Sensible heat loss from Muskoxen (Ovibos moschatus) feeding in winter: small calves are not at a thermal disadvantage compared with adult cows

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Abstract

Muskoxen (Ovibos moschatus) are large (>200 kg adult body mass) mammalian herbivores that overwinter in the polar regions. Calves are around one-third the body mass of mature females and may be expected to suffer greater thermal stresses in winter compared with adults because the ratio of surface area to volume (SA : vol) is much greater for calves than for adults. We found that during feeding bouts, when animals are fully exposed to environmental conditions, calves did lose sensible (dry) heat more readily than adults (W m(-2)) in still air conditions. However, calves and cows lost less than 2%-6% of their estimated daily digestible energy intake as conductive, convective, and radiant heat losses accumulated during feeding bouts. More important, calves did not lose relatively more heat than larger adults in terms of sensible losses as part of their daily energy intake. Coat surface temperatures were only 2 degrees-5 degrees C above ambient even when air temperature fell to -40 degrees C. Body temperatures recorded deep within the ear canal near the tympanum fluctuated in both cows and calves. Muskoxen combine peripheral heterothermy and an exceptional winter coat to minimize sensible heat loss in winter. These mechanisms appear to have circumvented some of the thermal problems normally associated with a high SA : vol ratio in calves, which reflects the strong selection to conserve energy in winter.

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Sensible Heat Loss from Muskoxen (*Ovibos moschatus*) Feeding in Winter: Small Calves Are Not at a Thermal Disadvantage Compared with Adult Cows

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ABSTRACT

Muskoxen (*Ovibos moschatus*) are large (>200 kg adult body mass) mammalian herbivores that overwinter in the polar regions. Calves are around one-third the body mass of mature females and may be expected to suffer greater thermal stresses in winter compared with adults because the ratio of surface area to volume (SA : vol) is much greater for calves than for adults. We found that during feeding bouts, when animals are fully exposed to environmental conditions, calves did lose sensible (dry) heat more readily than adults (W m^{-2}) in still air conditions. However, calves and cows lost less than 2%–6% of their estimated daily digestible energy intake as conductive, convective, and radiant heat losses accumulated during feeding bouts. More important, calves did not lose relatively more heat than larger adults in terms of sensible losses as part of their daily energy intake. Coat surface temperatures were only 2°–5°C above ambient even when air temperature fell to −40°C. Body temperatures recorded deep within the ear canal near the tympanum fluctuated in both cows and calves. Muskoxen combine peripheral heterothermy and an exceptional winter coat to minimize sensible heat loss in winter. These mechanisms appear to have circumvented some of the thermal problems normally associated with a high SA : vol ratio in calves, which reflects the strong selection to conserve energy in winter.

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Introduction

Feeding can be expensive; animals must expend energy to find, ingest, and process food while they may be exposed to environmental and predation risks. Risks of environmental exposure are especially prominent for species in polar regions, such as muskoxen (*Ovibos moschatus*). Muskoxen are large (>200 kg) grazing ruminants that spend winter where ambient temperature (T_a) routinely falls below −40°C and may reach an effective temperature as low as −80°C with wind chill (Blix 2005). Muskoxen conserve energy in winter by reducing activity (Forchhammer 1995; Munn and Barboza 2008) and rates of basal metabolism (Nilssen et al. 1994; Lawler and White 1997), without profound metabolic depressions such as torpor or hibernation. Consequently, these large herbivores must forage year-round, and feeding is their dominant activity in winter (Forchhammer 1995; Munn and Barboza 2008). Adult muskoxen are well equipped for winter, with a thick coat of underwool, known as qiviut, that affords exceptional insulation (Rowell et al. 2001). Additionally, adults carry substantial stores of body fat (Adamczewski et al. 1995) that provide further insulation as well as energy during food shortages or when extreme weather prevents foraging. Winter mortalities of adult muskoxen are typically low, but calves are more vulnerable than adults to the combined effects of exposure, starvation, and predation in winter (Thing et al. 1987; Aastrup and Mosbech 2000; Larter and Nagy 2001; Reynolds et al. 2002). In large mammalian herbivores, high rates of juvenile mortality are common and have profound consequences for the structure and growth of their populations (Saether 1997; Gaillard et al. 1998).

Muskoxen are born at 6–8 kg body mass shortly before spring (April–May), when snow and ice still cover the ground. Neonates are well equipped to manage cold conditions because they are insulated with qiviut and possess brown fat for non-shivering thermogenesis (Blix et al. 1984). Brown fat in muskoxen is apparently depleted over the first few weeks postpartum (Adamczewski et al. 1995). Under captive conditions, calves continue to grow through spring and summer, and by the onset of winter in October, they are normally around 70–80 kg body mass, or about one-third the size of adults (200–250 kg; Peltier and Barboza 2003; Knott et al. 2005). Muskox calves enter their first winter with half the body fat content (percent body mass) of mature cows (Adamczewski et al. 1995; Peltier and Barboza 2003). Small calves have higher ratios of surface area to volume (SA : vol) than adults and are therefore expected to lose heat more readily than adults with similar insulation. Consequently,
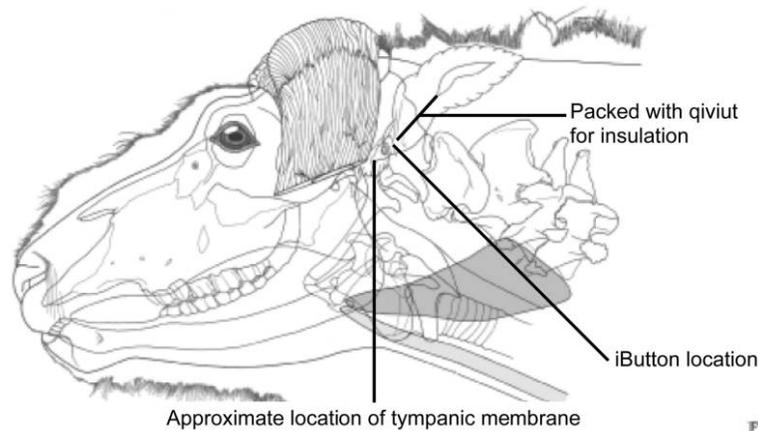
Figure 1. Left lateral view of an adult muskox indicating the approximate location of the tympanic membrane in relation to the placement of an iButton for the measurement of deep ear temperature. The external auditory meatus was packed with qiviut to provide insulation for the ear canal to allow iButton temperature to equilibrate with tympanic ear temperature (modified with permission from original artwork of Frey et al. 2006).

constraints related to thermoregulation are an obvious possible explanation for the apparent vulnerability of muskox calves to severe winters.

