SEASONAL METABOLIC ACCLIMATIZATION IN A NORTHERN POPULATION OF FREE-RANGING SNOWSHOE HARES, *LEPUS AMERICANUS*

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Seasonal acclimatization in high-latitude endotherms may involve increases or reductions in body size and metabolic rate to, respectively, augment thermoregulatory capacity or reduce energy requirements. We investigated seasonal acclimatization in a northern population of wild snowshoe hares (*Lepus americanus*) that is exposed to low food availability and extremely cold temperatures in winter. Snowshoe hares were livetrapped and transported to a nearby mobile laboratory. Hares were placed in a metabolic chamber and oxygen consumption was measured for 55 min at each of the following temperatures: 10°C, 0°C, −10°C, −15°C, and −20°C. Hair length and density were measured on a sample of collected hares. Snowshoe hares maintained similar body mass and body temperature between the seasons, but average resting metabolic rate and thermal conductance were, respectively, 20% and 32% lower in winter than in autumn. The lower critical temperature was −10°C to −15°C in winter and 0°C to −10°C in autumn. Guard hairs were 36% longer and 148% denser in winter than autumn, whereas downy hairs were the same length but 128% denser in winter than autumn. Collectively, these results suggest that resource constraints associated with a herbivorous diet in regions and seasons of poor forage quality favors an energetically conservative approach to winter acclimatization.

Key words: free-ranging northern mammals, fur insulation, indirect calorimetry, lagomorph, *Lepus americanus*, resting metabolic rate, thermal conductance, winter acclimatization

Seasonal changes in climate can cause energetic challenges for many animals. During summer months animals can be exposed to high temperatures, which may result in dehydration and heat stress. During winter months animals can be exposed to low temperatures, long nights, restricted food supplies, and high energetic costs of thermoregulation. Climatic differences between the seasons are further enhanced at high latitudes. Many endotherms living in these extreme seasonal climates are characterized by seasonal changes in body mass, body temperature (T_b), metabolic rate, thermal conductance, and pelage (Broggi et al. 2007; Dehnel 1949; Hart et al. 1965; Heldmaier 1989; Lovegrove 2005; Scholander et al. 1950).

Snowshoe hares (*Lepus americanus*) provide an excellent opportunity to investigate the effects of extreme seasonality on thermal energetics. They are widely distributed across the boreal forest of North America and are active at all times of the year (Hodges et al. 2001). As a result they must deal with large seasonal variations in ambient temperature (T_a) and daylight. Snowshoe hares do not make nests or use burrows, and thus differ from most other small to medium-sized mammals in the north that exploit these microhabitats to reduce heat stress at high T_a or heat loss at low T_a (Bazin and MacArthur 1992; Holleman et al. 1982; Merritt et al. 2001; Pauls 1978; Pierce and Vogt 1993). Thus, they are directly exposed to prevailing environmental conditions. Hares are most active at night, which exposes them to the coldest of winter temperatures. Food quality also varies seasonally for hares; during the summer months hares feed on herbaceous plants (high-quality food), whereas in the winter months hares feed on woody stems (low-quality food), with the forage quality reaching its annual minimum in the late winter (Sinclair et al. 1982).

In an earlier study on snowshoe hares in Ottawa, Ontario, Canada, Hart et al. (1965) showed that fur insulation played a

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large role in seasonal acclimatization. However, that study used captive hares fed a high-quality diet exposed to an average winter daily low of only $-8°C$. In a later study on snowshoe hares, Feist and Rosenmann (1975) found that seasonal acclimatization of snowshoe hares from Fairbanks, Alaska, involved enhanced nonshivering thermogenesis, increased sensitivity to norepinephrine and epinephrine, and an increase in the maximum metabolic rate during winter in Fairbanks. Here we investigated winter acclimatization in wild snowshoe hares in the Kluane region, Yukon, Canada, during an extreme cold period in late winter and during the early autumn when hares were no longer reproductively active yet still maintained their summer coat. Specifically, we tested for seasonal changes in body mass, T_b, resting metabolic rate (RMR), thermal conductance, and pelage. This is the 1st study to investigate thermal energetics on a free-ranging mammal that is directly exposed to environmental conditions during temperatures that average $-30°C$. Although hares experience these extremely cold temperatures during the winter months, we predict that RMR will decrease as T_a declines in order to conserve energy during this low-resource period. Furthermore, we predict that this decrease in RMR will be facilitated by a decrease in thermal conductance and an increase in pelage.

