EFFECT OF POSTURE, FEEDING, LOW TEMPERATURE, AND WIND ON ENERGY EXPENDITURES OF MOOSE CALVES

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Abstract: Energy expenditures of two moose calves (*Alces alces*) were studied during late fall and early winter. Interactions of level of feeding, temperature, and posture were examined using a closed-circuit indirect calorimeter. Interactions of temperature and wind were determined in a wind tunnel using the Douglas-bag technique. Increments in energy expenditure due to feeding were approximately 20% over resting metabolism. The energy cost of maintaining a standing posture was in the order of 35%. As temperature dropped from -20°C to -30°C, metabolic rate increased 36% while standing, but only 2% while lying. Wind speeds up to 8 m sec^{-1} increased energy expenditures consistently only at temperatures below -20°C.

Little information exists concerning the energetic relationships of moose to their winter habitat. Energy requirements for thermoregulation have been estimated by Gasaway and Coady (1974) but have not been determined empirically. Because of their northerly distribution and because of their large size, moose probably exhibit considerable tolerance to severe thermal environments. Markgren (1966) observed that captive moose did not appear stressed by temperatures as low as -28°C with a moderate wind. However, since many environmental and physiological factors influence the response of animals to cold, the energy costs of thermoregulation may become significant, particularly for calves, under certain conditions. This study attempts to define the thermal tolerance of moose calves and to define how posture, level of feeding, and wind influenced their metabolic

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response to low ambient temperatures.

METHODS

The study was conducted using the facilities of the Metabolism Unit at the University of Alberta from October until January of 1977-1978. Two bull moose calves used in this study were reared on lamb milk replacer and weaned in September onto a pelleted alfalfa-barley ration (Table 1). At the time of the experiment they weighed 80 to 95 kg.

Table 1. Ingredients and nutrient composition of pelleted alfalfa-barley ration.

Ingredient	Percent by weight
Alfalfa meal (minimum 15% protein)	26
Barley (coarse ground)	31
Wheat bran	14.5
Beet pulp	14
Wet molasses	7
Soybean meal	6
Trace mineral salt	0.005
Vitamin A, D_3, E premix	0.001
Nutrient	**Percent of sample (at 9.9% moisture)**
Protein	15.6
Fibre	14.2
Calcium	1.15
Phosphorus	0.66

Nitrate	0.33
Fat	2.1
Ash	8.3
Carotene (mg/lb)	1.6

Interactions of Feeding and Posture with Temperature

The energy cost of eating was evaluated at temperatures of 0°C and -20°C. The temperature of 0°C was considered thermoneutral, since it approximated the mean daily temperature for October and early November to which the animals were acclimatized. A preliminary experiment revealed that panting occurred at temperatures above 10°C and that the calves would lie down at temperatures below -10°C.

Following a 24 hour fast each calf was placed in a closed circuit indirect calorimeter (Young et al. 1975). Two kilograms of pelleted ration were offered before sealing the chamber and commencing measurements for a duration of 4 hours. The next day, 15 hours after the trial began, metabolic rate was measured for an additional 2 hours. Two series of measurements for each animal were made at temperatures of 0 and -20°C. During the series at -20°C, the temperature was decreased to -30°C in an attempt to determine the lower critical temperature for moose calves. Changes in posture were recorded at 10 minute intervals in order to determine the energy cost of standing versus lying at various temperatures.

Metabolic rates were calculated from respiratory gases by assuming a caloric equivalent at 4.86 kcal l^{-1} (McLean 1970). Chamber and rectal temperatures were monitored on a Honeywell multichannel recorder. Heart rate was measured with a Hewlett Packard heart sound amplifier and respiration rate with a mercury manometer.

Interactions of Wind with Temperature

The combined effects of temperature and wind were studied in a wind tunnel which simulated laminar air flows of up to 8 m sec^{-1}. Trials were conducted on selected days of contrasting temperatures during January.

Respiratory gases were collected using a face mask and a meteorologic balloon. The volume of air expired in three minutes was measured with a dry test meter and the extraction of oxygen was determined with a Beckman oxygen analyzer. Rectal and skin temperatures were measured with a battery-operated telethermometer.