We tested the hypothesis that juvenile muskoxen experienced greater thermal stress than adults in winter under captive conditions, where the effects of food availability and predation are excluded. We estimated sensible (nonevaporative) heat losses from captive muskoxen feeding in midwinter by using infrared technologies to measure their surface temperatures (reviewed by McCafferty [2007]). We focused on heat losses from animals during their feeding bouts because potential energy losses while feeding present tangible trade-offs in animal time-energy budgets. Successful foraging (i.e., achieving positive energy balance) may occur only when energy assimilation from feeding bouts markedly exceeds that lost as heat from the body surface when feeding, which may be substantial for arctic mammals in winter. Additionally, we monitored fluctuations in deep ear temperature (T_{ear}) to detect peripheral heterothermy in muskoxen during midwinter. We experienced two environmental extremes during our study, a relatively warm week (T_a ca. $-5°$C) and a cold week (T_a ca. $-30°$C), which allowed us to compare sensible heat losses of adults and juveniles in direct relation to their thermal environment.

Material and Methods

Animals

Mature female (cows; $n = 6$) and young-of-the-year (calves; $n = 3$ [2 male, 1 female]) muskoxen were studied at the R. G. White Large Animal Research Station (LARS), Institute of Arctic Biology, University of Alaska, Fairbanks (lat 65°N, long 146°W). Animals were studied through midwinter, between December 20, 2004, and January 14, 2005. Cows were not pregnant, were at least 10 yr old (mean ± SEM = 13.4 ± 0.8), and had a mean body mass of 231.3 ± 2.3 kg at the beginning of the study. Calves were born between April 8 and May 17, 2004.

At the beginning of the study, calves were 7.8 ± 0.4 mo of age (± SEM) and weighed 94.7 ± 4.9 kg. Individual cows and calves were identified using reflective ribbon (2 cm × 50 cm) braided into a small patch of fur.

Calves were separated from their mothers and weaned on December 1, 2004. The mothers of those calves were not used in this experiment. Thereafter, the calves were maintained in a large pen (0.2 ha) directly adjacent to a larger pen (0.5 ha) where the cows were maintained. Calves and cows were in visual contact, but a butting barrier on the calf side of the fence prevented physical interaction. Snow (water) and long (unchopped) Brome grass hay (*Bromus* sp.) were provided to calves and cows ad lib. (for dietary analysis, see Munn and Barboza 2008). Additionally, cows and calves received a daily pelleted ration of milled grain and alfalfa with minerals and vitamins (Alaska Pet and Garden, Anchorage) at 200 and 100 g pellet air dry mass d^{-1}, respectively (Munn and Barboza 2008). The ration is a balanced supplement of minerals to grass hay (Peltier and Barboza 2003). Pellet rations were offered equivalent to 3.0 g dry matter kg$^{-0.75}$ d^{-1} for the cows and calves and were always completely consumed. Animals were herded through a large barn and handling chute each day between 0800 and 0900 hours to record their body mass (± 0.5 kg; Tru-Test model 703 scale; San Antonio, TX) and to offer a ration of pellets.

Weather

We recorded ambient temperature (T_a; ± 0.2°–0.7°C between T_a 0° and -40°C; sensor model S-TMB-M006), black globe temperature (T_{bg}; ± 0.2°–0.7°C between T_a 0° and -40°C; sensor model S-TMB-M006), wind speed (± 1.1 m s^{-1}; sensor model S-WSA-M003), wind gust speed (± 1.1 m s^{-1}; sensor model S-WSA-M003), and solar radiation (± 10 W m^{-2} or ± 5% of measured input in daylight, whichever was greater; sensor model S-LIB-M003) by using a HOBO weather station (model H21-002; Onset Computer, Bourne, MA). Inputs from

Figure 2. Typical thermal image illustrating a cow (*left*) and calves (*right*) separated by a feeding station (*middle*; showing overhead CCD camera) filled with hay.

T_a, T_{bg}, and wind and solar sensors were logged every 10 min. Mean ($\pm$ SEM) values for T_a and T_{bg} differed by $0.8° \pm 0.02°C$ ($n = 1{,}430$) over the entire study, with a median difference of $0.6°C$, which was within the precision limits for each sensor. Wind speeds, T_a, and T_{bg} were measured at the height of adult female muskoxen (1.1 m). Ambient relative humidity was measured at the Geophysical Institute, University of Alaska, Fairbanks, approximately 2 km south of LARS. Snowfall was recorded 3 km south of LARS at the Agricultural and Forestry Experiment Station.

Feeding Behavior

Behavioral observations were carried out in two 5-d bouts in early January 2005. The first bout (week 1) was from 0900 hours on January 3 to 0800 hours on January 8, and the second bout (week 2) was from 0900 hours on January 9 to 0800 hours on January 14. Thus, during week 1 and week 2, animals were observed continuously over 23 h each day for five consecutive days. Observations were not recorded between 0800 and 0900 hours daily because the animals were disturbed for collection of feces, weighing, and other procedures (see Munn and Barboza 2008).

Animals were observed from a tower (height 4.3 m) overlooking both adjacent pens for cows and calves. A feeder containing grass hay was situated 14.5 ± 1.5 m from the base of the tower, allowing free access from either pen. Fresh hay was offered daily at irregular intervals to prevent entrainment. Animals were easily observed and identified by the naked eye or by using binoculars when there was sufficient daylight. Under low light conditions, animals were identified using a handheld night-vision scope (Infra-red Imager, Rostov Cyclops 8M). We recorded individual foraging times for each animal and noted the initiation and termination time for each foraging bout.

Deep Ear Temperature

The deep ear temperature (T_{ear}) of each animal was logged every 10 min, using an iButton (model DS1921H; Maxim Integrated Products, Sunnyvale, CA) calibrated to $\pm 0.1°C$. Two weeks before week 1, each animal was trained to tolerate an iButton inserted into the left ear (Fig. 1). Each iButton was secured to a modified fob-style holder (Maxim Integrated Products) wrapped with qiviut and inserted into the ear canal (see also Guidry and McDowell 1966). An iButton was placed at the terminal narrowing of the external auditory canal, approximately 2 cm from the tympanic membrane (Fig. 1; A. J. Munn, personal observation). This region is well insulated by the mane and by large cervical fat pads (Frey et al. 2006). After insertion, the ear canal was packed gently with cleaned qiviut until the entire external auditory canal was filled. To prevent the qiviut packing or iButton from dislodging, the ear was "sealed" by gluing a piece of surgical gauze to the external auditory meatus (Fig. 1). At the end of week 1, the iButton was removed, the data were downloaded, and the package was reinserted for week 2. By the end of week 2, iButton internal clocks had drifted by an average (± 1 SD) of 2.1 ± 0.5 s d^{-1} after synchronizing to Coordinated Universal Time (Atomic Clocksyc, ver. 2.7.0.3; Chaos Software, http://www.worldtimeserver.com/atomic-clock/) at the beginning of week 1. Average maxima and average minima of T_{ear} in week 1 and week 2 were quantified from the mean temperature peaks ($T_{ear\,max}$) and troughs ($T_{ear\,min}$) for each animal, recorded by iButtons.