Materials and Methods

This study was conducted during late winter, from 10 to 20 March 2007, and during autumn, from 1 to 10 October 2007, in the Kluane region in the Yukon ($60°57'N$, $138°12'W$). Snowshoe hares were in the 1st year of the decline phase of their population cycle, when the risk of predation is at its highest (Krebs et al. 1995). The Kluane region is located within the boreal forest at a relatively high elevation (600–1,100 m above sea level) within the rain shadow of the St. Elias mountain range. The study site was completely covered by snow (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*), with a mixed understory of gray willow (*Salix glauca*), bog birch (*Betula glandulosa*), soapberry (*Sheperdia canadensis*), and herbaceous plants. Average daily T_a maxima and minima, measured at 10–20 cm above substrate level (temperatures that hares encounter), were $-12.6°C$ and $-29.4°C$ during our winter study period, and $2.0°C$ and $-4.0°C$ during our autumn study period.

Hares were livetrapped using Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin; see Krebs et al. [1986] for details). Traps were set at 2000 h and checked the next morning at 0600 h. Because of the extreme cold in winter, traps were checked at 2400 h and hares were immediately transported to a holding facility and kept at $-10°C$ for the remainder of the night. Upon 1st capture hares were weighed and ear-tagged (No. 3 Monel tags; National Band and Tag Co., Newport, Kentucky), and sex was determined; reproductive status was assessed to ensure that no hares were reproductively active. A sample of hares also was shot to

determine changes in pelage. We collected T_b measurements from 9 hares in winter and 7 hares in autumn with a rectal thermometer (Miller and Weber Inc., New York, New York) during handling or immediately after being shot (<30 s). The thermometer was inserted 5 cm into the rectum and held there for 15 s. This distance and time was selected because any further penetration into the rectum or length of time held did not change the temperature reading.

Thirteen hares (5 males and 2 females for winter and 4 males and 2 females for autumn) were used to measure RMR in a mobile laboratory located 5–30 km from the study grids where hares were captured. Hares were fasted for a minimum of 8 h before 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). The chamber was made from a 20-liter opaque plastic bucket fitted with a raised wire-mesh floor and was large enough that a hare could easily move about. Chambers were placed on an activity detector (MAD-1; Sable Systems International Ltd., Las Vegas, Nevada) to determine when animals were resting in the chamber. Hares were habituated to the chamber for 2–3 h before the start of measurements. Each trial consisted of 4 or 5 temperatures increasing from coldest to warmest: $-20°C$, $-15°C$, $-10°C$, $0°C$, and $10°C$. Temperatures were measured using a TC-2000 thermocouple meter (Sable Systems International) inserted directly into the chamber. Hares remained at each temperature for a total of 55 min, a 20-min equilibration period was allowed between each temperature change (Hart et al. 1965), and thus hares were in the chamber for 8–9 h. All trials started 2–3 h after dawn. Hares were weighed and immediately released at the site of capture after testing.