RESULTS

Energy Cost of Feeding

Food consumption to satiation averaged 1.33% of body weight. The time spent eating was approximately 30 minutes. Chamber temperature did not have a significant effect on food intake.

During feeding, metabolic rate increased sharply then declined gradually with fluctuations after feeding due to abrupt changes in posture (Figure 1). The average increment in energy expenditure while eating was 0.52 kcal kg^{-1} h^{-1}, approximately 20.5% greater than that of the resting animals. The increment was similar at 0°C and at -20°C. However, in general, absolute levels were slightly lower (20 kcal $kg^{-0.75}$ d^{-1}) at lower ambient temperature.

A trial was terminated 2 hours after feeding if the animal became unduly stressed by the experimental conditions (Figure 1). Observations with no bars in Figures 1, 2, and 3 are indicative of single observations.

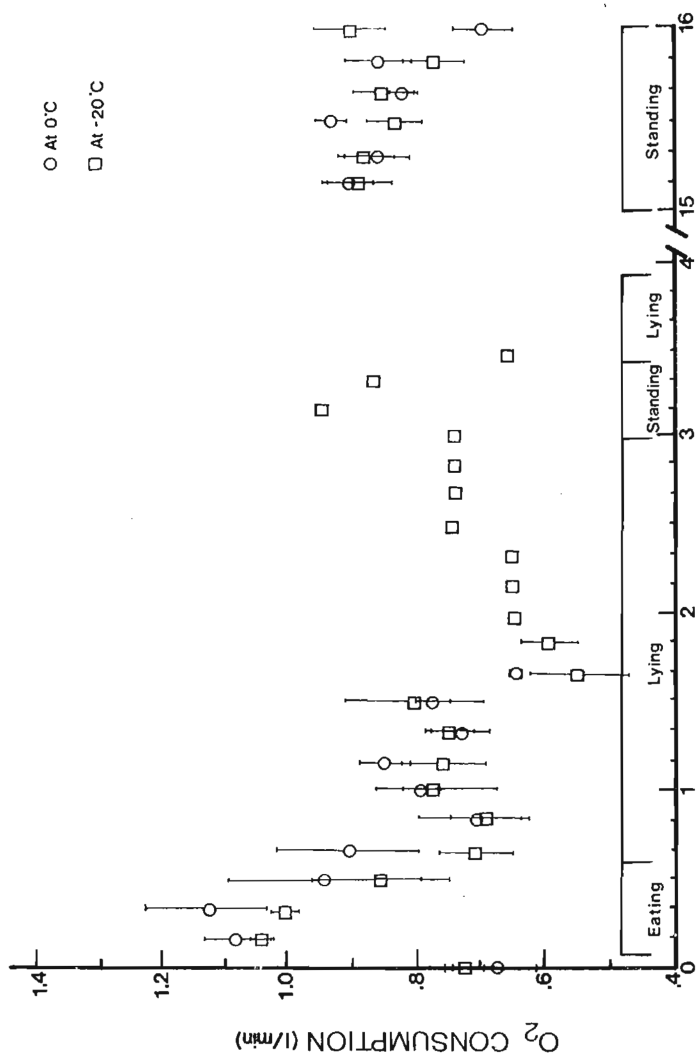

Figure 1. Mean energy expenditures (±SE) during and after eating at 0°C and -20°C.