Surface Temperature

Surface (coat) temperature (T_{sur}) was measured for animals during every feeding bout, using a forward-looking infrared radiometer (FLIR; ThermaCAM s40, FLIR Systems, Danderyd,

Table 1: Weather conditions during the feeding trials in the warm
week (week 1) and the cold week (week 2)

Parameter	Week 1 ($n = 5$ d)	Week 2 ($n = 5$ d)
Ambient temperature (°C):		
Average ($\pm$ SEM)	$-4.3 \pm .1$	$-32.2 \pm .3$
Maximum	$-.3$	-13.8
Minimum	-10.2	-41.1
Median	-4.4	-34.2
Wind speed (m s^{-1}):		
Average ($\pm$ SEM)	$.4 \pm .03$	$.02 \pm .004$
Maximum	4.2	1.1
Minimum	.0	.0
Median	.0	.0
Wind gust speed (m s^{-1}):[a]		
Average ($\pm$ SEM)	$3.1 \pm .1$	$.84 \pm .04$
Maximum	12.9	3.8
Minimum	.4	.0
Median	1.9	.8
Solar radiation (W m^{-2}):[b]		
Average ($\pm$ SEM)	$4.7 \pm .3$	16.2 ± 1.1
Maximum	16.3	56.3
Minimum	1.3	1.3
Median	5.0	12.5

[a] Averaged from detected wind gusts.
[b] Averaged for daylight hours with detectable solar input (i.e., >0 W m^{-2}).

Sweden). We used a 24° lens with a total angle of view of 7.0 m, capable of capturing both calves and cows feeding simultaneously. The FLIR was located in the observation tower, 15.1 ± 2.9 m from the midpoint of the feeder, providing a viewing angle of approximately 11° (see McCafferty 2007). At that distance, each pixel of captured image was equivalent to 1.8–2.2 cm^2 of animal surface. The FLIR viewed the feeder through an aperture covered with transparent window plastic (Frost King Window Insulation, V73/3; Thermwell, Mahwah, NJ) applied according to the manufacturer's instructions. Transmissivity of the window plastic was measured as 0.87 (FLIR Systems, Notting Hill, Victoria). Animals usually foraged perpendicular to the feeder, thereby presenting one side to the camera (Fig. 2). Importantly, interference from solar radiation (McCafferty 2007) was not a concern because the experimental yards were not in direct sunlight during our study (see "Weather"). As a check, we compared surface temperatures recorded by the FLIR against a black globe thermometer (i.e., a black body; 152 mm diameter; Esis Environmental Monitoring, New South Wales) from 177 images ($n = 87$ from week 1 and $n = 90$ from week 2, with approximately half of the images from each week from cows and half from calves); black globe temperatures recorded by the FLIR differed from those recorded by the black globe temperature sensor (i.e., input from the HOBO weather station) by an average of $0.39° \pm 0.04°$C, which was within the precision limits of the sensor (model S-TMB-M006; $\pm 0.2°$–$0.7°$C between T_a 0° and $-40°$C).

Images captured by the FLIR were recorded at 1-min intervals, stored on a portable flash drive, and downloaded to a personal computer between 0800 and 0900 hours each day; T_{sur} was measured along the length of each animal from the rump to the neck at shoulder height using the "line" function in the ThermaCAM Researcher Pro 2.7 (FLIR Systems) and assuming an animal emissivity of 0.98 (Monteith and Unsworth 1990). Notably, during most foraging bouts, the entire surface of animals was not visible, and the head and feet were typically obscured by the feeding apparatus or by other animals. Consequently, we were unable to measure surface temperatures from entire animals in most cases. However, we were able to isolate $n = 177$ images where the entire surface of an animal was visible ($n = 87$ from week 1 and $n = 90$ from week 2); approximately half of the images from each week were from cows and calves, respectively (e.g., see Fig. 2). Using FLIR images where the entire surface of the animal was visible, we found that the average surface temperature of whole animals (including the head and front and rear legs) and measured using the "area" function in the ThermaCAM Researcher Pro 2.7 (FLIR Systems) differed from that measured at shoulder height using the "line" function (Fig. 2) by an average of $0.01° \pm 0.07°$C. Therefore, T_{sur} measured at shoulder height was a reliable measure of the mean surface temperature of muskoxen in our experiment. For each animal, mean T_{sur} measured by FLIR was taken from the midpoint of each foraging bout or from 5 min pre- or postmidpoint (i.e., if a midpoint image was not available or obscured by other animals).

In addition to the FLIR recordings, animals were monitored continuously at the feeder, using a miniature CCD camera (B/W Miniature CCD, model KPC 190SWX; Korea Technology
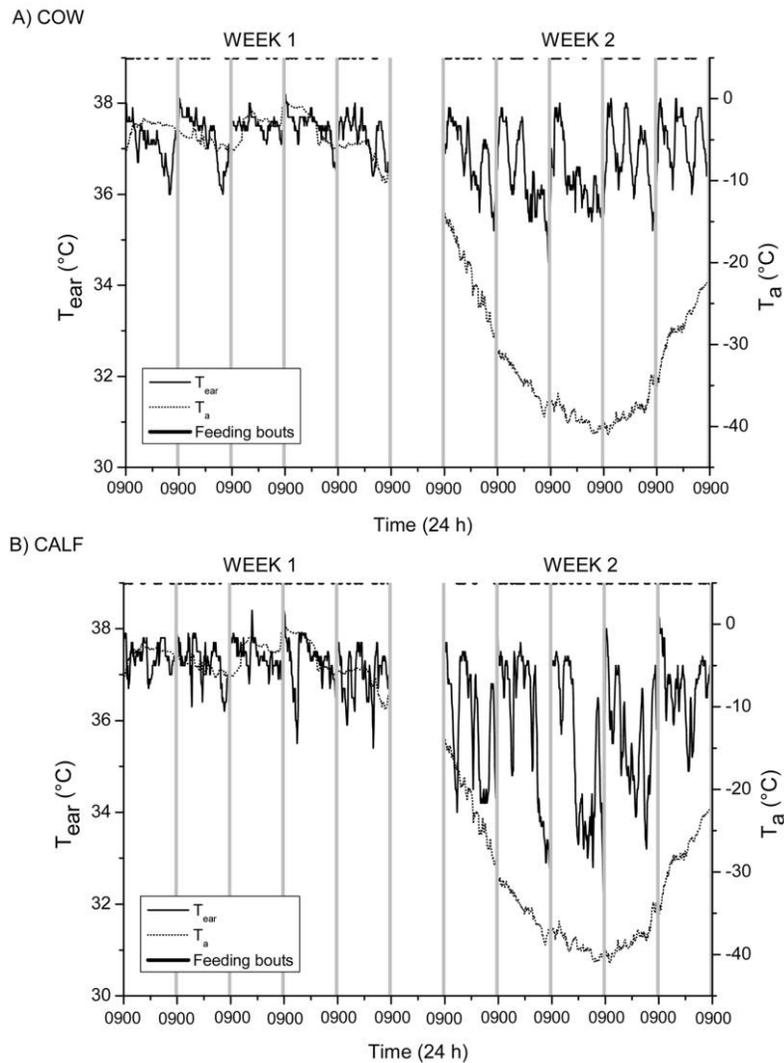
Figure 3. Representative traces for deep ear temperature (T_{ear}; *solid line*) and ambient temperature (T_a; *dotted line*) for a muskox cow (*A*) and calf (*B*) during a warm week (week 1) and a cold week (week 2) in midwinter Alaska. Feeding bouts are indicated by bars at the top of each plot. Note that vertical gray columns indicate the period when the animals were disturbed daily for body weight measurements and other procedures (see Munn and Barboza 2008).