Resting metabolic rate, as oxygen consumption, was determined using a flow-through respirometry system. Dry, CO_2-free air (drierite/ascarite/drierite scrubbed) was pumped through the chamber at a rate of 2,250 ml/min (Smart-Trak Series 100 Mass Flow Controllers; Sierra Instruments Inc., Monterrey, California), and a 147–153 ml/min subsample (SS-3 Gas Sub-Sampler; Sable Systems International) was passed through a drierite/ascarite/drierite scrubber before entering an oxygen analyzer (Oxzilla II Oxygen Analyzer; Sable Systems International). A computerized data acquisition system (Expedata Build V.1.0.18; Sable Systems International) controlled valves to measure baseline oxygen levels every 10 min during a trial with fresh-scrubbed air before reading and storing O_2 concentrations. RMR was calculated from the lowest stable level of oxygen consumption recorded for a 10-min period when the motion detector indicated that hares were at rest. Oxygen consumption was determined using the following formula, $VO_2 = V_e(F_i - F_e)/(1 - F_e)$ 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, respectively. The respiratory quotient does not need to be used in this situation because CO_2 was removed from the air (Koteja 1996; Withers 2001). We used least-squares regression analysis to describe
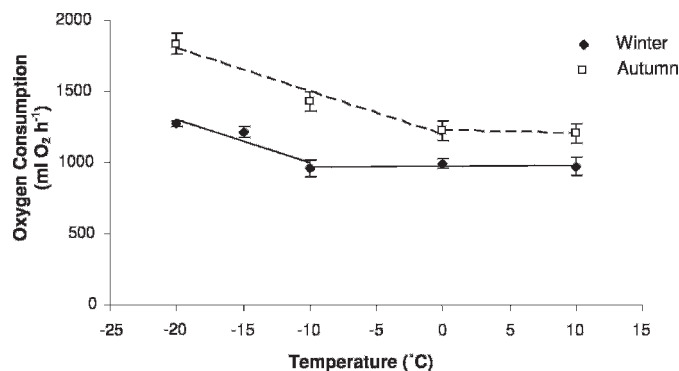
FIG. 1.—Oxygen consumption of resting snowshoe hares (*Lepus americanus*) from Yukon, Canada, over a range of ambient temperatures. Hares were wild-captured and measured during winter (diamond with solid line, $n = 7$) or autumn (open square with dashed line, $n = 6$) conditions (mean $\pm$ *SE*).
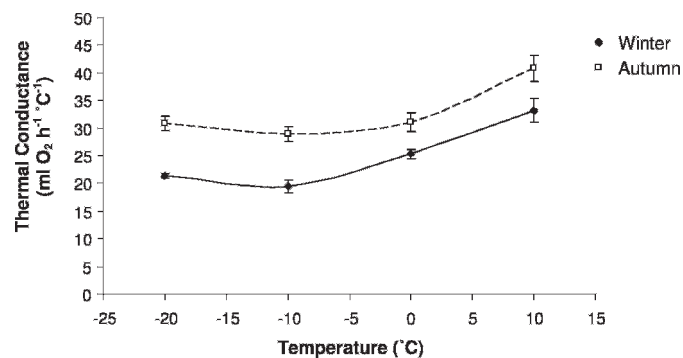

FIG. 2.—Thermal conductance of resting snowshoe hares (*Lepus americanus*) from Yukon, Canada, over a range of ambient temperatures. Hares were wild-captured and measured during winter (diamond with solid line, $n = 7$) or autumn (open square with dashed line, $n = 6$) conditions (mean $\pm$ *SE*).

the rate of increase in oxygen consumption with decreasing T_a below the lower critical temperature.

Thermal conductance was calculated using the Scholander–Irving model, $C = VO_2/(T_b - T_a)$ at each experimental temperature, where C is thermal conductance, VO_2 is the volume of oxygen consumed, T_b is body temperature, and T_a is ambient temperature (Katzner et al. 1997; Scholander et al. 1950). This model assumes that the level that T_b is held above T_a depends on the ratio of heat production (metabolic rate) to cooling rate (thermal conductance). We did not calculate thermal conductance as the slope of VO_2 versus T_a below thermal neutrality because the slope did not extrapolate to T_b.

Pelage characteristics were determined for 6 hares in winter and 6 hares in autumn. Pelts were cut from the midback of hares that were shot and mounted onto 100-cm^2 wooden planks in the field and immediately frozen. Two 1-cm^2 areas for each pelt were sampled to determine the length and density (number/cm^2) of guard hairs and downy hairs. Many studies show that heat flow and insulation are affected by hair length and density (Bozinovic and Merritt 1992; Hart et al. 1965; Ivanter 1994; McClure and Porter 1983; Rogowitz 1990; Sealander 1972; Webb and McClure 1988). Within each 1-cm^2 square, 6 guard hairs and 6 downy hairs were measured while still attached to the pelt. Hair within each square was then shaved to 0.5 mm and subdivided into a 100-square grid. Using a microscope, individual guard hairs and downy hairs were easily distinguishable and could be counted.