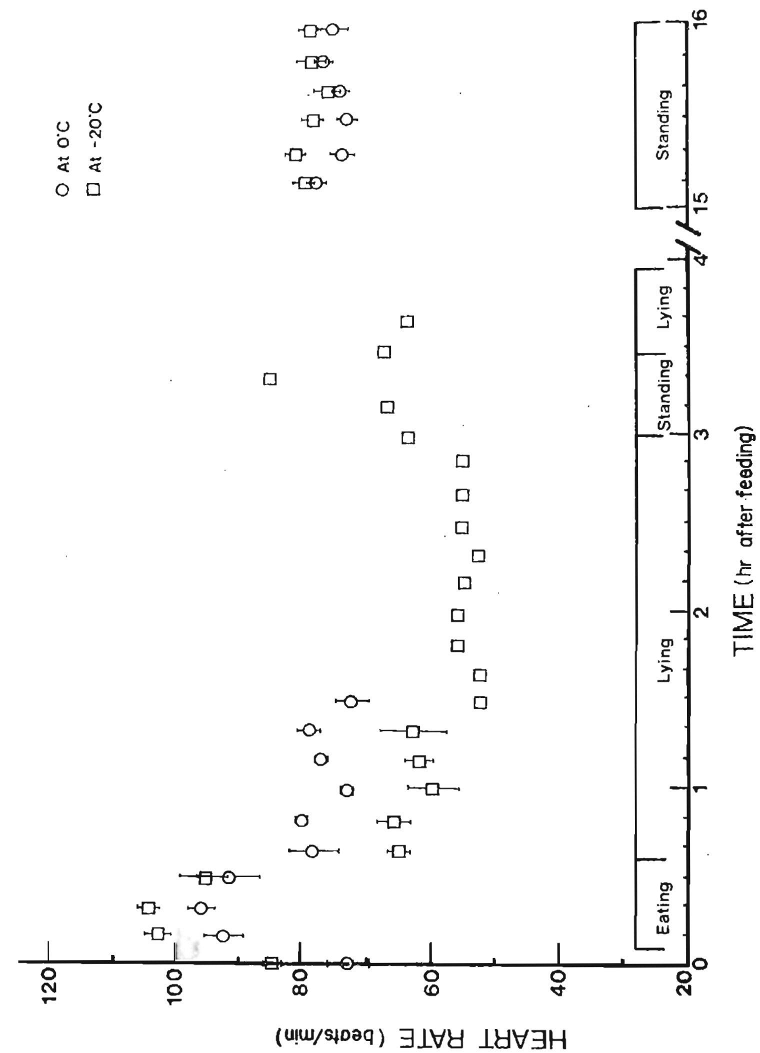

Figure 2. Mean heart rate (±SE) during and after eating at 0°C and -20°C.