and Communications) encased in foam insulation, mounted above the feeder, and illuminated with a 15-W red lightbulb. The CCD images were logged at 30-s intervals on a personal computer, using a digital video recording system (DICO-800, ver. 3.5, video surveillance and DVR system; Video-Surveillence.com, New York). Images from the CCD were cross-referenced with FLIR images for identification of individual muskoxen.

Surface Areas and Characteristic Diameters

Heat exchanges between an object and its environment depend on the object surface area (SA) available for exchange and the temperature gradient between the object surfaces and its sur-

roundings. To assess heat loss from muskoxen, we estimated SA (m^2) for average cows and calves by constructing three-dimensional-scale (1 : 10 cm) clay models according to the average body dimensions obtained from photographs. We modeled the basic muskox shape, including the head, coat skirt, and fore and hind limbs, as presented by foraging animals. The SA of each model (excluding hoof-to-ground contact area) was then traced using tissue paper and the area was measured using a digital planimeter (Graphtec Digitizer KD 4300, Graphtec, Tokyo). Estimated SAs for radiant and convective heat losses were 1.8 m^2 for calves and 3.7 m^2 for cows, comparable to those estimated for mature domestic cattle derived using digitally constructed, ellipsoid models (3.27 m^2; Keren and Olsen 2006). Average diameter (*d*) for cows and calves was measured as-

Table 2: Average deep ear temperatures (T_{ear}) for mature female (cow; $n = 6$) and young-of-the-year (calf; $n = 3$) muskoxen during a warm week (week 1) and a cold week (week 2) week in midwinter Alaska

T_{ear} (°C)	Week 1 (over 5 d)	Week 2 (over 5 d)	Age Effect P value
Average:			
Cow	37.0 ± .1[A]	35.7 ± .4[B]	NS
Calf	37.1 ± .1[A]	34.5 ± .8[B]	
Maximum:			
Cow	37.8 ± .2[A]	37.6 ± .1[A]	<.05
Calf	38.5 ± .0[A]	38.1 ± .3[A]	
Minimum:			
Cow	35.8 ± .3[A]	32.6 ± .9[B]	≤.05
Calf	34.6 ± .5[A]	28.9 ± 1.7[B]	

Note. Means (±SEM) with different superscript letters denote significant differences between weeks within age groups; $P \leq 0.05$. NS = not significant.

suming a cylindrical shape (Keren and Olsen 2006) and taking the mean circumference at the rump, middle, hump, neck, and head of each scale clay model (calves, 0.76 m; cows, 0.92 m).

Hoof-to-ground contact surface areas (SA_{hoof}; fore and hind) were estimated for cows and calves, using hoof width and length from photographs and assuming an elliptical shape; single fore-hoof $SA = 103 \pm 0.01$ cm^{-2} for cows and 56 ± 0.01 cm^{-2} for calves, and single hind hoof $SA = 104 \pm 0.01$ cm^{-2} for cows and 54.0 ± 0.01 cm^{-2} for calves.

Sensible Heat Loss during Feeding Bouts

Sensible or nonevaporative heat exchange can occur between an animal's surface and its environment via three paths: radiation (long- and shortwave), convection, and conduction (Monteith and Unsworth 1990). The thermal environment in our study was simplified because solar (shortwave) radiant influxes were negligible (Table 1) and thus had minimal impact on the overall heat budget of cows or calves. Thus, we constructed a model of sensible heat loss (G_S) from muskoxen during feeding bouts, according to (Monteith and Unsworth 1990; Maia et al. 2005)

$$G_S = K + C + L, \tag{1}$$

where K is conductive heat loss from hooves in contact with the ground/ice (W m^{-2}), C is convective heat exchange (W m^{-2}), and L is heat exchange by longwave radiation (W m^{-2}).

Conductive heat loss (K) occurred between hooves and the ice (compacted snow surrounding the feeder) and was measured according to (Blaxter 1989; see also Gatenby 1977)

$$K = \frac{\rho C_p}{r_S} \cdot (T_{hoof} - T_g), \tag{2}$$

where ρC_p is volumetric specific heat capacity of the hoof (1.99 J cm^{-3} K^{-1}), estimated from the density of keratin (1.3 g cm^{-3}; Withers 1992) and the specific heat capacity of bovid horn

sheath keratin (1.53 J g^{-1} K^{-1}; Picard et al. 1999); r_S is the thermal resistance of hoof keratin; T_{hoof} is hoof surface temperature (K); and T_g is ground temperature (K; assumed = T_a). The thermal resistance (m^{-1}) of hoof keratin was estimated according to (Withers 1992)

$$r_S = \frac{\rho C_p \cdot l}{k}, \tag{3}$$

where l is hoof thickness (assumed = 2.5 cm) and k is the coefficient of conductive heat exchange for bovid horn sheath keratin (6.3 × 10^{-3} W cm^{-1} °C^{-1}; Picard et al. 1999). Hooves were rarely visible during feeding bouts, making it difficult to estimate conductive heat loss via this route. Therefore, we isolated FLIR images for each animal ($n = 18$–21 images per animal) where hoofs were visible (fore and hind) and measured T_{hoof} across the full range of T_a in both weeks. For each animal there was a tight, significant relationship between T_a and T_{hoof} ($P < 0.01$; see "Results"), and the regression equations were used to estimate T_{hoof} from T_a at the midpoint of each animal's feeding bout. We measured T_{hoof} from FLIR images using the "line" function reporting the maximum temperature for the distalmost 1.8–2.5 cm of the hoof (i.e., laterally and immediately adjacent to the ground); this represents the temperature gradient through which heat flowed from the animal to the ground/ice. We did not use temperatures from the dorsal hoof surface (as might be used for measures of convective and radiant heat loss) because these temperatures are not indicative of the gradient between hoof and ground because the dorsal hoof surface of ungulates is less protected by ketrain and fat than the sole (Budras 2003). We assumed a hoof thickness for the heat-exchanging layer of 2.5 cm, typical of the width trimmed from captive muskoxen without interfering with the vascular layer (P. S. Barboza, personal observation). Total K (W m^{-2}) via the hooves was estimated for cows and calves from forehooves and hind hooves combined.