All data are expressed as means $\pm$ 1 *SE*, unless otherwise stated. Analyses of varince, *t*-tests, and regression analyses were performed using the software package STATISTICA 6 (StatSoft, Inc., Tulsa, Oklahoma). The assumption of normality was tested with Shapiro–Wilks tests and homogeneity of variances with Levene's tests. If these assumptions were not met the appropriate adjustment was made (log-transformation of data or Greenhouse–Geisser adjustment—Quinn and Keough 2003). Comparisons of the means were considered significant if $P < 0.05$. Differences between sexes were not tested because of the unequal sex ratio; however, this ratio was even between seasons and thus sex would not have played a

role in seasonal differences. This research was conducted according to the guidelines approved for animal care and use by the American Society of Mammalogists (Gannon et al. 2007) and approved by the University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council for Animal Care.

RESULTS

Hares were not characterized by reduced body mass or T_b in winter compared with autumn. Hares weighed an average of $1,398 \pm 29$ g in winter and $1,438 \pm 51$ g in autumn ($t = -0.66$, *d.f.* $= 11$, $P > 0.05$). Rectal temperature ranged from $38.2°C$ to $39.9°C$ in winter and $38.6°C$ to $40.0°C$ in autumn ($t = 0.86$, *d.f.* $= 14$, $P > 0.05$) and showed no consistent relationship with T_a.

Resting metabolic rate was significantly lower in winter compared with autumn ($F = 12.88$, *d.f.* $= 4, 8$, $P < 0.005$; Fig. 1). This seasonal difference remained significant when body mass was included as a covariate in the analysis (season: $F = 33.87$, *d.f.* $= 4, 8$, $P < 0.0005$; mass: $F = 5.82$, *d.f.* $= 4, 8$, $P < 0.05$). The lower critical temperature shifted approximately $10°C$ from autumn to winter, from $0°C$ to $-10°C$ in autumn to $-10°C$ to $-15°C$ in winter. Within the thermoneutral zone, average RMR was 20% lower in winter (976.68 ± 50.15 ml O_2/h) than in autumn ($1,215.64 \pm 64.82$ ml O_2/h; $t = -4.63$, *d.f.* $= 31$, $P < 0.0001$). Least-squares regression equations of the relationship between T_a and oxygen consumption below thermoneutrality were $VO_2 = 686.14 - 30.897(T_a)$ ($r^2 = 0.89$) in winter and $VO_2 = 1,192.30 - 30.61(T_a)$ ($r^2 = 0.97$) in autumn.

Thermal conductance was 32% lower in winter (20.50 ± 0.64 ml O_2 h^{-1} °C^{-1}) compared with autumn (30.28 ± 0.81 ml O_2 h^{-1} °C^{-1}) at temperatures below the thermoneutral zone ($t = -9.04$, *d.f.* $= 30$, $P < 0.0001$), with the largest seasonal differences occurring at the coldest trial temperatures (Fig. 2). Thermal conductance declined with decreasing air temperature from $20°C$ to $0°C$ and $-10°C$, in autumn and winter, respectively, then plateaued until $-20°C$ in both seasons.
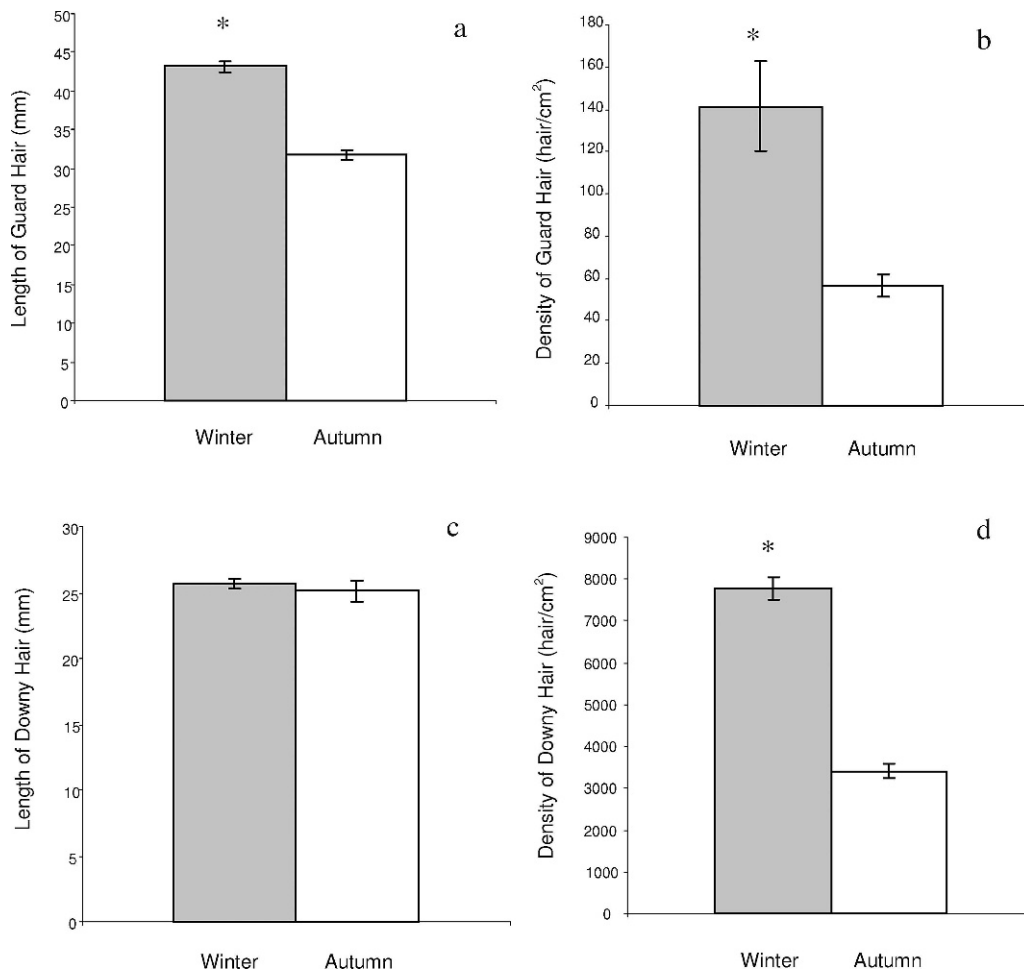
FIG. 3.—Pelage characteristics of snowshoe hares (*Lepus americanus*) from Yukon, Canada, during winter ($n = 6$) or autumn ($n = 6$) (mean ± *SE*). a) Length of guard hairs; b) density of guard hairs; c) length of downy hairs; d) and density of downy hairs. An asterisk denotes a significant difference ($P < 0.05$).

