

The cold shoulder: free-ranging snowshoe hares maintain a low cost of living in cold climates

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Abstract: The hypothesis that cold air temperatures (T_a) constrain the metabolic diversity of high-latitude endotherms is based on the observation among birds and mammals that mean field metabolic rate (FMR) increases, whereas the variability of FMR decreases, from the warm tropics to the cold poles. However, there is a paucity of FMR measurements from above 60° latitude and below 0 °C. We measured the daily energy expenditure of a high-latitude population of free-ranging snowshoe hares (*Lepus americanus* Erxleben, 1777) in Yukon, Canada, in winter ($T_{a\text{-mean}} = -16.4$ °C) and in autumn ($T_{a\text{-mean}} = 0.5$ °C). Doubly labelled water measures of FMR were approximately 20% lower in winter than in autumn, and were a similar, low multiple of resting metabolic rate in both seasons (2.04 and 1.94, respectively). The mass-corrected FMR of snowshoe hares in winter was only half the value predicted by extrapolating the relationship between FMR and $T_a > 0$ to -16.4 °C. These results contribute to an emerging pattern of a reversal in the relationship between FMR and T_a in free-ranging mammals from negative above 0 °C to positive below 0 °C. We refer to the positive, low T_a portion of this relationship as the cold shoulder, and suggest that it may reflect the general necessity for free-ranging mammals to use behavioural and (or) physiological means to conserve energy during long winters when cold conditions coincide with resource scarcity.

Résumé : L'hypothèse qui veut que les températures froides de l'air (T_a) restreignent la diversité métabolique chez les endothermes de haute latitude est basée sur l'observation que, chez les oiseaux et les mammifères, le taux métabolique moyen en nature (FMR) augmente des régions tropicales chaudes vers les régions polaires froides, alors que la variabilité du FMR diminue. Il existe cependant peu de mesures de FMR aux latitudes supérieures à 60° et aux températures inférieures à 0 °C. Nous avons déterminé la dépense quotidienne d'énergie dans une population de haute latitude de lièvres d'Amérique (*Lepus americanus* Erxleben, 1777) au Yukon, Canada, en hiver ($T_{a\text{-moyen}} = -16,4$ °C) et en automne ($T_{a\text{-moyen}} = 0,5$ °C). Les mesures du FMR à l'eau doublement marquée sont environ 20 % inférieures en hiver qu'en automne et représentent aux deux saisons un multiple faible mais semblable du taux de métabolisme de repos (2,04 et 1,94 respectivement). Le FMR des lièvres d'Amérique en hiver corrigé en fonction de la masse représente seulement la moitié de la valeur prédictive par l'extrapolation de la relation entre FMR et $T_a > 0$ jusqu'à $-16,4$ °C. Ces résultats contribuent à l'émergence d'un patron de renversement de la relation entre FMR et T_a chez les mammifères libres en nature, de relation négative au-dessus de 0 °C à positive sous 0 °C. Nous référerons à la portion positive de la T_a basse comme à un « épaulement froid » et croyons qu'il doit refléter la nécessité générale pour les mammifères en liberté en nature d'utiliser des moyens comportementaux et/ou physiologiques pour conserver l'énergie durant les longs hivers pendant lesquels les conditions frigides s'accompagnent de pénurie des ressources.

[Traduit par la Rédaction]

Introduction

The rate of energy expenditure of a free-living animal is among the most important determinants of its ecology (Brown et al. 2004). The ability of an animal to acquire sufficient energy to satisfy its daily requirements shapes its behaviour and distribution, and is critical to survival and reproductive success. Understanding the variables that influ-

ence energy expenditure is not only critical to understanding an animal at the individual level, but may provide a potential mechanistic link between the individual, population, and ecosystem (Brown et al. 2004).

There have been many reviews of factors that account for interspecific variation in energy expenditure (e.g., Speakman 1999; Anderson and Jetz 2005; Nagy 2005). Field metabolic rate (FMR) is a measure of the daily energy expenditure of

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free-living animals experiencing natural conditions (Speakman 1999). Although FMR scales allometrically with body mass like other measures of metabolic rate, the residual variation is substantial and can amount to a sixfold range in mass-adjusted values of FMR (Nagy 1994). Many traits have been shown to contribute to the remaining variation, including phylogeny, life stage, diet, habitat, latitude, season, and ambient temperature (T_a) (Bryant 1997; Corp et al. 1999; Speakman 1999; Anderson and Jetz 2005). A recent broad-scale review of FMR by Anderson and Jetz (2005) showed that across latitude, mass-corrected (mc) FMR of birds and mammals fell between two constraint lines: (1) an upper bound that does not change with latitude and may represent an upper physiological limit and (2) a lower bound that increases with increasing latitude and is driven by environmental factors. Furthermore, they found that T_a is among the best environmental predictor of mcFMR, with the highest levels of energy expenditure coinciding with the lowest temperatures. Collectively, they suggested that these patterns show decreasing metabolic niche space from the tropics to the poles. However, a major limitation to the Anderson and Jetz (2005) study was the paucity of FMR measurements at latitudes above 60° (two studies) and at temperatures below 0 °C (three studies). With so few FMR studies conducted at the extreme end of latitudinal and environmental axes, it is difficult to evaluate whether FMR continues to increase at high latitudes and low T_a and even more difficult to assess its variability. This is a critical limitation, because the apparent uniformity of mcFMR at high latitudes has been translated into a constrained metabolic niche hypothesis. This hypothesis proposes that species diversity declines at high latitudes because cold T_a limits diversity by restricting the range of energetically feasible lifestyles (Anderson and Jetz 2005; Clarke and Gaston 2006).