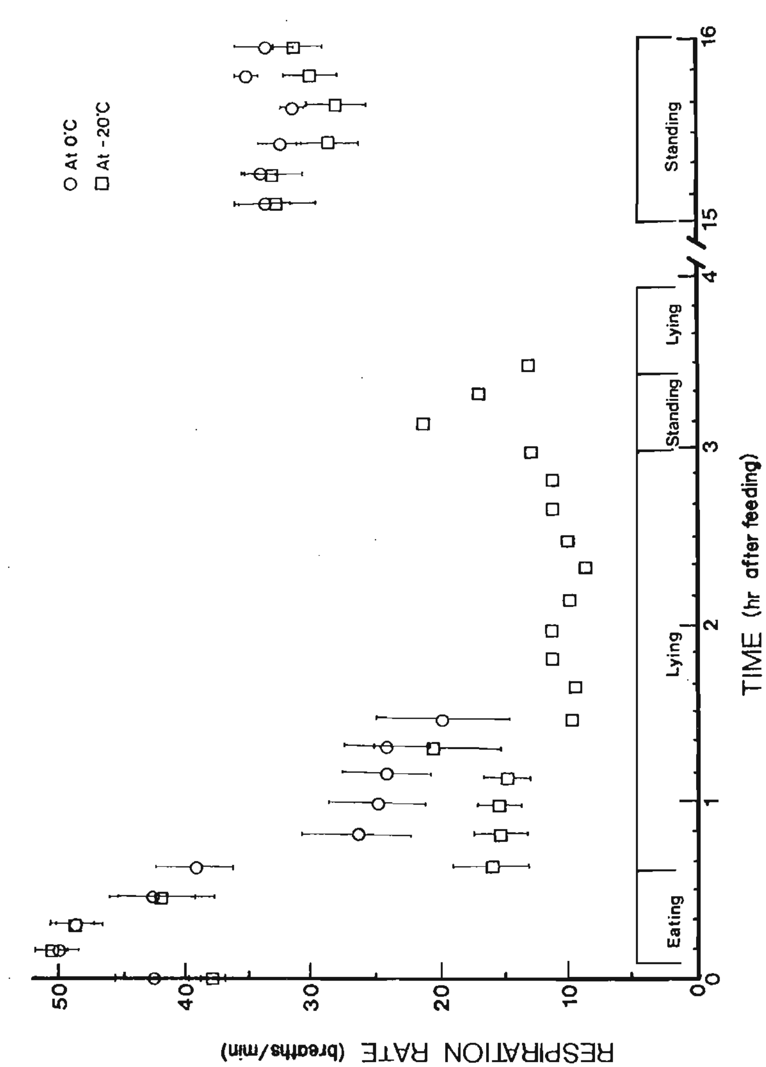

Figure 3. Mean respiration rate (±SE) during and after eating at 0°C and -20°C.

Heart rates and respiration rates paralleled changes in energy expenditure (Figures 2, 3). Regressions (Figures 4, 5) accounted for 59.7% and 54.8% of variation in metabolic rate, respectively.

Energy Cost of Standing

Energy expenditures while standing and lying at temperatures of 0°C, -20°C, and -30°C are shown in Table 2. Heat production at -20°C was somewhat lower than at 0°C but this was not significant. This appeared to result from decreased restlessness at colder temperatures.

The energy cost of standing in a thermoneutral environment was about 0.65 kcal kg^{-1} h^{-1} or 35% of energy expenditure while lying. As the temperature decreased to -30°C, the energy increment to maintain a standing posture rose to 1.48 kcal kg^{-1} h^{-1}, or 78%.

At the lower temperature, the calves assumed a prone position with their legs under their bodies and their noses tucked into their flanks. The approximate hair length of the winter pelage was 7.6 cm and piloerection occurred between -20°C and -30°C. Heart and respiration rates declined to 48 beats min^{-1} and 8 respirations min^{-1}, respectively, while lying at the lower temperatures.

Table 2. Energy expenditures of moose calves while standing and lying at temperatures of 0°C, -20°C, and -30°C ($\bar{x}$ ± SE).

Posture	Temperature (°C)	N	Heat Production (kcal $kg^{-0.75}$ d^{-1})
Standing	0	33	197.5±7.09
	-20	33	189.8±3.44
	-30	6	259.3±3.59
Lying	0	17	144.7±6.76
	-20	27	142.8±4.17
	-30	7	146.0±11.45

