, field metabolic rate (FMR) represents the energy throughput maintained by animals under natural circumstances (Speakman 2000). Because FMR reflects both the amount of energy individuals need to acquire from the environment and the amount of energy metabolized for maintenance, growth and reproduction, it provides a potential mechanistic link between individual, population and ecosystem processes (Brown *et al.* 2004). The advent

and application of the doubly labelled water technique (Lifson *et al.* 1955, Nagy 1983, Speakman 1997), which estimates the carbon dioxide production of free-ranging animals based on the differential washout of injected hydrogen and oxygen isotopes, has resulted in a proliferation of FMR measures across an impressive array of taxa and environments (reviewed in Nagy *et al.* 1999; Speakman 2000; Anderson & Jetz 2005; Nagy 2005).

Several comprehensive reviews have established a suite of biotic and abiotic variables as general predictors of inter-specific variation in FMR. Foremost among these is body

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mass; allometric models of FMR variation typically have a greater intercept and slightly different exponent than basal metabolic rate (BMR) models (Nagy *et al.* 1999; Speakman 2000; Anderson & Jetz 2005; Nagy 2005). Once mass-related variation in FMR is statistically accounted for, additional significant predictors typically include phylogeny, diet, habitat and ambient temperature (Speakman 2000; Anderson & Jetz 2005; Nagy 2005). Anderson & Jetz's (2005) recent broad-scale review of doubly labelled water studies found ambient temperature during the sampling interval (typically measured at a nearby weather station) to be among the strongest and most consistent environmental predictors of FMR in birds and mammals, with the highest levels of expenditure coinciding with the coldest ambient temperatures. A negative relationship between ambient temperature (T_a) and FMR is not surprising, given that first principles of thermal exchange predict the metabolic rate of a homeotherm will increase with decreasing T_a along a slope equal to thermal conductance (McNab 2002). Nevertheless, the significance and consistency of the effect of T_a on FMR, despite the capacity of many endotherms to occupy thermally buffered microenvironments (e.g. nests, subnivean tunnels, etc.) and to respond physiologically to declining temperatures in various ways (Heldmaier 1989; Lovegrove 2005), indicates that most endotherms either choose to or are forced to thermally engage with prevailing T_a across the range documented.

When considered in a broader physiological or ecological context, perpetual increases in FMR in response to increasingly low ambient temperatures become, at some point, biologically implausible. As suggested by Anderson & Jetz (2005) and many others (e.g. Drent & Daan 1980; Hammond & Diamond 1997; Speakman 2000), increases in FMR may be intrinsically limited by central or peripheral energy processing constraints. If BMR (the metabolic rate of a resting, post-absorptive endotherm measured within its thermoneutral zone; McNab 2002) largely represents the cost of maintaining the machinery involved in the acquisition, distribution and expenditure of energy (e.g. gut, muscle, liver, heart) and so is a reliable index of the size and capacity of these systems (e.g. Daan *et al.* 1990, but see Speakman *et al.* 2004), then a steeper slope for FMR vs. T_a than for BMR vs. T_a [i.e. metabolic scope (FMR/BMR) increases with declining T_a] would indicate that energy throughput is increasing faster than the capacity to ingest and process energy. However, if energy processing capacity increases in concert with energy throughput, as indicated by a parallel increase in BMR and FMR and constant metabolic scope with declining T_a , then intrinsic constraints are less likely to occur, unless they act directly on FMR independent of BMR (*sensu* Anderson & Jetz 2005). Cold climate elevation of FMR in nature should also frequently be prohibited by extrinsic limits involving the abundance and accessibility of food resources in the environment (Tinber-

gen & Verhulst 2000; Speakman *et al.* 2003), given that high rates of energy expenditure must be compensated by high rates of energy intake.

