

Brief communication

Seasonal changes in metabolic rates in muskoxen following twenty- four hours of starvation

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Abstract: Timing of seasonal trends in post-prandial energy expenditure (EE) was measured in muskoxen (2 males and 1 female) given a standardized meal followed by a 24–26 h starvation during 10 months over the course of a year. EE was significantly lower in winter than summer. CH₄ production (E_{CH₄}) was reversed with winter highs and summer lows. Ratio of E_{CH₄}:EE indicates a change in dietary efficiency but this difference was not associated with a seasonal shift in RQ which was constant. The main increase in EE from winter to summer occurred between April and May and the summer to winter decrease between August and September.

Key words: *Ovibos moschatus*, energy expenditure, seasonality, methane.

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Introduction

A seasonal lowering of resting metabolic rate typifies a north temperate adaptation to limiting winter food supply in a cold environment (Wood *et al.*, 1962; Feist & White, 1989). Nilssen *et al.* (1994) documented a significantly lower resting metabolic rate for ad. lib. fed and starved muskoxen (*Ovibos moschatus*) during the winter compared to summer. However, timing of the down regulation in winter and up regulation in summer was not determined. The objective of this study was to determine the timing of seasonal trends in metabolism of muskoxen given a standardized meal followed by a 24–26 h starvation.

Materials and methods

Energy expenditure was measured in two intact males and one intact non-pregnant female musko-

xen during 10 months over the course of a year. All were 3 year olds and had been used in similar metabolic trials since yearlings. Animals were calm during metabolic trials. Before and after each trial, animals were maintained in a brome pasture (*Bromus inermis*) with *ad. lib.* access to brome hay. Twice a week, animals were offered high-protein pellets (Quality Texture, Alaska Mill and Feed, Anchorage) fed at a daily rate of 14 g (DM) per kg BW^{0.75}. At the start of an experiment each animal was brought into an unheated barn, offered 1 standard meal of 50% chopped brome hay and 50% pellets fed at 10 g (DM) per kg BW^{0.75} and then starved for 24–26 h. Each was then placed in an open circuit metabolic chamber (White *et al.*, 1984) to measure oxygen consumption, and carbon dioxide and methane production at 2 min intervals over a 2 h period. Temperature and barometric pressure was

Table 1. Comparison of winter with summer mean standardized energy expenditures, methane production and RQ of three 3 year muskoxen.

	Summer ¹		Winter ²		<i>p</i>
	<i>mean</i>	<i>SEM</i>	<i>mean</i>	<i>SEM</i>	
Daily Energy Expenditure ³	447	8.5	370	5.6	<0.001
Energy Expenditure (W/kg)	1.40	0.03	1.20	0.02	<0.001
CH ₄ Energy	17.0	1.16	24.0	0.92	0.001
CH ₄ Energy / Energy Expenditure	0.038	0.003	0.063	0.002	<0.001
RQ	0.88	0.01	0.90	0.01	NS

¹ June (*n*=3: Where *n* is the number of trials per month), July (*n*=3) and August (*n*=3)

² November (*n*=3), January (*n*=15), February (*n*=14) and March (*n*=19)