The constrained metabolic niche hypothesis was challenged in a recent study of winter FMR of a northern population of red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), living above 60° latitude and regularly experiencing temperatures below -20 °C (Humphries et al. 2005). Contrary to the interspecific pattern described by Anderson and Jetz (2005), red squirrels, occupying high latitudes and exposed to very low T_a , had FMR levels among the lowest reported in mammals and that FMR decreased at lower T_a . Humphries et al. (2005) suggested that the reduction in FMR is an adaptive response to low resource availability and the limited benefits of maintaining a high FMR during winter when there is no growth or reproduction. Red squirrels were able to maintain this extremely low cost of living by combining three strategies. First, they have access to a secure, concentrated food source that is larder-hoarded in autumn (Steel 1998). Second, they construct well-insulated nests with southern exposures to capitalize on the heat benefits of the brief daylight during the subarctic winter (A.G. McAdam and S. Boutin, unpublished data). Third, they spend much of the winter inactive within their nests, only venturing out for brief forays at times that coincide with the warmest periods of the warmest days (Pauls 1978). A more general indication that the energy expenditure of free-ranging mammals does not always increase with decreasing air temperature is provided by Nagy et al.'s (1999) finding of no sig-

nificant increase in FMR from summer to winter across 19 mammal species.

In the present study we document the FMR of snowshoe hares (*Lepus americanus* Erxleben, 1777) occupying the same cold high-latitude environment as the red squirrels studied by Humphries et al. (2005). Snowshoe hares are widely distributed across the boreal forest of North America and are active at all times of the year (Krebs et al. 2001). As a result they must deal with a winter T_a that can be as low as -50 °C. However, unlike red squirrels, snowshoe hares do not make nests or use burrows and are thus directly exposed to the prevailing environmental conditions. They also lack access to hoarded food and must actively forage, exposing themselves to prevailing ambient conditions even during bouts of extreme cold in winter. Consequently, snowshoe hares are much more likely than red squirrels to be characterized by high FMR at very low temperatures, which would extend the pattern of high, invariant FMR at high latitudes and cold temperatures documented by Anderson and Jetz (2005) and support the constrained metabolic niche hypothesis.

Awareness of the existence and the significance of differences in the metabolic design of arctic and tropical endotherms date back to classic work conducted by P.F. Scholander and colleagues in the 1950s (Scholander et al. 1950a; Scholander et al. 1950b; Scholander 1955). Development of field techniques for measuring metabolism, behaviour, and thermal ecology of free-ranging animals makes it now possible to re-evaluate these patterns in a natural ecological context in light of recent hypotheses about the ecological significance of large-scale metabolic variation. The main objective of this study was to document the daily energy expenditure of a high-latitude population of free-ranging snowshoe hares experiencing a wide range of air temperatures. In addition, we examine the influence of mass and age on FMR, as well as microclimate exposure of hares as potential means for manipulating thermal exposure and cold climate energetics. Emerging data (shown here and in Humphries et al. 2005) contradict the metabolic constraint hypothesis by showing that free-ranging mammals reduce energy expenditure at high latitudes and low temperatures. We refer to this reversal of the relationship between T_a and FMR as the cold shoulder of FMR variation.

Materials and methods

Animals and field procedures

The study was conducted during late winter, from 17 to 21 March 2007, and during autumn, from 14 to 19 October 2007, in the Kluane region, Yukon (60°57'N, 138°12'W). Snowshoe hares were in the first year of the decline phase of their population cycle when the risk of predation was at its highest (Sheriff et al. 2009a). The Kluane region is located within the boreal forest at a relatively high elevation (600–1100 m) within the rain shadow of the St. Elias mountain range. The study site was completely snow covered (1–3 m deep) during winter and completely snow free during autumn. This region is dominated by a single conifer species, white spruce (*Picea glauca* (Moench) Voss), with a mixed understory of grayleaf willow (*Salix glauca* L.), bog birch (*Betula glandulosa* Michx.), western soapberry (*Sa-*

pindus saponaria L.), and herbaceous plants. Mean daily highs and lows measured at 10–20 cm above substrate level (temperatures that hares encounter) were –6.43 and –26.30 °C during our winter study period, and 9.70 and –8.71 °C during our autumn study period.