Table 3: Average animal and environmental properties for mature female
(cow; $n = 6$) and young-of-the-year (calf; $n = 3$) muskoxen during
feeding bouts in a warm week (week 1) and a cold week (week 2) in
midwinter Alaska

Parameter	Week 1	Week 2	Age Effect P value
Total feeding time (min d^{-1}):[a]			
Cow	320 ± 16^A	343 ± 13^B	<.05
Calf	354 ± 5^A	387 ± 14^B	
T_a (°C):			
Cow	$-4.1 \pm .1^A$	$-32.5 \pm .7^B$	NS
Calf	$-4.0 \pm .2^A$	$-33.5 \pm .3^B$	
T_{ear} (°C):			
Cow	$37.1 \pm .1^A$	$35.9 \pm .4^B$	NS
Calf	$37.2 \pm .1^A$	$34.6 \pm .7^B$	
T_{sur} (°C):			
Cow	$-1.7 \pm .1^A$	$-28.4 \pm .6^B$	NS
Calf	$-1.3 \pm .2^A$	$-28.5 \pm .7^B$	
$T_{sur} - T_a$ (°C):			
Cow	$2.4 \pm .1^A$	$4.2 \pm .1^B$	NS
Calf	$2.7 \pm .1^A$	$4.9 \pm .4^B$	

Note. T_a = ambient temperature; T_{ear} = deep ear temperature; T_{sur} = coat surface temper-
ature. Means ($\pm$ SEM) with different superscript letters denote significant differences between
weeks within age groups; $P \leq 0.05$. NS = not significant.
[a] After Munn and Barboza 2008.

Convective heat loss was estimated as (Monteith and Uns-
worth 1990; Turnpenny et al. 2000; Maia et al. 2005)

$$C = \frac{\rho C_p}{r_H} \cdot (T_{sur} - T_a), \qquad (4)$$

where ρC_p is the volumetric specific heat capacity of air at T_a
(J m^{-3} K^{-1}; estimated from known values; Monteith and Uns-
worth 1990) and r_H is boundary layer resistance to convective
heat flow, calculated as

$$r_H = \frac{\rho C_p d}{k Nu}, \qquad (5)$$

where d is the average diameter of the body (m), k is thermal
conductivity of air at T_a (W m^{-1} K^{-1}; calculated from known
values; Monteith and Unsworth 1990), and Nu is a dimen-
sionless Nusselt number. Nu was calculated according to either
free convection or forced convection scenarios (Blaxter 1989;
Monteith and Unsworth 1990), respectively,

$$Nu = BGr^m, \qquad (6)$$

$$Nu = ARe^n, \qquad (7)$$

where Gr is a dimensionless Grashof number, Re is a dimen-
sionless Renyolds number, and A, B, m, and n are constants
(Monteith and Unsworth 1990; see descriptions for eq. [9]).
These dimensionless numbers are used to estimate heat ex-

change by convection as a consequence of a temperature gra-
dient between an object surface, its shape, and the temperature,
velocity, inertia, viscosity, and buoyancy of the surrounding air
(Monteith and Unsworth 1990). Gr was calculated as (Monteith
and Unsworth 1990)

$$Gr = \frac{a g d^3 (T_{sur} - T_a)}{v^2}, \qquad (8)$$

where a is the thermal expansion coefficient of air ($1/T_a$; K), g
is the acceleration of gravity (9.8 m s^{-1}), and v is the kinematic
viscosity of dry air at T_a (m^2 s^{-1}; calculated from known values;
Monteith and Unsworth 1990). Re was calculated as (Mount
1979; Monteith and Unsworth 1990; Keren and Olsen 2006)

$$Re = \frac{Vd}{v}, \qquad (9)$$

where V is the velocity of air (average wind speed during feeding
bout; m s^{-1}). Constants for equations (6) and (7) were from
Monteith and Unsworth (1990) and were estimated for free
convection laminar flow ($10^4 < Gr < 10^9$) over a horizontal
cylinder ($B = 0.48$; $m = 0.25$) and for forced convection
($4 \times 10^3 < Re < 4 \times 10^5$) over a cylinder ($A = 0.17$; $n = 0.62$).
Note that when we assumed free laminar convection across a
vertical rather than a horizontal cylinder (i.e., $B = 0.58$), es-
timated heat losses changed by just 0.4 W m^{-2}.

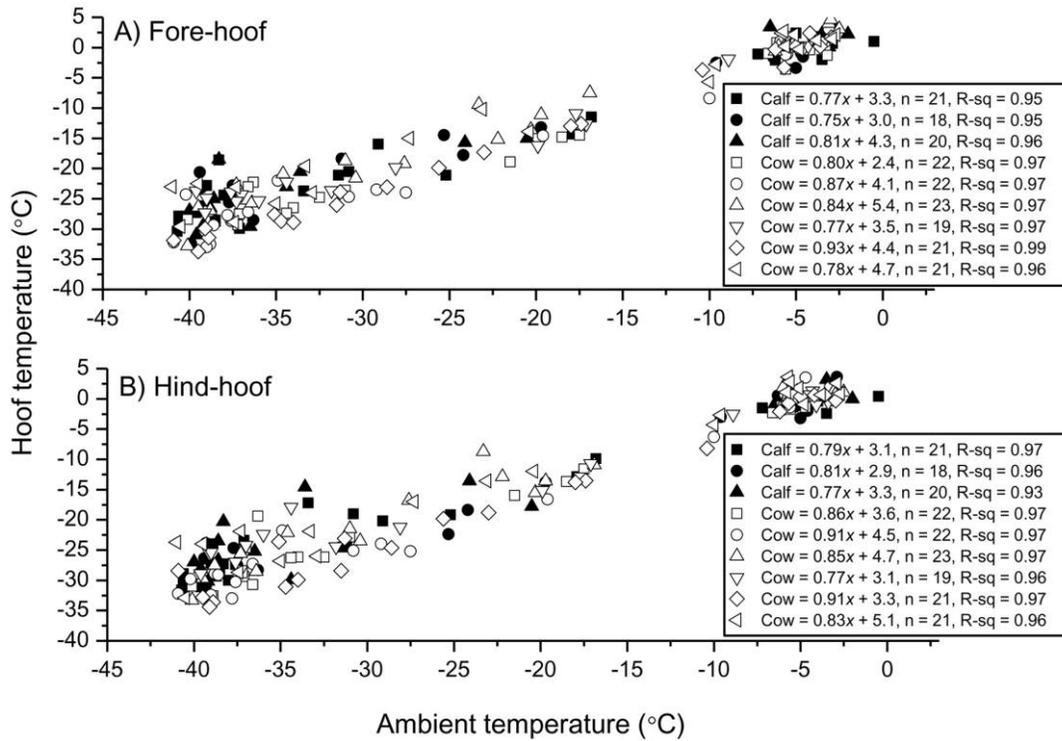Longwave radiant heat exchange (L) was estimated as (Mon-