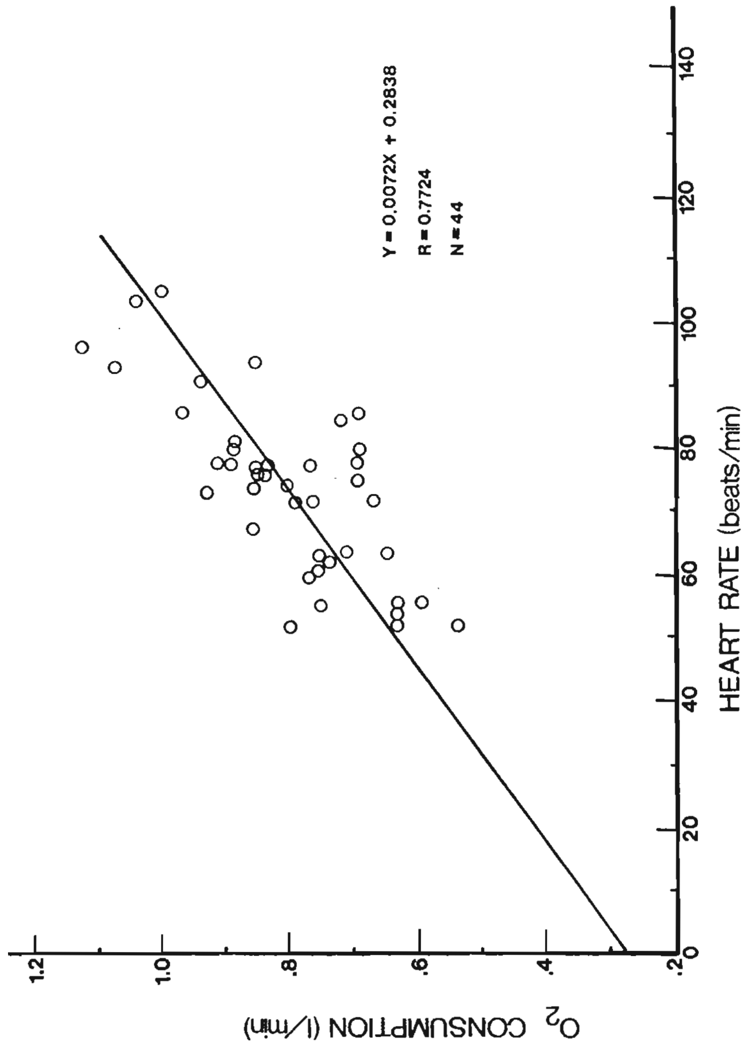

Figure 4. Relationship between heart rate and oxygen consumption.

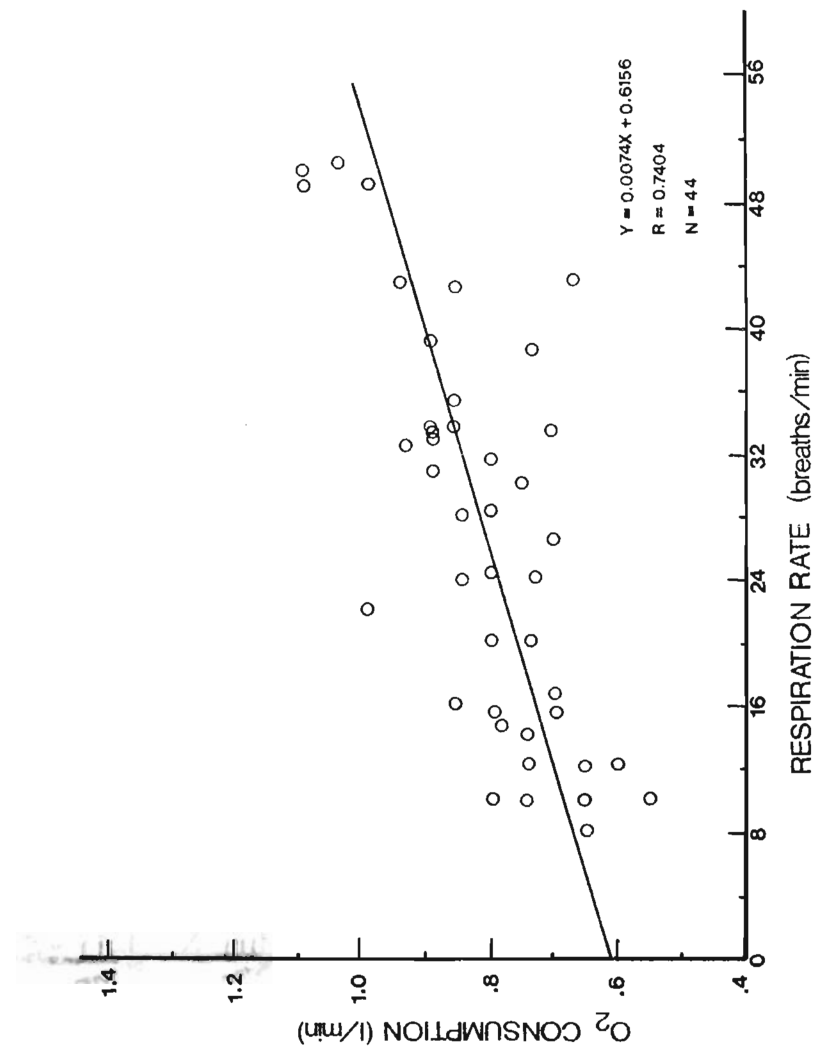

Figure 5. Relationship between respiration rate and oxygen consumption.