³ kJ per kg BW^{0.75}

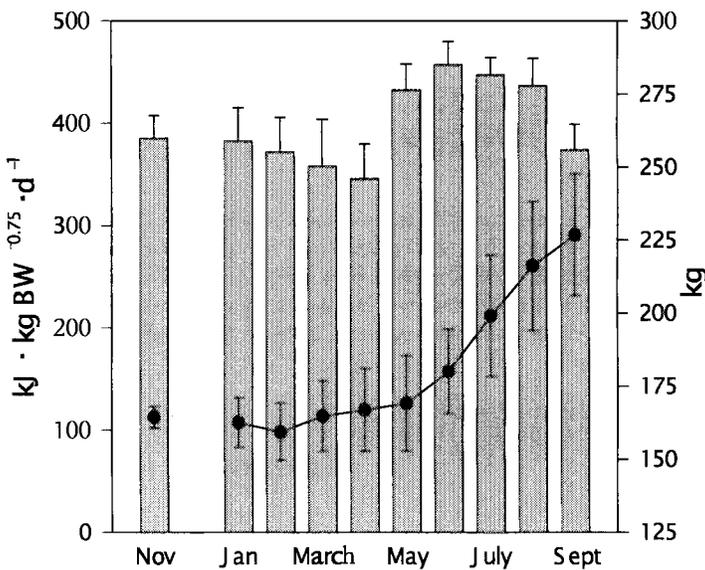


Fig. 1. Seasonal trends in mean energy expenditure and mean body weight of 3 muskoxen following a standardized meal and 24 hours of starvation. Seasonal patterns of summer highs and winter lows in energy expenditure and body weight were not synchronized.

logged by computer. Energy expenditure (EE) and methane energy loss (E_{CH_4}) was calculated from gas concentrations, and flow rates (Kokjer, 1981). Calculations were performed using the entire 2 h interval. Therefore, differences in EEs associated with different activities were not calculated. Respiratory quotient (RQ) was calculated as CO_2 expired/ O_2 consumed. Differences in energy expenditure were assessed by a two-factor analysis of variance. Sources of variance for the analysis were season, animal, and animal by season. Significance was determined at a 5 percent confidence level.

Results and discussion

EE was significantly lower in winter (November through March) than summer (June, July, August) (Fig. 1 and Table 1, $P < 0.001$). Mean EE ($n=3$) was lowest in April at 343 ± 15 (SEM) kJ per kg BW^{0.75} (1.11 ± 0.03 W per kg) and highest in June at 457 ± 16 kJ per kg BW^{0.75} (1.45 ± 0.05 W per kg). The 33% difference was significant ($P=0.006$) but less divergent than the seasonal values for 7-10 h starved animals reported by Nilssen *et al.* (1994) who found winter and summer metabolic rates of 0.86 ± 0.10 and 1.74 ± 0.27 W per kg respectively (a 49% difference). The difference in winter-summer extremes more closely resemble the 30% difference recorded by Nilssen *et al.* (1994) for 6 d starved animals

(winter values of 0.62 ± 0.07 W per kg and summer values of 0.77 ± 0.03 W per kg). Values reported for our muskoxen, represent both lying and standing-active animals, whereas those for Nilssen *et al.* (1994) are for the lying period. Low EEs occurred when body mass was at maintenance (November through April) and highest values during a period of weight gain (June through September) (Fig. 1). Summer and winter mean values were 53% and 27% respectively above the predicted BMR using the Kleiber equation (Kleiber, 1975).

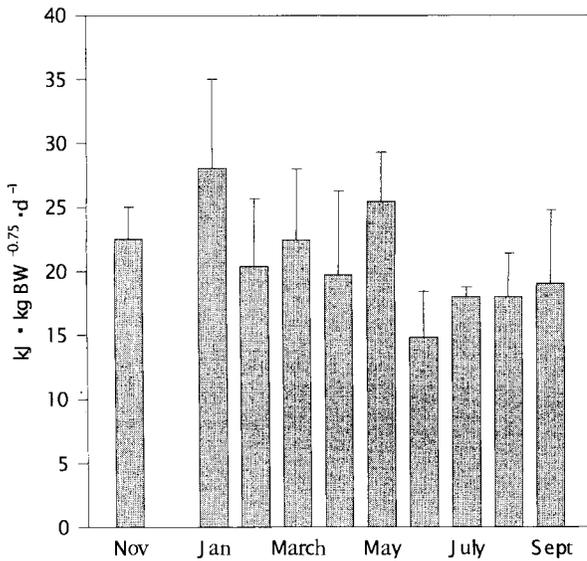


Fig. 2. Trends in mean CH₄ energy loss of 3 muskoxen following a standardized meal and 24 hours of starvation. Methane energy loss was higher in winter than in summer.