All described animal use procedures were approved by the University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council on Animal Care. Hares were live-trapped using Tomahawk traps (Tomahawk Live Trap Co., Tomahawk Wisconsin, USA; for details see Krebs et al. 1986). Since hares are most active between dusk and dawn, traps were set at 2000 and checked the next morning at 0600. Upon capture, hares were weighed and sexed; reproductive status was assessed to ensure that no hares were reproductively active. All hares had been previously captured for a monitoring study (Sheriff et al. 2009a) and were of a known age. In summer, juveniles can be distinguished by their small size. In autumn, juveniles can be distinguished by the soft brown fur on their feet, whereas adults have coarse white fur on their feet. In winter, there is no distinguishable features of young born the previous summer. However, for our study, all our winter hares had been previously aged. Hares were then transported to the Kluane Lake Research Station for FMR measurements. Because of the extreme cold in winter, traps were checked at 2400 (instead of 0600) and hares were immediately transported to a holding facility at KLRS and kept at –10 °C prior to FMR measurements.

Field metabolic rate

We measured the FMR of 20 snowshoe hares (6 male and 4 female winter adults; 2 male and 2 female autumn adults; 4 male and 2 female autumn juveniles) using the doubly labelled water (DLW) technique (Butler et al. 2004). Hares were transferred to a burlap bag for holding and allowed to habituate to laboratory conditions for 2 h prior to injections. Intraperitoneal injections with 1.6 or 1.8 mL DLW (10% APE-enriched ^{18}O water (Enritech Ltd., Rehovot, Israel) and 99% ^2H water (MSD Isotopes, Pointe-Claire, Quebec, Canada) mixed in a ratio of 20:1) were made between 0900 and 1100. Hares were left for 2 h prior to initial bleed to allow for the isotope to equilibrate in the body water (validation of equilibrium time was run on two hares each season and shows that there is no change in DLW concentrations by 2 h; Fig. 1). A 100 μL initial blood sample was taken from the ear artery using a 28 gauge heparinised insulin syringe (Becton, Dickinson and Company, Franklin Lakes, New Jersey, USA) and transferred to two 100 μL micropipettes (Fisherbrand disposable micropipettes; Fisher Scientific, Fair Lawn, New Jersey, USA), which were immediately flame-sealed using a butane gas burner. Hares were recaptured 4–5 days later and a final blood sample was taken within 2 h of a 24 h interval. Sampling across multiple days increases the precision of the method because it evens out day-to-day variation in FMR, which can be substantial in small mammals (Speakman et al. 1994; Berteaux et al. 1996). Sampling as close as possible to 24 h intervals minimizes the impact of circadian effects on metabolism (Speakman and Racey 1988). To determine background levels of ^{18}O and ^2H , blood samples were taken from six hares prior to injection (method D in Speakman and Racey 1987).

All animals were released at their site of capture within 2 h of blood sampling.

Blood samples were vacuum-distilled (Nagy 1983), and water from the resulting distillate was used to produce CO_2 and H_2 (methods for CO_2 in Speakman 1998 and for H_2 in Speakman and Król 2005). The isotope ratios $^{18}\text{O} : ^{16}\text{O}$ and $^2\text{H} : ^1\text{H}$ were analysed using gas source isotope ratio mass spectrometry (Isochrom µG and Isoprime, respectively; Micromass, Manchester, UK). Isotope enrichments were converted to values of CO_2 production using a single-pool model as recommended for this size of animal by Speakman (1993). There are several alternative approaches for the treatment of evaporative water loss (Visser and Schekerman 1999). We assumed a fixed evaporation of 25% of the water flux (eq. 7.17 in Speakman 1997), which is known to minimize error in a range of conditions (Visser and Schekerman 1999; Van Trigt et al. 2002). To convert CO_2 production to kiloJoules per day, we assumed a RQ of 0.85. A RQ of 0.85 minimizes the error in the conversion of CO_2 production into energy expenditure when the substrate utilization is unknown (Speakman 1997).