Fur insulation was higher in winter than in autumn ($F = 77.35$, *d.f.* = 4, 8, $P < 0.0001$; Fig. 3). Using a Tukey honestly significant difference post hoc test we found that length of guard hairs in winter (43.19 ± 0.69 mm) was 36% longer than in autumn (31.67 ± 0.62 mm; $P < 0.0005$) and that guard hair density in winter (141.50 ± 21.42 hairs/cm^2) was 148% greater than in autumn (57.00 ± 5.34 hairs/cm^2; $P < 0.005$). Length of downy hairs did not change between winter (25.64 ± 0.38 mm) and autumn (25.15 ± 1.02 mm; $P > 0.05$), but density of downy hairs in winter ($7,788.83 \pm 266.63$ hairs/cm^2) was 128% greater than in autumn ($3,411.50 \pm 169.41$ hairs/cm^2; $P < 0.0005$). Winter guard hairs were also wider and flatter compared with early-autumn hairs.

DISCUSSION

Observed daily temperature highs and daily lows during our study period were 15°C and 26°C lower in winter than in autumn. This decline in T_a can be expected to directly affect an animal's energy budget. If they did not acclimatize, snowshoe hares would have to substantially increase their thermoregulatory expenditure at a time of reduced food

quantity and quality. Thus, hares must have an overwintering strategy to reduce energy requirements and improve cold tolerance under this new set of environmental conditions. We found that winter acclimatization in snowshoe hares consisted of hares maintaining body mass and T_b, reducing RMR, reducing thermal conductance, and increasing pelage length and density.