Although the observed relationship between T_a and FMR is strongly negative across the entire range documented (Anderson & Jetz 2005), there is a notable paucity of FMR measures obtained under climatic conditions below 0 °C. In fact, although free-ranging terrestrial mammals present at high elevations and high latitudes frequently operate at temperatures well below -20 °C, the coldest mammalian FMR measure included in Anderson & Jetz's (2005) analysis was at an ambient temperature of -3 °C, and only three of 112 mammal studies involved temperatures < 0 °C. The only additional FMR study we are aware of that has been conducted at colder T_a s is that of Holleman *et al.* (1982) on five, free-ranging red-backed voles (*Clethrionomys rutilus*) exposed to -23 °C during an Alaskan winter. As a result, it is presently unknown if the general, negative relationship between metabolism and T_a continues, reaches an asymptote, or even reverses at low temperatures, and if such changes occur, where and why they do so.

In the present study, we evaluate three alternative hypotheses regarding the response of mammalian FMR to cold ambient temperatures. One possibility is that FMR continues to increase at low ambient temperatures, facilitated by concordant increases in BMR that maintain metabolic scopes (i.e. FMR/BMR) at physiological sustainable levels. A second possibility is that FMR plateaus at low ambient temperatures, due to intrinsic constraints that impose maximum mass-specific levels of FMR independent of BMR. A third possibility is that FMR decreases at low ambient temperatures, facilitated by behavioural avoidance of cold exposure and possibly reduced BMR. We evaluate the effect of air temperature on the metabolic scope of small mammals in general by comparing how inter-specific variation in BMR, FMR and measured metabolic scope vary with T_a . We then present new data on the FMR of North American red squirrels (*Tamiasciurus hudsonicus*) while exposed to very cold ambient temperatures. At 200–250 g body mass, this species is the smallest boreal mammal active above the snow in winter, and therefore should face very high thermoregulatory requirements due to their high surface area to volume ratios (Pruitt & Lucier 1958). By studying a northern population of red squirrels during mid-winter, we were able to examine the energetic impact of ambient temperatures 20 °C colder than any previous mammal FMR study, with the exception of Holleman *et al.* (1982).

MATERIALS AND METHODS

We obtained BMR data from Table 3 of Lovegrove (2003) and FMR data from Appendix S1 of Anderson & Jetz

(2005). Both of these studies report significant negative relationships between air temperature and metabolic rate, with the BMR analysis based on climatic norms such as average annual air temperature ($T_{a \text{ avg ann}}$) and the FMR analysis based on prevailing air temperature during a doubly labelled water sampling interval ($T_{a \text{ FMR}}$). Both studies also report significant influence not only of additional variables, most notably body mass and taxonomy, but also of biogeographical zone, rainfall variables and day length. However, because our present study focuses on the influence of temperature on mammalian metabolism, and both Lovegrove (2003) and Anderson & Jetz (2005) found body mass, phylogeny and air temperature to be the strongest predictors of inter-specific variation in metabolic rate, here we focus on the influence of only these variables.

To compare how BMR and FMR vary with air temperature, and thus to generate a broad-scale prediction of how metabolic scope (FMR/BMR) should vary across climatic gradients, we used multiple regression analysis to evaluate how \log_{10} BMR (converted to kJ day^{-1} , assuming respiratory quotient (RQ) = 0.8) varies with \log_{10} body mass (g) and $T_{a \text{ avg ann}}$ ($^{\circ}\text{C}$) and how \log_{10} FMR (kJ day^{-1}) varies with \log_{10} body mass (g) and $T_{a \text{ FMR}}$ ($^{\circ}\text{C}$). We then compared the slopes of the temperature regression coefficients from the two regression equations following Zar (1999). We also compared the effects of temperature on inter-specific variation in BMR and FMR based on Felsenstein's (1985) method of independent contrasts calculated using the PDAP software package (Midford *et al.* 2002) implemented in Mesquite version 1.05 (Maddison & Maddison 2004). We used the same phylogenies for the BMR and FMR data sets as presented by the original authors (Lovegrove 2003; Anderson & Jetz 2005). Effects of body mass were statistically accounted for following procedures described by Garland *et al.* (1992), permitting comparison of the mass- and phylogenetically-independent effects of T_a variation on BMR and FMR using regression through the origin.