Figure 4. Forehoof (*A*) and hind hoof (*B*) distalmost surface temperatures (°C) relative to ambient temperature (°C) from muskox calves and cows through midwinter in Alaska (regressions were significant at $P < 0.01$ in all cases).

teith and Unsworth 1990; Turnpenny et al. 2000; Maia et al. 2005)

$$L = \frac{\rho C_{\mathrm{p}}}{r_{\mathrm{R}}} \cdot (T_{\mathrm{sur}} - T_{\mathrm{a}}), \tag{10}$$

where r_{R} is radiative resistance from an object, estimated as (Monteith and Unsworth 1990; Turnpenny et al. 2000; Maia et al. 2005)

$$r_{\mathrm{R}} = \frac{\rho C_{\mathrm{p}}}{4\sigma \overline{T}_{\mathrm{sur,a}}^3}, \tag{11}$$

where σ is the Stefan-Boltzmann constant (5.67×10^{-8} W m^{-2} K^{-4}) and $\overline{T}_{\mathrm{sur,a}}$ is the average of T_{sur} and T_{a} (K). Radiant heat exchange can occur between an animal's surface, the sky, and the ground. During our study there was no significant difference between T_{a} measured at LARS and sky radiant temperatures measured nearby at the Geophysical Institute, the University of Alaska, Fairbanks ($t_{(2), 2,858} = 2.0$, $P > 0.05$), and we assumed that ground surface temperature was equal to T_{a}.

Cumulative sensible heat losses by muskoxen while feeding (feeding G_{S}; kJ d^{-1}) was estimated for each animal as

$$\text{feeding } G_{\mathrm{S}} = \frac{[(C + L) \cdot \mathrm{SA}_{\mathrm{body}} + (K \cdot \mathrm{SA}_{\mathrm{hoof}})] \cdot t_{\mathrm{feed}}}{1{,}000}, \tag{12}$$

where *C*, *L*, and *K* are in watts per square meter, $\mathrm{SA}_{\mathrm{body}}$ is the

body surface area (excluding hoof SA; m^2), $\mathrm{SA}_{\mathrm{hoof}}$ is the hoof surface area (fore and hind combined; m^2), and t_{feed} is the total daily feed time (s).

Statistical Procedures

Statistical tests were performed using Statistica (StatSoft, Tulsa, OK). Means are reported $\pm$ SE (SEM). We used repeated-measures ANOVAs to compare data within ages and between weeks. Assumptions for statistical analysis were tested using the Kolmogorov-Smirnov test for normality ($\alpha = 0.05$) and Levene's test for homogeneity of variances ($\alpha = 0.05$). Heteroscedastic data (T_{ear} and $T_{\mathrm{ear\,min}}$) were $\log_{10}$ transformed before analysis. Proportional data were arcsine transformed for analysis.

Results

Weather

Average T_{a} dropped by 28°C from week 1, a relatively "warm" period, to week 2, which we defined as a "cold" period (Table 1). Wind and incident (total) solar radiation were low throughout the entire study (Table 1). Notably, on day 2 of week 1, clouds prevented any solar input from being detected at the site, and for the remaining 4 d of the trial, solar input was intercepted (i.e., >0 W m^{-2}) for an average ($\pm$ SEM) of 198 ± 21 min d^{-1}; solar interception was 314 ± 2.5 min d^{-1} over 5 d in week 2. Detected solar radiation peaked in week 2 at just 56 W m^{-2}; average solar influxes during daylight hours

Table 4: Average hoof (fore and hind) temperatures estimated for mature female (cow; $n = 6$) and young-of-the-year (calf; $n = 3$) muskoxen during feeding bouts in a warm week (week 1) and a cold week (week 2) in midwinter Alaska

Parameter	Week 1	Week 2	Age Effect P value
Fore T_{hoof} (°C):			
Cow	$-.9 \pm .1^A$	$-23.7 \pm .5^B$	NS
Calf	$-.8 \pm .2^A$	$-24.4 \pm .2^B$	
Hind T_{hoof} (°C):			
Cow	$.5 \pm .3^A$	-23.8 ± 1.0^B	NS
Calf	$-.1 \pm .2^A$	$-23.3 \pm .4^B$	
Fore $T_{hoof} - T_{ground}$ (°C):			
Cow	$3.2 \pm .0^A$	$8.9 \pm .1^B$	NS
Calf	$3.2 \pm .0^A$	$9.1 \pm .1^B$	
Hind $T_{hoof} - T_{ground}$ (°C):			
Cow	$4.6 \pm .3^A$	$8.8 \pm .7^B$	NS
Calf	$3.9 \pm .2^A$	$10.1 \pm .6^B$	

Note. T_{hoof} = maximum hoof surface temperature at 1.8–2.5 cm lateral to the hoof-ground contact surface and estimated from feeding bout ambient temperature (T_a) using the regressions for individual animals described in Figure 4; T_{ground} = ground temperature, assumed to equal T_a (°C). Means ($\pm$ SEM) with different superscript letters denote significant differences between weeks within age groups; $P \leq 0.05$. NS = not significant.

ranged between 4.7 and 16.2 W m^{-2} throughout the experiment (Table 1). Snow fell only during week 1: 83 mm on day 2, 31 mm on day 3, and 171 mm on day 4.

Continuous T_{ear}

Overall, T_{ear} fluctuated widely over the entire study but was generally higher and less variable during the warm period (week 1) than the cold period (week 2) in both cows and calves (Fig. 3; Table 2). Maximum temperature ($T_{ear max}$) was higher in calves than in cows in both weeks but did not differ significantly within age groups between weeks (Table 2). Conversely, cows and calves showed lower $T_{ear min}$ in week 2 than in week 1; $T_{ear min}$ was significantly lower in calves than in cows in both weeks (Table 2).

Feeding Bout T_a, T_{ear}, *and* T_{sur}

Average T_a at the midpoint of each feeding bout was similar to the average T_a in each week (Table 3). Although T_a decreased by 29°C during feeding bouts between week 1 and week 2, deep ear temperatures (T_{ear}) declined during feeding by only 1.2°–2.6°C (Table 3). Within each week, average T_{ear} when feeding was not significantly different between cows and calves (Table 3).