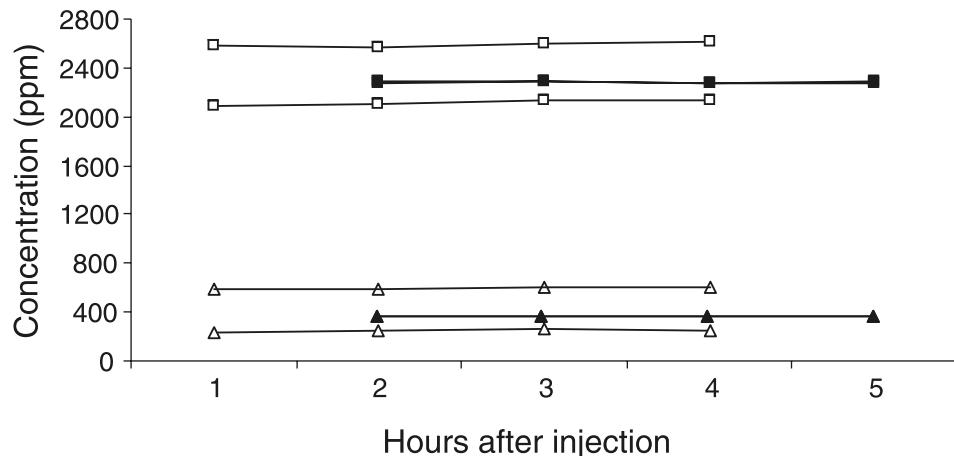
Metabolic scope (FMR/RMR), an index of how hard an animal is working, was determined in both seasons using measures of resting metabolic rate (RMR) reported in Sheriff et al. (2009b). Briefly, RMR, measured as oxygen consumption, was determined using a flow-through respirometry system in a mobile laboratory positioned 5–30 km from the study grids where hares were captured. Hares were fasted for a minimum of 8 h prior to the start of measurements. Each hare was placed in a metabolic chamber in a temperature-controlled environmental cabinet (model LU-113; Espec Canada, Hudsonville, Michigan, USA). Hares were habituated to the chamber for 2–3 h prior to the start of measurements. RMR was measured for a total of 55 min within their thermal neutral zone. Oxygen consumption was determined using the following formula, $\text{VO}_2 = V_e(F_i - F_e)/(1 - F_e)$, where VO_2 is oxygen consumption, V_e is the volume of air flowing out of the chamber, and F_i and F_e are the fractional concentrations of oxygen entering and leaving the chamber. The respiratory quotient does not need to be used in this situation, as CO_2 was removed from the air (Koteja 1996). Different individuals were used for FMR and RMR measurements; however, the animals were from the same population and measurements were taken within 1-week of each other.

Microclimate exposure

We evaluated the potential for snowshoe hares to avoid temperature extremes by measuring air temperatures in microhabitats (T_h) used by active and resting hares and comparing this to ambient temperature (T_a) measured at two nearby (within 5 km), shaded weather stations. We also attached temperature data loggers between the shoulder blades of hares to measure the temperature at the pelage surface (T_p).

To measure the T_h , iButtons (1-wire Thermocron DS1922L; each iButton was placed in a unsealed Ziploc® bag), programmed to record time and temperature every 10 min, were suspended from a branch or stick 10–20 cm above the surface of the snow in each of 3 different habitat types: (1) in a meadow habitat, which consists of an open

Fig. 1. Changes in the concentration (ppm) of ^{18}O (squares) and ^2H (triangles) in the blood following an injection with doubly labelled water (10% APE-enriched ^{18}O water and 99% ^2H water mixed in a ratio of 20:1) in snowshoe hares (*Lepus americanus*) in winter ($n = 2$; closed symbols) and in autumn ($n = 2$; open symbols). Note the differences in initial concentrations are due to different injection amounts. In all cases, concentrations had reached equilibrium after 2 h.



area with some small willows and spruce trees; (2) in a willow stand, which consists mainly of tall, 2–3 m, willows with some open spaces between each plant; and (3) a spruce stand, which consists mainly of tall, 10 m, trees with some open spaces between trees. In each of these habitat types, solar radiation and convection effects could potentially vary. Duplicate areas were found for each habitat type, and within each locale, one iButton was placed in an open exposed area and one in a sheltered area. In the meadow, the sheltered area was a snow cave, formed when snow accumulates and bends the branches of willows to the surface of the snow, eventually forming a snow cavity at the base of the willow. In the willow stand, the sheltered area was at the base of a willow. In the spruce stand, the sheltered area was in a tree well at the base of a spruce tree. Each of these microhabitats were previously used by hares, but were not occupied during the measurement period as evidenced by the absence of fresh tracks and pellets.

To measure the T_p , we attached iButtons (Maxim Integrated Products, Sunnyvale, California, USA), again programmed to record time and temperature every 10 min, between the shoulder blades of six hares immediately after the initial FMR blood sample. iButtons were attached to a 5 cm tag, which was glued into each hare's fur, causing the iButton to rest atop the pelage and measure temperature immediately external to the hare. Thus, the recorded temperature may be influenced by heat flux from the hare, objects that come into contact with the hare's dorsal surface, as well as T_a or T_h (Hind and Gurney 1998). We were also able to remove the iButton, immediately following the final FMR blood sample, without the need to remove a section of fur from the hare in winter.