To evaluate how measured metabolic scope varies with T_a , we identified 23 mammal species in the two data sets whose FMR and BMR had been measured in the same region ($\pm 3^{\circ}$ latitude, $\pm 3^{\circ}$ longitude). We converted whole animal BMR values (presented by Lovegrove 2003 in $\text{mL O}_2 \text{ h}^{-1}$) to kJ day^{-1} (assuming RQ = 0.8), then divided these into whole animal FMR (presented by Anderson & Jetz 2005 in kJ day^{-1}) to obtain an estimate of metabolic scope. If multiple FMR values were available for a given species, we randomly selected one of these measures and its associated $T_{a \text{ FMR}}$ for inclusion in statistical analysis. We then used ordinary least squares regression to evaluate whether metabolic scope varied significantly with $T_{a \text{ FMR}}$, with body mass included as a covariate if significant. We also assessed whether metabolic scope varied with $T_{a \text{ FMR}}$

when phylogenetic relationships were account for, using Felsenstein's (1985) method of independent contrasts and the phylogeny presented by Anderson & Jetz (2005).

We studied a free-ranging population of North American red squirrels in south-western Yukon, Canada (61° N, 138° W) where $T_{a \text{ avg ann}}$ is -3.8°C (Burwash Yukon Environment Canada Station, <http://climate.weather.office.ec.gc.ca/>). This population has been the subject of long-term research by SB and collaborators, and details of research methodology, the study site, and this population's ecology and evolutionary biology are published elsewhere (Berteaux & Boutin 2000; Humphries & Boutin 2000; McAdam & Boutin 2003). Red squirrels are conifer cone specialists, relying on a larger hoard of cones clipped from trees in late summer/autumn to support winter and spring energy requirements (Steele 1998). Cones are stored in underground tunnels contained within middens, which serve as a focal point of each individual's territory. Territories are food-based, consisting of one to several middens and surrounding cone-bearing trees, and are maintained year-round by both sexes. Red squirrels do not hibernate and are not known to express torpor (Pauls 1978a). Instead, they survive winter at euthermic body temperatures by relying on food hoarded in their midden and occupying well-insulated tree nests (Pauls 1978b). The presence of only a single conifer species (white spruce, *Picea glauca*) at our Yukon study site results in extreme annual variation in food availability for squirrels between mast and non-mast years (McAdam & Boutin 2003). The present study was conducted from January to February 2002, during a period of low natural food availability (third successive mast crop failure) and declining population density. Nevertheless, most of the individuals included in our study survived winter and reproduced in spring.

We measured the FMR (or daily energy expenditure) of 61 female squirrels between 9 January and 28 February 2002 using the doubly labelled water technique (Speakman 1997). Winter measures preceded the mating season, and coincided with a period of cold ambient temperatures, complete snow cover and low resource availability except for food present in the midden. To obtain FMR measurements, animals were captured, weighed and injected intraperitoneally with 0.5 mL DLW [10% APE-enriched ^{18}O water (Enritech, Rehovot, Israel) and 99% APE-enriched ^2H water (MSD Isotopes, Pointe-Claire, Quebec, Canada) mixed in a ratio of 20 : 1], left in the trap for 60 min to allow the isotopes to equilibrate in the body, and then bled via a clipped toenail to obtain initial blood samples for isotope analysis. Squirrels were then recaptured, weighed and bled 48–120 h after the initial blood sample, within 0–3.5 h of a 24-h interval (25th percentile = 0.11 h, median = 0.8 h, 75th percentile = 1.75 h). Analysis of isotope concentrations in blood samples was conducted according to methods described by Ergon

et al. (2004). We estimated CO₂ production using the single pool equation from Speakman (1997; eqn 7.17) and converted CO₂ production to FMR (kJ day⁻¹) assuming RQ = 0.8. To compare our winter FMR values to levels of expenditure expressed by red squirrels experiencing warmer ambient temperatures, we also present the average FMR of three, non-reproducing females measured at the same study site but in a different year (1997) using doubly labelled water methodology described by Thomas *et al.* (1994). An index of T_a during all FMR sampling measures was obtained by calculating the mean of hourly temperature readings between each individual's initial and final blood sample, as recorded by an automated weather station located within the study site.