CH₄ production showed a significant but reverse seasonal pattern with winter highs and summer lows (Fig. 2 and Table 1, $P=0.001$). Mean daily E_{CH_4} loss after the standardized starvation was lowest in June at 15 ± 2.6 kJ per kg BW^{0.75} and highest in January at 28 ± 2.1 kJ per kg BW^{0.75} ($P=0.02$) (Fig. 2). Ratio of E_{CH_4} :EE indicates a change in dietary efficiency (Fig. 3) but this difference was not associated with a seasonal shift in RQ which was constant at 0.88.

Variation exists between individuals and between seasons in voluntary levels of dietary intake, passage rate, and digestibility in muskoxen (Holleman *et al.*, 1984; White *et al.*, 1984; Adamczewski *et al.*, 1994). Each of these factors alter the heat increment of feeding and make it difficult to determine when a ruminant animal will reach a post-absorptive state (Blaxter, 1962). Usually methane production would be low or non-existent when ruminants are truly post absorptive, thus our estimate of significant production shows heat increment is present. However, in some species, starving an animal to the point that it reaches a post-absorptive state has been shown to cause hyperactivity and restlessness (Robbins, 1994). These factors and those imposed by new animal welfare concerns make it difficult to achieve the

conditions required to directly measure BMR in large ruminants.

An alternative approach to long-term starvation is to measure EE under standardized conditions (Blaxter & Boyne, 1982), with the realization that some effects of heat increment may be carried over to add an indeterminate contribution to the variability in EE. As depicted by trends in body weight (Fig. 1), muskoxen were at maintenance levels in winter, but in positive energy balance in the summer. Thus the seasonal pattern in EE for these 24 h starved muskoxen, even when preceded by a standardized meal, undoubtedly reflect some residual heat increment and other metabolic effects associated with body weight gain and food intake. However, the 33% shift in seasonal extremes in this study closely resembles that for long-starved muskoxen (Nilssen *et al.*, 1994) which suggests that endogenous regulations could partially contribute to these seasonal EEs. Nilssen *et al.* (1994) argue that the 30% decrease in EE in long starved muskoxen is a down regulation and not due to heat increment.

For the first time, we report on the timing of seasonal changes. The main increase in EE from winter to summer occurred between April and May and the summer to winter decrease

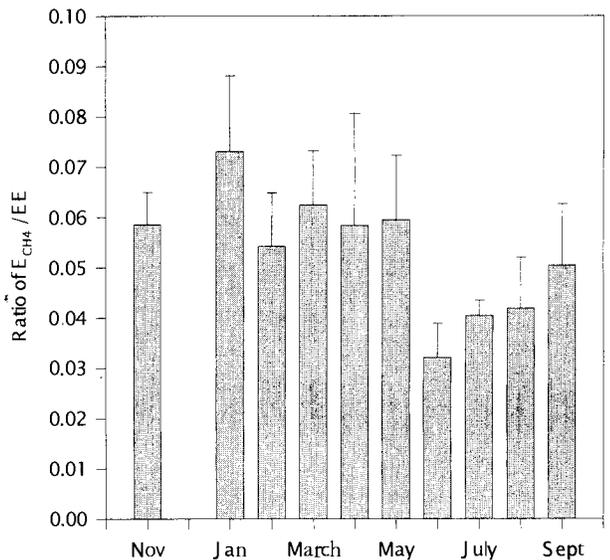


Fig. 3. Ratio of monthly mean methane energy loss to monthly mean energy expenditure indicating changes in dietary efficiency. Animals were more efficient in summer than in winter.

between August and September (Fig. 1). Possible cues that initiate seasonal shifts include seasonal photoperiod and forage quality and quantity. Under the conditions of this study in Fairbanks, Alaska (latitude 65° N) the month of April provides a summer cue, while the month of August provides that for winter, the month after and the month before equinox respectively. From a natural history viewpoint, it is significant that the initiation of calving occurs in April, and initiation of the rutting season, and a shift of nutrient partitioning in adult females from milk production to body reserves, occurs in early August (White *et al.*, 1989), precisely when we observe significant shifts in seasonal EE.

Acknowledgments

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