Statistical analysis

All data are expressed as mean \pm 1 SE, unless otherwise stated. The influence of age, season, and mass on FMR were evaluated with ANCOVAs performed using the software package STATISTICA version 6 (StatSoft Inc., Tulsa, Oklahoma, USA). The assumption of normality was tested with the Shapiro–Wilk test and homogeneity of variances with

Levene's test. If these assumptions were not met, the data were log-transformed. Comparisons of the means were considered significant if $P < 0.05$. The influence of T_a on the differential between T_p and T_a was evaluated with a LOESS curve fit using least squares, with a re-descending M estimator with Tukey's bi-weight function, a span = 0.7 and a polynomial up to degree = 2 in R version 2.7.2 (R Development Core Team 2008).

Results

Field metabolic rate

FMR in snowshoe hares was lower in winter (960.97 ± 34.64 kJ/day) than in autumn (1154.73 ± 31.47 kJ/day; Fig. 2), whether or not mass was included as a covariate. With mass included as a covariate, FMR did not vary according to gender ($F_{[1,17]} = 0.4$, $P > 0.05$) but did vary with age ($F_{[1,8]} = 8.67$, $P < 0.05$) and season ($F_{[1,11]} = 14.54$, $P < 0.005$). Juvenile hares in autumn were characterized by a FMR that was lower than adults in autumn. Since adults had lower FMR in winter than in autumn, juvenile FMR in autumn was similar to adult FMR in winter (Fig. 2). RMR also significantly declined from autumn to winter (inset of Fig. 2), and the metabolic scope of adults was similar in both seasons, averaging 2.04 ± 0.07 in winter and 1.94 ± 0.05 in autumn. Autumn juveniles had a lower metabolic scope than adults, averaging 1.59 ± 0.06 .

Microclimate exposure

The mean daily highs and lows of T_h was approximately 6 °C warmer and 1 °C colder, respectively, than the mean daily highs and lows of T_a measured at two nearby shaded weather stations (Table 1). The microhabitats with the lowest and highest mean daily highs had T_h s that were, respectively, 2.4 °C colder (sheltered spruce forest) and 13.8 °C warmer (snow cave) than mean daily high T_a . Mean daily low T_h and T_a were consistently much more similar; microhabitats with the lowest and highest mean daily lows had T_h s that were, respectively, 3.2 °C colder (exposed meadow) and 1.7 °C warmer (exposed spruce forest) than mean daily

Fig. 2. Field metabolic rates (FMR) of a free-ranging population of snowshoe hares (*Lepus americanus*) in southern Yukon, Canada, during winter (adults) and autumn (adults and juveniles). Inset shows the resting metabolic rate (RMR) of the same population of snowshoe hares (adults only with similar body masses) measured at the same time (winter: $n = 7$; autumn: $n = 6$; adapted from Sheriff et al. 2009b).

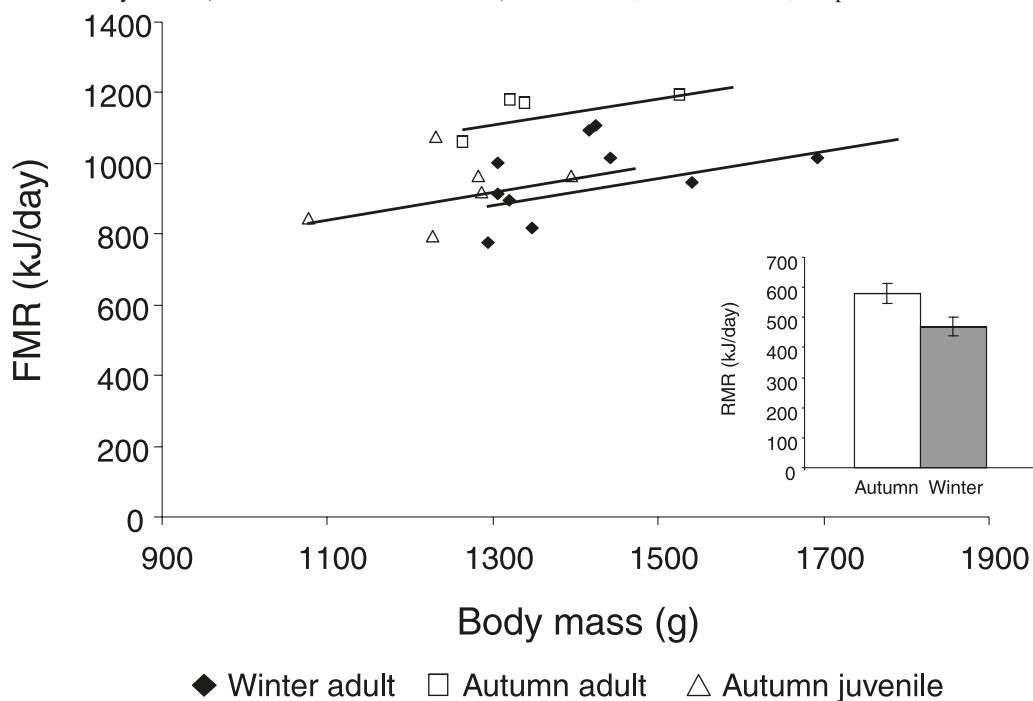


Table 1. Mean daily highs and lows ($^{\circ}\text{C}$; mean \pm SE) of the weather station temperature (T_a) and the microhabitat temperatures experienced by snowshoe hares (*Lepus americanus*) in southern Yukon, Canada, from 17 to 21 March 2007.