Resting metabolic rate at thermoneutral temperatures (RMRt) was measured on a subset of individuals for which we obtained FMR measures. Animals were captured 0–30 days following collection of their final DLW blood sample, transported to a temporary facility 30 km from the study site at around sunset, weighed, and placed in a 2-L metabolic chamber positioned in a temperature-controlled incubator. Dry CO₂-free air (ascarite and drierite) was pumped through each chamber at a rate of 640 mL min⁻¹, and a 100 mL min⁻¹ subsample was directed first through an ascarite/drierite scrubber and then through an oxygen analyzer (Sable Systems FC-1, Henderson, NV, USA) for each chamber. A computerized data acquisition system (Sable Systems Datacan V) controlled valves to first calibrate the oxygen analyzers at the start and end of each trial with fresh scrubbed air before reading and storing O₂ concentration in the chamber outflow at 5-s intervals. The computer also regulated the incubator temperature at 20 °C, within the 15 °C to *c.* 30 °C thermoneutral zone of winter-acclimatized red squirrels (Pauls 1978a). RMR was calculated from the lowest baseline level of oxygen consumption recorded for at least 15 min during a 1–2 h run. Animals were provided with water, apple and peanut butter at all times other than when in metabolic chambers and were re-released at their original trap location the following morning. This feeding, combined with the short period for which red squirrels were held in captivity, causes us to classify our metabolic measurements as thermoneutral resting metabolic rate (RMRt) rather than BMR, which forms the basis of Lovegrove's (2003) analysis. The difference between BMR and RMRt varies across taxa, but among small, granivorous rodents RMRt typically exceeds BMR by 5–15% (Nespolo *et al.* 2003).

An index of behavioural activity in the field was obtained by visiting the primary middens of a subset of female squirrels (median 21 females per day, range 8–27) on 35 days with varying ambient temperatures (T_a during sampling round: median -9.5 °C, range -26.1–0.6 °C). We always conducted these midden visits during the afternoon

(median start time = 15:08, range 13:15–17:08) to coincide with the daily activity peak of red squirrels in winter. We remained at each squirrel's midden for 7 min, and noted whether the owner, identified via colour combinations of wires threaded through ear tags, was observed outside the nest. Because squirrels are highly vocal with spatially concentrated activity around middens during winter, owners were frequently observed during these short visits (average proportion of owners observed = 0.30, see Results). However, because focal squirrels were not radio-collared, we cannot be sure that unobserved squirrels were in fact in the nest. Thus, while this behavioural sampling approach does not provide a reliable measure of individual squirrel nest occupancy, when observations are pooled across multiple individuals, it does provide a population index of out-of-nest activity as a function of ambient temperature. Behavioural estimates of the proportion of squirrels observed outside the nest were arcsine transformed prior to statistical analysis to normalize proportional data.

We evaluated the influence of T_a FMR on red squirrel FMR and metabolic scope using least-squares linear regression with body mass included as a covariate in the models. Both FMR and RMR varied significantly with body mass. In both cases, regressions based on log-transformed values had lower explanatory power than regressions based on untransformed values, and thus only the latter were used in statistical analyses. Unless otherwise indicated, the unit of all metabolic measures analysed or presented is kJ day⁻¹ and means are presented as ± 1 standard error.

RESULTS

The BMR of small mammals increased with body size and decreased with T_a (\log_{10} BMR = 0.55 + 0.66 \log_{10} mass - 0.011 T_a avg ann; Fig. 1a, open squares) along similar slopes as FMR (\log_{10} FMR = 0.89 + 0.68 \log_{10} mass - 0.009 T_a FMR; Fig. 1a, open circles). The T_a regression coefficients from the two models were both significantly different from zero (BMR, $t_{265} = -10.2$, $P < 0.001$; FMR, $t_{75} = -3.7$, $P < 0.001$), but were not significantly different from each other ($t_{339} = 1.67$, $P = 0.10$). Analyses based on independent contrasts also revealed equivalent, mass-independent effects of T_a on BMR (regression coefficient -0.007 T_a avg ann; $F_{1,266} = 49.3$, $P < 0.001$) and FMR (regression coefficient -0.007 T_a FMR; $F_{1,76} = 8.5$, $P < 0.005$).