Surface temperatures of cows and calves during feeding bouts were 27°C lower in week 2 than in week 1. Surface temperatures of calves were similar to those of cows during each week (Table 3). The difference between T_{sur} and T_a was greater in the cold week (ca. 5°C) than in the warm week (ca. 3°C; Table 3).

There was a significant relationship between distal hoof surface temperature (T_{hoof}) and T_a for all animals across T_a ranges

of −40° to +5°C (Fig. 4). Thus, using the significant regression equations derived for each individual, we estimated T_{hoof} for animals during feeding bouts according to T_a (Table 4). Average T_{hoof} during feeding bouts was not significantly different between cows and calves within weeks but was significantly lower for both age classes during the colder week 2 (Table 4). Differences between T_{hoof} and T_{ground} were similar for forehooves and hind hooves in cows and calves, being ca. 3.2°–4.6°C in week 1 and 8.9°–10.1°C in week 2, but small sample sizes preclude statistical comparisons of forehoof versus hind hoof temperatures or heat losses by conduction.

Feeding Bout Sensible Heat Loss

Instantaneous sensible heat losses (i.e., W m^{-2}) during feeding bouts were greater in week 2 than in week 1 for all routes (K, C, and L) from cows and calves (Table 5). Total sensible heat loss (kJ d^{-1}) during feeding (feeding G_S) was greater for cows compared with calves by 1.5–1.6-fold (kJ d^{-1}; Table 6). When feeding G_S (kJ d^{-1}) was expressed on the basis of metabolic body mass (i.e., kJ kg$^{-0.75}$ d^{-1}), calves exhibited significantly greater sensible heat losses when feeding by around 1.2–1.3-fold (kJ kg$^{-0.75}$ d^{-1}; Table 6). However, feeding G_S by cows and calves was a small proportion of daily digestible energy intake (DEI), ranging between 2.0% and 5.5% across both weeks (Table 6). Notably, feeding G_S (%DEI) was significantly higher in cows relative to calves in both weeks (Table 6).

Discussion

For arctic ungulates, the amount of energy lost during winter feeding bouts may present a significant trade-off in their daily energy budget. However, such a trade-off is probably negligible

Table 5: Sensible heat losses via conduction (K; hoof-to-ground forehooves and hind hooves combined), convection (C) and longwave radiation (L) from mature female (cow; $n = 6$) and young-of-the-year (calf; $n = 3$) muskoxen during feeding bouts in a warm week (week 1) and a cold week (week 2) in midwinter Alaska

Parameter	Week 1	Week 2	Age Effect P value
K (W m^{-2}):			
Cow	197 ± 9[A]	445 ± 19[B]	NS
Calf	178 ± 5[A]	484 ± 16[B]	
C (W m^{-2}):			
Cow	6.3 ± .4[A]	8.9 ± .4[B]	<.01
Calf	7.6 ± .3[A]	10.9 ± 1.0[B]	
L (W m^{-2}):			
Cow	10.9 ± .5[A]	13.5 ± .3[B]	≤.05
Calf	11.9 ± .2[A]	15.9 ± 1.4[B]	
K (%feeding G_S):			
Cow	6.0 ± .3[A]	10.0 ± .5[B]	NS
Calf	5.3 ± .3[A]	10.1 ± 1.1[B]	
C (%feeding G_S):			
Cow	34.4 ± 1.2[A]	35.7 ± .7[A]	NS
Calf	36.7 ± .7[A]	36.6 ± .8[A]	
L (%feeding G_S):			
Cow	59.6 ± 1.0[A]	54.3 ± .5[B]	NS
Calf	58.0 ± .4[A]	53.3 ± .8[B]	

Note. Heat losses are expressed per unit surface area available for heat exchange (W m^{-2}) and as a proportion of total sensible heat losses accumulated during feeding bouts (%feeding G_S; see Table 6). Means (±SEM) with different superscript letters denote significant differences between weeks within age groups; $P < 0.05$. NS = not significant.

for muskox, at least down to T_a of −40°C without wind. Overall, sensible heat losses accumulated by calves and cows when feeding amounted to just 22–41 kJ kg$^{-0.75}$ d^{-1} (Table 6), less than 2%–6% of the digestible energy they accumulated from feeding bouts (see Munn and Barboza 2008). Importantly, the internal heat loads generated from feeding could balance this level of sensible heat loss from the body surface. The heat increment of feeding for muskoxen eating brome hay in winter was 34–39 kJ kg$^{-0.75}$ d^{-1} (Lawler and White 2003), comparable to that lost as sensible heat by the adult and juvenile muskoxen in our study (Table 6).

It is intuitive that high SA : vol ratios combined with low ambient temperatures might adversely affect young muskoxen in winter. However, temperature alone could not explain muskox population dynamics across Greenland (Forchhammer and Boertmann 1993), and there were zero calf mortalities over a two-year study of newly established muskox populations in Alaska, despite severe winter conditions (Jingfors and Klein 1982). Moreover, muskox calves did not increase food (energy) intake more so than did adults when T_a declined from −5° to −30°C, suggesting that calves did not have greater thermal costs relative to those of cows (Munn and Barboza 2008). There were significant differences in the instantaneous sensible heat losses (K, C, L; W m^{-2}) by calves and cows in week 2, suggesting that calves did lose more heat than adults in the colder conditions. However, total sensible heat losses by calves amounted to a smaller proportion of their daily energy intakes as compared with that of cows (Table 6). Of note, we did not measure the total daily heat losses by each animal over 24 h, and the higher sensible heat losses (W m^{-2}) of calves in week 2 indicate that they may have significantly more sensible losses from their body surface relative to cows over an entire day under these conditions.

Overall, K was by far the largest contributor to instantaneous sensible heat loss (i.e., W m^{-2}) among calves and cows. However, the surface contact area of hooves (fore and hind) was around only 1.1% and 1.2% of total body SA for cows and calves, respectively. As such, conductive heat loss via hooves composed ca. 6% of total feeding bout heat losses by cows and calves in week 1 and ca. 10% in week 2. A small sample size precludes statistical comparisons of heat losses by the different routes within or between cows and calves (e.g., K vs. C) across weeks. Nonetheless, it is noteworthy that conductive heat losses from the hooves of cows and calves amounted to just 0.1%–0.2% of their DEIs in week 1, increasing only slightly to 0.4%–0.6% of their DEIs in week 2. Moreover, our measure of conduction via the hooves is probably an overestimate. First, it is based on a steady state model that does not account for the potential warming of the ground/ice from the hoof itself (see Blaxter 1989, p. 106), which would reduce the gradient for heat loss. A non–steady state model of K from hooves (which would account for ground warming; e.g., see Gatenby 1977) was not

Table 6: Sensible heat loss as a proportion of digestible energy intake (%DEI) from mature female (cow; $n = 6$) and young-of-the-year (calf; $n = 3$) muskoxen during feeding bouts in a warm week (week 1) and a cold week (week 2) in midwinter Alaska

Parameter	Week 1	Week 2	Age Effect P value
Feeding G_S (kJ d^{-1}):			
Cow	$1,278 \pm 84^A$	$1,893 \pm 61^B$	$<.001$
Calf	788 ± 28^A	$1,243 \pm 132^B$	
Feeding G_S (kJ kg$^{-0.75}$ d^{-1}):			
Cow	21.8 ± 1.5^A	$32.2 \pm .9^B$	$<.01$
Calf	$25.7 \pm .5^A$	40.7 ± 2.7^B	
Feeding G_S (%DEI[a]):			
Cow	$2.8 \pm .2^A$	$5.5 \pm .4^B$	$\leq.01$
Calf	$2.0 \pm .1^A$	$4.2 \pm .9^B$	

Note. Means ($\pm$SEM) with different superscript letters denote significant differences between weeks within age groups; $P \leq 0.01$.