Habitat type	Daily temperature ($^{\circ}\text{C}$)	
	High	Low
Weather station (T_a)	$-6.4 \pm 2.0\text{c}$	-26.3 ± 3.4
Willow		
Exposed	$-1.9 \pm 2.0\text{cb}$	-28.0 ± 3.8
Sheltered	$-3.9 \pm 2.1\text{cb}$	-27.9 ± 3.6
Spruce forest		
Exposed	$4.7 \pm 2.0\text{ab}$	-24.7 ± 3.9
Sheltered	$-8.9 \pm 2.5\text{c}$	-24.7 ± 4.0
Meadow		
Exposed	$-4.3 \pm 1.9\text{cb}$	-29.5 ± 3.5
Snow cave	$11.9 \pm 1.87\text{a}$	-29.4 ± 3.2

Note: Letters denote significant differences ($P < 0.05$).

low T_a . The greater variability in mean daily highs for T_h was likely due to exposure to solar radiation and shelter from wind, especially in the case of the snow cave.

The T_p of snowshoe hares varied between daily highs averaging $11.4 \pm 1.4\text{ }^{\circ}\text{C}$ and daily lows averaging $-6.2 \pm 1.2\text{ }^{\circ}\text{C}$ (Fig. 3). Across all hares, the differential between T_p and T_a averaged $18.4 \pm 0.2\text{ }^{\circ}\text{C}$, with 98% of observations exceeding $10\text{ }^{\circ}\text{C}$ (inset of Fig. 3). There was a scattering of very large differentials ($>25\text{ }^{\circ}\text{C}$) observed during the day (18 of 216 observations between sunrise and sunset) and at night (26 of 396 observations between sunset and sunrise), likely associated with inactive hares basking in the sun or occupying snow caves. Otherwise, changes in T_p were proportional to changes in T_a until T_a reached $-20\text{ }^{\circ}\text{C}$, at which point

there was an upward acceleration of $T_p - T_a$ differentials. T_p rarely declined below $-10\text{ }^{\circ}\text{C}$ (4% of the observations) even though $T_a < -28\text{ }^{\circ}\text{C}$ was not uncommon (18% of observations). Thus, although T_a and T_p have similar patterns, T_p tends to decouple from T_a in extreme cold.