For the 23 species on which FMR and BMR have both been measured in the same locality, metabolic scope averaged 2.96 ± 0.27 and also did not vary significantly with T_a during FMR measures ($t_{20} = 1.49$, $P = 0.15$; Fig. 1b, open diamonds) or body mass ($t_{20} = 0.24$, $P = 0.81$; total model $F_{2,20} = 1.16$, $P = 0.34$). The relationship between T_a and measured metabolic scope became margin-

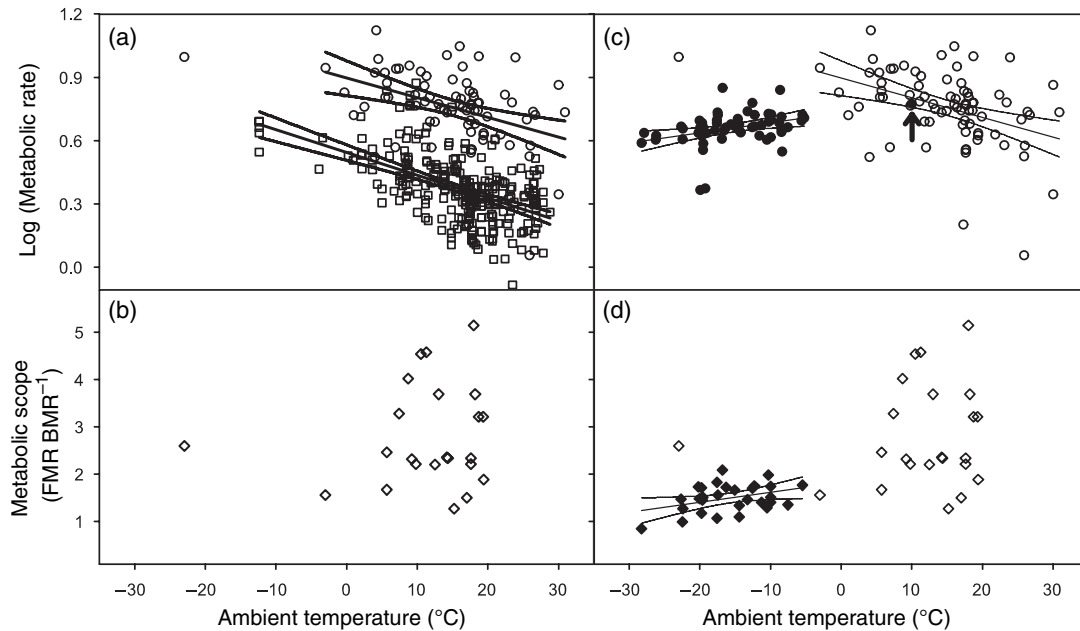


Figure 1 (a) The influence of ambient temperature on mass-independent variation in mammalian FMR (open circles; $n = 77$ species, recalculated from Anderson & Jetz 2005) and BMR (open squares; $n = 268$ species, recalculated from Lovegrove 2003). Values presented are measured \log_{10} FMR $- 0.68 \log_{10}$ mass and measured \log_{10} BMR $- 0.66 \log_{10}$ mass, both in kJ day^{-1} . Lines represent the least-square regression slopes and 95% confidence intervals. The open circle in the upper left is the FMR of *Clethrionomys rutilus* in winter (Holleman *et al.* 1982) that was not included in Anderson & Jetz's (2005) analysis. (b) The influence of ambient temperature on inter-specific variation in measured metabolic scope (FMR/BMR). The open triangle on the left is the measured metabolic scope of *C. rutilus* based on Holleman *et al.*'s (1982) FMR measures and Rosenmann *et al.*'s (1975) winter-acclimatized RMR measures. (c) The influence of ambient temperature on Yukon red squirrel FMR during winter (closed circles) in comparison with temperature effects on the average FMR of other mammals (open circles). To facilitate visual comparison, red squirrel FMR is presented as residual \log_{10} FMR using the same calculation used in (a). Solid lines are the least-square regression equations and 95% confidence intervals. The single closed circle indicated by the arrow is the average residual \log_{10} FMR of three non-reproductive female red squirrels from the same population measured during spring. (d) The influence of ambient temperature on the measured metabolic scope of red squirrels (closed diamonds) in comparison with other mammals (open diamonds).

ally significant when analysed using independent contrasts ($t_{21} = 1.51$, $P = 0.05$), but the direction of this relationship was for metabolic scope to increase with increasing T_a .