Interactions of Wind and Temperature

The wind tunnel trials were conducted in January. The calves were exposed to ambient temperatures from -25°C to 0°C and wind speeds of 0 m sec^{-1} to 8 m sec^{-1}. Under this range of conditions the effect of temperature was significant but wind and wind by temperature interactions were not. Falling temperatures to -20°C decreased metabolic rate although a sharp rise occurred from -20°C to -25°C (Table 3). In general, increased wind speeds also depressed metabolic rates down to -20°C but increased metabolic rates at the coldest temperature. A slight increase in metabolic rate occurred during the lowest wind speed at all temperatures but this appeared due to a behavioural reaction to activating the fan in the wind tunnel.

Table 3. Energy expenditures (kcal $kg^{-0.75}$ d^{-1} + SE) of moose calves exposed to ambient temperatures of 0°C to -25°C and wind speeds of 0 m sec^{-1} to 8 m sec^{-1}.

Temperature (°C)	Wind speeds (m sec^{-1})				
	0	2	5	8	Mean
-25 to -20	150 ±2	229 ±11	202 ±4	229 ±18	206 ±10
-19 to -15	133 ±22	165 ±35	116 ±21	118 ±16	132 ±10
-14 to -9	147 ±16	157 ±17	134 ±36	107 ±38	139 ±12
-8 to 0	- -	223 ± 0	180 ± 4	180 ±16	188 ±13
Mean	142 ±10	178 ±15	156 ±13	159 ±18	159 ±10

DISCUSSION

The thermogenic effect of food ingestion is believed to be one factor increasing the resistance of animals to cold. In this study, the activity of feeding was considerably more important than simply the presence of food in the digestive tract. The energy increment of feeding (0.52 kcal kg^{-1} h^{-1}) was comparable to that observed in studies on other ruminants. Chappel (1978) found values of 0.43 - 0.46 kcal kg^{-1} h^{-1} in bighorn sheep (Ovis canadensis) consuming alfalfa brome hay. Values for domestic sheep range from 0.54 (Graham 1964) to 0.83 kcal kg^{-1} h^{-1} (Webster and Hays 1968). Energy costs of eating appear to be more a function of the time spent eating than the type or weight of material ingested (Osuji et al. 1975). Since temperatures during trials on the energy costs of eating were above the lower critical temperature of the moose calves it is not possible to determine if heat generated during feeding spares heat of thermoregulation. Since the energy increment of eating was similar at 0°C and -20°C, the increment could not be attributed to the energy cost of warming ingested food. Considering the weight, temperature gradient and specific heat of the pelleted ration, the maximum cost of warming would be approximately .03 kcal kg^{-1} h^{-1}.

Energy costs of standing for moose calves in this study (0.65 kcal kg^{-1} h^{-1}) were several times higher than those reported for domestic livestock in which an average increment of 10% was observed (Osuji 1974). However, the energy increment of standing in moose appears considerably lower than reported for smaller wild ruminants such as white-tailed deer (Odocoileus virginianus borealis) (Mattfeld 1973), roe deer (Capreolus capreolus) (Weiner 1977), and pronghorn antelope (Antilocapra americana) (Wesley et al. 1973). Chappel and Hudson (1978) suggested that these differences may be related to body conformation, particularly the angles of the limbs. Although this conformation may increase energy costs of standing, it probably has functional advantages.

The importance of posture in regulating heat loss was amply demonstrated in this study. The energetic advantages of remaining bedded on cold days are obvious since this posture reduces the lower critical temperature to far below -30°C. Lying postures may increase thermal insulation by reducing heat loss through the extremities. Use of this form of behavioural thermoregulation has been well documents in white-tailed deer (Holter et al. 1975).

Moose respond to falling temperatures by lowering metabolic rate slightly to their lower critical temperature (between -20°C and -30°C for moose calves) then increase metabolic rate sharply to maintain body temperature and prevent the deterioration of tissue function. Bison calves (Bison bison) reduce metabolic rates more markedly and have slightly lower critical temperatures (Christopherson et al. 1978). Wind is probably not a major factor over most of the northern range of moose, since wind speeds up to 8 m sec^{-1} did not have a major effect at temperatures below -20°C. The great resistance of moose to cold thermal environments is not unexpected because of their large size and the environments which they have successfully exploited.

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