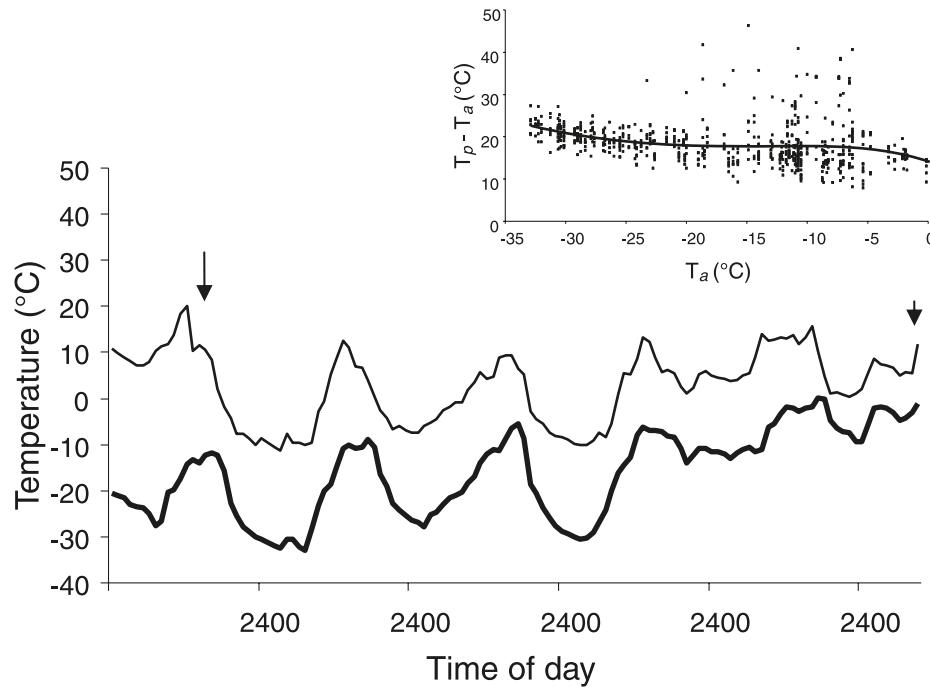
Discussion

Field metabolic rate

In the present study, snowshoe hares were characterized by a significantly lower FMR in winter, when T_a averaged $-16.4\text{ }^{\circ}\text{C}$, than in autumn, when T_a averaged $0.5\text{ }^{\circ}\text{C}$ (Fig. 2). Animals could be expected to minimize energy expenditure in the winter (Masman et al. 1988; Nolet and Rosell 1994). However, in a broad review, Nagy et al. (1999) concluded that there was no overall consistent seasonal effect on FMR across 19 mammal species. Within individual species though, several studies have shown FMR to vary seasonally, including studies on black-tailed jackrabbits (*Lepus californicus* Gray, 1837) (Shoemaker et al. 1976); swift foxes (*Vulpes velox* (Say, 1823)) (Covell et al. 1996); house mice (*Mus domesticus* L., 1758) (Mutze et al. 1991); Merriam's kangaroo rats (*Dipodomys merriami* Mearns, 1890) (Nagy and Gruchacz 1994); Sundevall's jirds (*Meriones crassus* Sundevall, 1842) and pygmy gerbils (*Gerbillus henleyi* (de Winton, 1903)) (Degen et al. 1997); and degus (*Octodon degus* (Molina, 1782)) (Bozinovic et al. 2004). Although these studies all showed FMR to be greater in winter than summer (with the exception of Shoemaker et al. 1976 and Covell et al. 1996), prevailing winter temperatures generally exceeded $0\text{ }^{\circ}\text{C}$ (except that of Covell et al. 1996, with a winter T_a of $-2.6 \pm 2.2\text{ }^{\circ}\text{C}$).

The metabolic scopes (FMR/RMR) of snowshoe hares in

Fig. 3. Mean pelage temperatures (T_p ; thin line) experienced by six snowshoe hares (*Lepus americanus*) in relation to ambient temperature (T_a ; thick line) in southern Yukon, Canada, from 17 to 21 March 2007. The arrows represent the time of release and recapture, and the spike in T_p prior to release is due to hares being placed in burlap bags for transport (this is not shown for recapture). The inset figure shows the differential between T_p and T_a as a function of T_a for all hares, plus a LOESS curve reflecting the mean $T_p - T_a$ differential across all hares.



autumn (1.94) and winter (2.04) are much lower than the mean value of 3.4 calculated by Speakman (1999) for 60 mammal species weighing <4 kg. Metabolic scope usually falls between 2 and 5 in free-ranging animals, with maximal values around 7 (Koteja 1991; Weiner 1992; Speakman 1997). Other studies on small mammals occupying high latitudes have reported low metabolic scopes similar to our results for snowshoe hares; 2.6 for red-backed voles (*Clethrionomys rutilus* (Pallas, 1779)) in Alaska (Rosenmann et al. 1975; Holleman et al. 1982), 2.4 for common shrew (*Sorex araneus* L., 1758) in northeastern Poland (Ochocińska and Taylor 2005), and 1.5 for red squirrel in southwestern Yukon, Canada (Humphries et al. 2005).

Since the metabolic scope of snowshoe hares was at the lower end of values predicted for small mammals, and FMR paralleled the direction of seasonal changes in RMR, we believe that the decline in FMR is not caused by intrinsic constraints (a maximum size or capacity of energy-supplying organs that would limit energy throughput), but is likely limited by the abundance and accessibility of food resources. During the summer hares feed on herbaceous plants (high-quality food), while in the winter hares feed on woody stems (low-quality food), with forage quality reaching its annual minimum in late winter (Sinclair et al. 1982). An animal can respond to nutrient deprivation in two ways. The first is to increase foraging activity; however, this may also increase energetic demands. The second is to decrease activity and enter a physiological condition of adaptive fasting. Covell et al. (1996) found that swift foxes decrease their FMR in winter and suggested that this may be due to lower feeding rates during this time. It is not known whether snowshoe hares increase or decrease foraging activity during winter.

However, snowshoe hares do not accumulate substantial fat reserves during winter and therefore must feed continuously during winter to survive.

Microclimate exposure

Whether an animal increases or decreases foraging activity during nutrient deprivation, a behavioural avoidance strategy to reduce cold exposure will help decrease energy demand for thermoregulation. Animals may build well-insulated nests (Holleman et al. 1982; Redman et al. 1999) and increase nest occupation by restricting activity at cold T_a (Pauls 1978). Snowshoe hares lack an obvious nest or burrow and forage on the snow surface at night when T_a is the coldest. However, they use various microhabitats at rest and while foraging that may provide some thermal advantage at extremely cold T_a . Although the daily lows we recorded in microhabitats closely approximated daily low T_a , the daily high T_h recorded in some microhabitats (e.g., snow caves) was considerably higher than daily high T_a . Since hares are most often inactive during the day (Krebs et al. 2001), microhabitats like snow caves could offer substantial thermal advantages, particularly on cold, sunny days. This possibility warrants further investigation by documenting the occupation and thermal characteristics of different microenvironments across a range of climate conditions through a combination of radio-tracking and snow-tracking of hares and documentation of operative temperature using heated taxidermic mounts (for review see Bakken 1992).