The average winter FMR of Yukon red squirrels experiencing ambient temperatures ranging between -5 and -28 °C was $196 \pm 5 \text{ kJ day}^{-1}$, and varied significantly with body mass ($t_{56} = 3.05$, $P = 0.004$) and temperature [$t_{56} = 2.70$, $P = 0.009$; total model $F_{2,56} = 9.80$, $P < 0.0001$, $r^2 = 0.26$, regression equation: $\text{FMR} (\text{kJ day}^{-1}) = 52.5 + 0.613 \text{ mass (g)} + 2.017 T_a \text{ FMR (}^\circ\text{C)}$]. FMR was positively related to temperature, such that the lowest levels of FMR were expressed by individuals exposed to the coldest ambient temperatures (Fig. 1c, closed circles). The average FMR of three non-reproducing females in spring ($253 \pm 13 \text{ kJ day}^{-1}$) was significantly higher than average winter FMR (Mann–Whitney $U_{3,59} = 10$, $P = 0.01$), and was within 10% of the value predicted by extrapolating the winter FMR vs. T_a relationship to the average T_a prevailing during these spring measurements (Fig. 1c, closed circle indicated by arrow).

The average winter RMRt of red squirrels was $290 \text{ mL O}_2 \text{ h}^{-1}$ or 138 kJ day^{-1} , and also varied significantly with mass ($\text{RMRt} = 43.70 + 0.40 \text{ mass}$, $r^2 = 0.15$, $F_{1,33} = 5.62$, $P = 0.02$). Among the subset of 26 female red squirrels for which we successfully obtained measures of both field and resting metabolism, metabolic scope averaged only 1.47 ± 0.06 and tended to increase with increasing T_a (scope = $1.18 + 0.021 T_a$, $r^2 = 0.15$, $F_{1,27} = 4.58$, $P = 0.04$; Fig. 1d, closed diamonds). The proportion of female red squirrels observed outside of the nest increased significantly with ambient temperature [$\arcsin(\text{proportion observed}) = 0.408 + 0.009 T_a$, $r^2 = 0.22$, $F_{1,33} = 9.26$, $P = 0.005$; Fig. 2].

DISCUSSION

These results demonstrate that the widespread tendency for mammals to increase FMR with declining ambient temperature does not generalize to very cold temperatures. Although the mass-independent FMR of red-backed voles

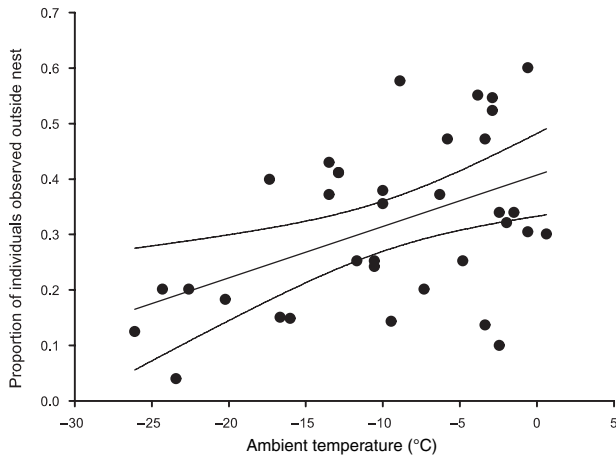


Figure 2 The influence of ambient temperature on the proportion of red squirrels observed outside the nest during afternoon territory visits. Proportions have been arcsine transformed. Lines represent the least-square regression slope and 95% confidence interval.

from Alaska experiencing $T_a = -23\text{ }^\circ\text{C}$ [$\log(\text{FMR}) = 0.996\text{ kJ day}^{-1}$; Holleman *et al.* 1982] is in the 95th percentile of published mammal values, the mass-independent FMR of red squirrels measured at a mean T_a of $-15.4\text{ }^\circ\text{C}$ (0.660 kJ day^{-1}) occupies only the 27th percentile and approximates the FMR predicted for a mammal experiencing $23\text{ }^\circ\text{C}$ (Anderson & Jetz 2005). Red squirrel FMR is not always unusually low – the FMR of non-reproductive females experiencing spring $T_a \sim 10\text{ }^\circ\text{C}$ is close to the average predicted for other small mammals at this temperature. Instead, the uniqueness of our winter FMR measures appears to result from a surprising capacity for red squirrels to minimize energy expenditure during cold winter conditions.