Although changes in body mass are a component of seasonal acclimatization in many mammals, snowshoe hares maintained the same body mass in autumn and winter. Some mammals reduce body mass in winter, presumably as a means to decrease total daily energy expenditure (Dehnel 1949; Heldmaier 1989; Lovegrove 2005; Merritt 1995). Alternatively, mammals may increase body mass in response to extremely cold winters because an increase in size allows for greater insulation (Hart 1956; Nilssen et al. 1984; Prestrud and Nilssen 1992), a reduced ratio of surface area to volume (Vaughan 1986), and prolonged fasting endurance (Lindstedt and Boyce 1985). Several northern mammals are known to increase body mass in winter (Li et al. 2001; Merritt 1986; Merritt et al. 2001; Nagy 1993), but this approach is only feasible if access to resources is sufficient in autumn to

increase mass and in winter to sustain the elevated total energy requirements associated with increased mass. Many of these species seem to find a release from winter food limitation by employing a variety of other strategies to reduce energy expenditure such as torpor, food caching, and communal nesting. Snowshoe hares employ none of these energy conservation strategies. Snowshoe hares survive the winter with a marrow fat content very close to starvation (M. J. Sheriff, pers. obs.), thus decreasing body fat may not be possible. Reductions in lean body mass may not be favored because of the low energy yield per unit mass of nonlipid tissues and the considerable cost of reconstituting these tissues in spring (Speakman 2000). This will especially be the case for herbivorous snowshoe hares at high latitudes that become reproductively active when winter climate and forage conditions persist (Stefan and Krebs 2001). Increasing body mass may not be possible either, because of the decrease in food quantity and quality during autumn and winter (Sinclair et al. 1982).

A reduction in T_b also would reduce total daily energy expenditure and this is seen in some winter-acclimatized mammals (Fuglesteg et al. 2006; Merritt et al. 2001). However, we found that snowshoe hares were characterized by similar rectal temperatures (average of 39.4°C in both seasons) over a wide range of T_a. This is consistent with the findings of Hart et al. (1965), who found that snowshoe hares maintained rectal temperatures of 39.8°C. Substernal temperatures of 38.9°C also were maintained across seasons; however, these were significantly lower than rectal temperatures (Hart et al. 1965). The T_b of lagomorphs, including the snowshoe hare, is often higher than predicted by allometric models and only 1 study has shown seasonal variation in T_b. Rogowitz (1990) showed that *Lepus townsendii* increased T_b from 38.2°C to 38.9°C from the summer to the winter. Even though the snowshoe hare is a northern species, its T_b is comparable to, and possibly higher than, that of most other lagomorphs (*L. arcticus*, 38.9°C [Wang et al. 1973]; *Sylvilagus audubonii*, 38.5°C [Hinds 1973]; *Ochotona princeps*, 40.1°C [MacArthur and Wang 1973]; *L. californicus*, 38.8°C [Hinds 1977]; *L. alleni*, 38.1°C [Hinds 1977]; *L. timidus*, 39.7°C [Pyornila et al. 1992]; and *Brachylagus idahoensis*, 38.5°C [Katzner et al. 1997]).

There have been many conflicting studies on cold acclimatization in basal metabolic rate or RMR. Many studies show that an increase in metabolic rate may be adaptive to maintain euthermy in cold conditions (Hinds 1973, 1977; Li et al. 2001; McDevitt and Speakman 1994; Merritt 1995; Merritt et al. 2001; Rogowitz 1990; Tomasi and Horwitz 1987), whereas others show that a decrease in metabolic rate may be adaptive in order to decrease energy expenditure during periods of scarce resources that tend to coincide with cold conditions (Corp et al. 1997; Grodzinski et al. 1977; Maddocks and Geiser 2000; Wunder et al. 1977). However, these studies have primarily involved captive or semicaptive animals acclimated to unnatural resource conditions and temperatures above −5°C. Fuglesteg et al. (2006) investigated

seasonal variation in basal metabolic rate of arctic foxes (*Vulpes lagopus*), acclimatized to their natural environment, at T_a as low as −30°C in the summer and −45°C in the winter. They found that basal metabolic rate was reduced by 36% in the winter. Other studies on arctic species also have shown depressed RMR values in the winter, presumably to reduce energy expenditure in response to overwinter food shortage and starvation (Fuglei and Oritsland 1999; Mortensen and Blix 1986; Nilssen et al. 1984). In snowshoe hares, we found that RMR was reduced by 20% between winter (1,215.64 ± 64.82 ml O_2/h) and autumn (976.68 ± 50.15 ml O_2/h). In comparison to previous work presenting snowshoe hare RMR as milliliters of O_2 per gram per hour, our winter RMR value of 0.70 ml O_2 g^{-1} h^{-1} is similar to what Irving et al. (1957) found for a single snowshoe hare in the winter in Anchorage, Alaska, but lower than that reported by Hart et al. (1965), who found a RMR value of approximately 0.9 ml O_2 g^{-1} h^{-1} for hares from southern Ontario, Canada. Furthermore, Hart et al. (1965) found that RMR was lower in the winter compared with the summer only at temperatures below the thermoneutral zone, but within the thermoneutral zone there was no difference. The winter decline in RMR we found in free-ranging hares in the Yukon is likely due to the longer and harsher winter experienced by this northern population. The hares in the study of Hart et al. (1965) were captive (and thus fed ad libitum, artificial diets) and experienced daily minimum temperatures in winter (coinciding with the active period of hares) only 3°C lower than their lower critical temperature. In the present study, hares were free-ranging in the wild immediately before RMR measurements and therefore experienced natural winter food scarcity and average winter daily lows approximately 20°C lower than their lower critical temperature. In order to reduce energy expenditure, a decline in RMR may be the normal overwinter strategy of northern populations that face extremely cold temperatures accompanied by reductions in food quality and quantity.