Pelage temperature may also provide evidence that hares have the potential means for manipulating thermal exposure and cold climate energetics. Nassuna-Musoke et al. (2007)

found that T_a accounted for between 45%–51% of the variation in T_p in Friesian cows and that these animals would utilize areas of greater shade to reduce heat stress. We found that the pelage temperature recorded by the iButton mounted on the snowshoe hares averaged 18 °C higher than T_a and all T_h s other than the snow cave. The occasional, extreme $T_p - T_a$ differential that we documented may be indicative of hares exploiting microhabitats. Otherwise, we found changes in T_p to be proportional to changes in T_a until T_a reached –20 °C, at which point T_p remained relatively constant, at –10 °C, as T_a continued to decline to as low as –35 °C (Fig. 3). In an earlier study on snowshoe hares, we found that the lower critical temperature (LCT) during winter was approximately –10 °C (Sheriff et al. 2009b). Thus, the temperature at the hare's thermal boundary varies with T_a above the LCT but does not decline below the LCT even when temperatures drop to –35 °C.

There are two ways in which T_p might be decoupled from T_a in the extreme cold. Since hares are at or below their LCT under these conditions, increased heat production will become necessary to maintain homeothermy, which may result in increased heat flux across the pelage surface that warms the temperature probe. Feist and Rosenmann (1975) found that winter-acclimatized hares had a maximum metabolic rate eight times that of their RMR. Thus, when conditions require, snowshoe hares have potent capacity for increasing heat production. The second way in which snowshoe hares may regulate T_p is through behavioural avoidance. As T_a declines to extremely low temperatures, hares may occupy thermally advantageous microhabitats that warm to around –10 °C when occupied by hares. Since hares need to actively forage during the night, it is unlikely that behavioural avoidance accounts for all the T_p warming that we have observed. But a mixed strategy of alternating bouts of foraging and thermal refuge occupation remains a possibility. Further work needs to be done to investigate the behavioural and microhabitat adjustments hares use to maintain low rates of energy expenditure and elevated T_p on the coldest of nights.

The cold shoulder of FMR

Although it has been proposed that endotherm FMR increases as latitude increases and T_a decreases (Anderson and Jetz 2005), the paucity of FMR measurements at latitudes above 60° and at temperatures below 0 °C makes it difficult to evaluate whether FMR continues to increase at high latitudes and low T_a . Here we showed that within a high-latitude cold-climate endotherm population, FMR decreased as T_a decreased. Snowshoe hares had mcFMR values during autumn and winter that were 92% and 52%, respectively, of the values predicted for mammals by Anderson and Jetz (2005). Humphries et al. (2005) also found that in a northern population of red squirrels as T_a decreased FMR decreased. In an earlier study on the same free-ranging population of hares, we found that individuals were characterized by increased pelage insulation, as well as reduced RMR, LCT, and thermal conductance in winter compared with autumn (Sheriff et al. 2009b). These adaptations likely allowed hares to decrease their FMR and maintain a low metabolic scope during winter. Other studies of free-ranging northern species have also shown a decline in RMR values

in the winter (Nilssen et al. 1984; Mortensen and Blix 1986; Fuglei and Oritsland 1999; Humphries et al. 2005; Fuglesteg et al. 2006). We suggest that the reduction in FMR at low T_{as} may be a general adaptive response in high-latitude environments to reduce energetic costs during the extremely cold winters when resource availability is low and that this response is facilitated, in part, by a reduction in RMR. Thus, a cold shoulder of decreasing FMR with declining T_a below 0 °C that switches to a decrease in FMR with increasing T_a above 0 °C, as originally reported by Anderson and Jetz (2005), may be a general feature of the relationship between T_a and FMR in free-ranging mammals.

In conclusion, we found that snowshoe hares had a lower FMR in winter than in autumn and maintained a very low metabolic scope across the seasons. We also found that air temperatures measured at the surface of hare's pelage did not drop below their lower critical temperature, even at winter air temperatures < –30 °C. We believe that these adaptations are facilitated by a decline in lower critical temperature, thermal conductance, and RMR during winter (Sheriff et al. 2009b), and potentially the occupation of thermally buffered microhabitats during periods of inactivity. More generally, we hypothesize that a reduction in FMR at low T_{as} will be an adaptive response of most high-latitude mammals to reduce energetic costs during cold winters when resource availability is low.

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