Our re-analysis of recent multi-species comparisons of BMR and FMR variation (Lovegrove 2003; Anderson & Jetz 2005) provides no indication that cold-climate reduction of FMR is imposed by intrinsic ceilings on sustainable metabolism, given that predicted metabolic scope does not increase with declining ambient temperature. In fact, if anything, the trend is for metabolic scope to increase with increasing ambient temperatures. Thus, although red-backed voles have unusually high mass-residual FMR, they are also characterized by a winter-acclimatized mass-residual BMR that is higher than most mammals (Rosenmann *et al.* 1975), and therefore express a routine metabolic scope of 2.6 during winter. Red squirrels, with their unusually low winter FMR combined with moderately high RMR_t, have a metabolic scope of only 1.47, which is among the lowest ever recorded for endotherms, and is lower than both sloths (*Bradypus variegatus*; Nagy & Montgomery 1980) and humans living in affluent societies (Black *et al.* 1996).

We suggest that the reduction in FMR at low ambient temperatures expressed by red squirrels is an adaptive response to low resource availability and the limited benefits of maintaining elevated energy throughput during winter when animals are not growing or reproducing. Red squirrels achieve this extraordinarily low cost of winter living by combining three strategies familiar to human occupants of cold-weather climes. A secure food source is stock-piled in autumn in a central, underground location (Steele 1998). Well-insulated nests are constructed, preferentially with southern exposures to capitalize on the brief daily periods of subarctic winter sunlight (McAdam & Boutin, unpublished data). Then much of the winter is spent inactive in these nests and any outside forays are timed to coincide with the warmest periods of the warmest days (this study, Pauls 1978b). The tendency for red squirrels to increase out-of-nest activity on warmer days, as documented in this and previous studies (Pruitt & Lucier 1958; Pauls 1978b), likely accounts for the observed positive relationship between FMR and ambient temperature. We are currently pursuing additional field research on this population to quantify the thermal environment experienced by red squirrels when inside and outside of their above-ground tree nests and to evaluate how nest occupancy is influenced by food availability.

The potential for energy storage, microhabitat selection and related behavioural strategies to compensate for seasonal mismatches of energy supply and demand has been recognized for a long time (e.g. King & Murphy 1985). The particular tendency for red squirrels to occupy nests and express temperature-sensitive activity during winter has been known for even longer (Pruitt & Lucier 1958; Pauls 1978b). Thus, our observation that red squirrels do not have an extremely high cost of winter living may come as no surprise to some readers. Nevertheless, this study is only the second to quantify the energetic effectiveness of a free-ranging mammal's behavioural compensation for very cold environmental temperatures, and the first to show that this compensation can be so effective as to actually reverse the normal influence of ambient temperature on homeotherm metabolism. Although red-backed voles also make extensive use of nests and the subnivean space, they are characterized by much higher winter energy expenditure than red squirrels, perhaps owing to their smaller body size and lack of access to hoarded food (Holleman *et al.* 1982). Snowshoe hares (*Lepus americanus*), which lack access to both subnivean environments and hoarded food, might be a candidate for even higher costs of winter living.

More field energetics research is needed to evaluate whether cold air temperatures cause other temperate- and polar-zone mammals to express sufficiently high winter FMR to be subject to intrinsic constraints, operating

either directly on FMR (*sensu* Anderson & Jetz 2005) or on the metabolic scope separating FMR and BMR (*sensu* Drent & Daan 1980; Peterson *et al.* 1990; Hammond & Diamond 1997; Speakman 2000, this study). Alternatively, extrinsic constraints on environmental energy availability during winter may force most cold climate endotherms to maintain conservative levels of winter energy expenditure, far below levels imposed by intrinsic constraints. As long as both possibilities remain, the metabolic niches (*sensu* Anderson & Jetz 2005) of high latitude species should be recognized to have the potential to be as highly diversified as those of low latitude species.

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