[a] DEIs (kJ kg$^{-0.75}$ d^{-1}) were for animals feeding on brome hay ad lib. plus a pellet supplement: cows, 693 ± 65 and 588 ± 25 kJ kg$^{-0.75}$ d^{-1} for week 1 and week 2, respectively; calves, $1,292 \pm 92$ and $1,042 \pm 168$ kJ kg$^{-0.75}$ d^{-1} for week 1 and week 2, respectively (after Munn and Barboza 2008).

possible in our study because we could not measure the hoof-ground contact time during feeding; animal movements were not restricted. Our model also assumes that the ice-hoof contact surface is smooth, but surface roughness can reduce conductive heat loss by trapping pockets of insulating air. Last, the ground contact SA we used was probably overestimated. For example, in two adult muskoxen, we estimated that only around 67% of the hoof directly contacted a flat surface (unpublished results, based on photographs of the sole, indicating regions of wear and soil staining).

We did not measure heat losses experienced by muskoxen via paths other than sensible losses from the body surface or by heat exchanges occurring outside of feeding bouts. But there was evidence that our muskoxen were actively thermoregulating via vasomotor adjustments throughout the study, as indicated by fluctuations in their deep ear canal/tympanic temperature (T_{ear}). Drops in T_{ear} were indicative of peripheral vasoconstriction, at least in the cranial region surrounding the ear canal and tympanic membrane. Maxima for T_{ear} were consistent across ambient temperatures in the study, which suggests that T_{ear} reflects periodic blood perfusion. Maximum T_{ear} (Table 2) was close to tympanic temperatures measured for muskoxen under controlled conditions (36.5 ± 0.6; $n = 4$; F. Kohl and P. S. Barboza, unpublished data) and was lower than rumen temperatures of $38.8° \pm 0.3°C$ reported for muskoxen feeding on brome hay in winter (Crater and Barboza 2007); rumen temperatures are typically higher than core or carotid blood temperatures (Beatty et al. 2008). We did not measure blood flows, but our data strongly suggest that muskox calves and cows routinely use peripheral heterothermy to manage winter conditions. Similar strategies have been reported for red deer (Arnold et al. 2004) and for a range of arctic mammals (Feist and White 1989). Peripheral vasoconstriction probably contributed to the low estimate of heat loss from the muskox's body surface. Surface temperatures of muskoxen were only 5°C above am-

bient temperatures at $-30°C$, a testament to the substantial insulation provided by their coat but probably also reflective of cutaneous vasoconstriction.

We were unable to examine the potential impacts that wind would have on muskox daily heat balance. Wind can have profound impacts on thermal exchanges by disrupting the insulative layer of the coat (Blix et al. 1984) and exacerbating convective and radiant heat loss (Monteith and Unsworth 1990). It is uncertain how wind might affect feeding patterns of muskoxen, but high winds restricted feeding times in free-ranging domestic sheep (*Ovis aries*) and interfered with their optimal foraging strategies (Armstrong and Robsertson 2000). In this regard, wind effects may be especially important for smaller, younger animals with higher SA : vol ratios. Notably, instantaneous convective heat losses (C; W m^{-2}) from muskox calves were significantly higher than those of cows (Table 5), even though wind was negligible in week 2 (Table 1). As such, convection would be exacerbated from calves in windy conditions, likely increasing their energy debts relative to those of cows, particularly when fully exposed during feeding bouts. Additionally, wetter and heavier snowfalls in winter could compromise calves (e.g., Parker 1988) by depressing the coat, thereby reducing insulation and increasing convective losses, but further studies on the thermal properties of muskox coats in relation to wind, wetness, and snow are needed. Calves can shelter from the wind and rain by lying or standing behind their mothers, but that shelter may not be available during feeding if adults continue to move when calves are deterred from feeding. Adverse weather that interrupts feeding may be more problematic for calves because they require a proportionately higher intake of digestible energy than cows (Munn and Barboza 2008).

The larger daily energy requirements of muskox calves may be related to higher metabolic demands associated with a proportionately greater mass of intestine relative to that of adults

(Munn and Barboza 2008). Higher metabolic rates could compromise calf heat budgets in midwinter, being typically associated with increased breathing rates and concomitant heat losses via respiratory evaporation and convection. Additionally, Lawler and White (2003) found that the energetic costs of standing while feeding are disproportionately greater for smaller muskoxen. Calves have been shown to spend more time feeding than adults under captive (Munn and Barboza 2008) and free-ranging (Forchhammer 1995) conditions. Other costs of feeding in midwinter include the ingestion of cold food and snow that may impact energy budgets; ingested food and water must be heated internally, which can account for 3%–14% of the DEI of adult muskoxen (Crater and Barboza 2007). Clearly, further research is needed to fully appreciate differences in the energy budgets of muskox cows and calves, but thermal constraints in the form of sensible heat loss from the body surface are of negligible concern for animals fully exposed during feeding bouts.

Our observation that juvenile muskoxen did not lose a greater proportion of their energy intake as heat loss from the body surface than did the larger cows suggests that selection pressure for energy conservation alleviates some of the thermoregulatory problems normally associated with a smaller body size (i.e., high SA : vol ratio). Selection may favor much greater thermal tolerances at lower temperatures and greater wind strengths than we could test in captivity at Fairbanks. Interestingly, Smith et al. (2002) found no clinal- or temperature-related variation in body size for adult muskoxen across a latitudinal range of 60°–83°N. This is contrary to Bergmann's rule (see Ashton et al. 2000; Smith et al. 2002) that endotherms should be larger nearer the poles because selection should favor lower SA : vol ratios that minimize heat loss. Lyberth et al. (2007) did report spatial differences in body sizes for mature muskoxen, but the effect was most pronounced for males and was attributed to the interplay between resource availability, density dependence, and sexual selection rather than to weather-induced phenotypic variations.

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