The lower critical temperature for snowshoe hares shifted approximately 10°C from 0°C to −10°C in autumn to −10°C to −15°C in winter. Hart et al. (1965) found that hares shifted their lower critical temperature from 10°C in the summer to −5°C in the winter. As with the difference in RMR, the difference in lower critical temperature for each population likely reflects the different climate hares experience at each location. The downward shift in lower critical temperature during cold acclimatization, and associated reductions in energy expenditure below the lower critical temperature, has been shown in many other species and results in a reduction of energy expenditure (e.g., Fuglesteg et al. 2006; Hinds 1973, 1977; Rogowitz 1990).

Thermal conductance in snowshoe hares declined by 30% in winter compared with autumn. A seasonal difference in thermal conductance has been shown in 3 other leporids (Hinds 1973, 1977; Rogowitz 1990) and other northern species (Fuglesteg et al. 2006; Mortensen and Blix 1986; Nilssen et al. 1984). In comparison with previous work presenting snowshoe hare thermal conductance on a per gram basis, our estimated

conductance of 0.015 ml O_2 g^{-1} h^{-1} $°C^{-1}$ in winter is similar to the values of Irving et al. (1957) for Alaskan snowshoe hares (0.016 ml O_2 g^{-1} h^{-1} $°C^{-1}$) and lower than the values of Hart et al. (1965) for hares in Ontario (0.023 ml O_2 g^{-1} h^{-1} $°C^{-1}$). The lower thermal conductance of northern populations of snowshoe hares (this study and that of Irving et al. [1957] compared to the study of Hart et al. [1965]) presumably adapts them to the more northerly climate they inhabit by reducing thermoregulatory requirements at the low T_a they encounter.

Scholander (1955) 1st stated that small mammals could not accumulate enough body fat or hair insulation to contend with low winter T_a without compromising locomotion. However, many studies now show that winter-active small mammals increase pelage insulation in order to reduce thermal conductance (Bozinovic and Merritt 1992; Hart et al. 1965; Ivanter 1994; McClure and Porter 1983; Rogowitz 1990; Sealander 1972; Webb and McClure 1988). These studies show that hair length, density, and quality can all affect heat flow and insulation. We found that snowshoe hares increased guard hair length by 36%, and that guard hair and downy hair density increased by 148% and 128%, respectively. Winter guard hairs also were wider and flatter compared with those in early autumn. These changes could account for most, if not all, of the documented decrease in thermal conductance in the winter.

In the present study, we found that a decline in lower critical temperature and thermal conductance, associated with an increase in pelage insulation, allows a northern population of snowshoe hares to maintain their T_b while reducing their RMR in winter. Energy conservation in winter is essential for wild snowshoe hares because they are directly exposed to cold environmental conditions while simultaneously experiencing greatly reduced food quantity and quality. In contrast, Hart et al. (1965) found that insulative changes alone were sufficient to compensate for seasonal changes in temperature experienced by snowshoe hares in southern Ontario, Canada. We suggest that these differences demonstrate the ability of snowshoe hares to adjust components of seasonal acclimatization depending on the environment they experience. This phenotypic plasticity in thermal biology may be one reason why the distribution of snowshoe hares extends from the shrub tundra of the southern arctic to mountainous forests of New Mexico and Tennessee.

ACKNOWLEDGMENTS

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