PREDICTION OF ENERGY EXPENDITURES BY ROCKY MOUNTAIN BIGHORN SHEEP

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ABSTRACT

Factors influencing the metabolic rate of Rocky Mountain bighorn sheep were analysed by multiple classification analysis. Factors considered were sex, date, body weight, exposure temperature, adaptation temperature, time since last feeding, and previous gross energy intake. The overall mean energy expenditure was 2632 kcal.d^{-1} (110 kcal.kg^{-} 75.d^{-1}). When factors were tested independently, body weight, sex and exposure temperature, in order of importance, contributed significantly to differences in energy expenditures. The total statistical model accounted for 87% of variance in the rate of energy expenditure.

INTRODUCTION

Energy metabolism represents an important adaptation of wild ruminants to their environment. The value of being able to predict energy expenditures of free-ranging animals has been highlighted in a number of studies on the consequences of behavioural patterns and, particularly, the impact of harassment. Unfortunately, energy expenditure is difficult to measure in wild species and information has accumulated slowly.

The usual procedure used to estimate energy expenditure is to estimate basal metabolism from body weight, increment it arbitrarily to obtain

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resting metabolic rate, the appropriate base, and then add the estimated energy costs of activity and thermoregulation. However, a number of factors influence resting metabolic rate. These include body weight, age, sex, season, nutritional status, ambient temperature, and adaptation to prevailing thermal environments. Several studies on wild ruminants have attempted to determine the importance of these factors. In the _Cervidae_, most studies have dealt with seasonal cycles of energy metabolism (Silver _et al_., 1971) or the effects of exposure temperature (Holter _et al_., 1975), age (Wesley _et al_., 1973) and feeding level (Weiner, 1977).

Rather than determine the importance of these factors in controlled experiments, we have attempted to develop a predictive equation based on measurement of energy expenditures of bighorn sheep under a variety of conditions throughout the winter season. This study represents an extension of an approach applied by Graham _et al_. (1974) in a study on domestic sheep.

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METHODS

Animals available for this study included two adult male and two adult female Rocky Mountain bighorn sheep (_Ovis canadensis_). One ewe was captured in Jasper National Park while the remaining subjects were reared in captivity. They were held in a large enclosure and maintained on grass hay and a pelleted alfalfa-barley ration throughout the period of study (Chappel, 1978).

Indirect calorimetry, using the respiratory pattern analyzer described by Young *et al.* (1975), was used to determine metabolic rates at controlled temperatures of 10°C to -30°C. Oxygen consumption and carbon dioxide production were converted to an energetic equivalent using the equation of Brouwer (1965). From September to May, measurements of RMR and FMR (after a 72-hour fast) were made at monthly intervals, and body weights and mean environmental temperatures for three days prior to the trail were recorded. Mean gross energy intakes of the pelleted ration were recorded in individual feeding stalls for the two weeks preceding each trial. A total of 124 measurements of metabolic rate provided the data base for this study.

Explanation of variability in energy expenditure, under a variety of experimental conditions, was sought through multivariate analysis of the interrelationship of the dependent variable (metabolic rate) and several independent variables (body weight, sex, month, exposure temperature, adaptation temperature, time since last feeding, and previous gross energy intake). Multiple Classification Analysis (MCA, Andrews *et al.* 1973) was chosen to examine the correlation of a set of predictors with the dependent variable in the context of a linear additive model.

Several statistics were employed to determine the fit of both individual predictors alone and with others of the same set. The *Eta*-squared coefficient (correlation ratio) denoted the proportions of variance explained solely by that predictor. *Beta* coefficients expressed the value of each predictor after adjusting for the effects of all other predictors. Category coefficients were obtained through solution of least squares equation (Anderson and Bancroft, 1952). The fit of the total model was determined by an R-squared value. Significance was tested using the F test.

This analysis produces a coefficient for each category of every predictor in the model. The sum of coefficients for the appropriate categories, plus the value of the grand mean, provide a prediction of metabolic rate.

RESULTS AND DISCUSSION

The grand mean metabolic rate of bighorn sheep was 2632 kcal.d^{-1}. Collectively, the seven independent variables accounted for 87% of variation.

When effects were examined independently, body weight, sex, ambient temperature at the time of measurement and month accounted for significant variation (Table 1). When effects were partitioned, month emerged as one of the most important variables followed by exposure temperature, body weight, adaptation temperature measured 3 days prior to the trial, sex, previous nutrition and time since last feeding.

Body Weight

As an independent effect, body weight explained the greatest proportion of variance in metabolic rate. When variance was partitioned, it lost some of its former importance. Least squares-adjusted means of metabolic rate as a function of body weight are shown in Figure 1. Over the restricted range of weights observed, the increase per unit body weight was approximately linear. Expressed on the basis of metabolic rate the overall mean metabolic rate was 110 kcal.w^{-} 75.d^{-1}.

TABLE 1

STATISTICAL SUMMARY OF FACTORS INFLUENCING METABOLIC RATE
OF BIGHORN SHEEP

Predictor variable and categories	Eta^2	Beta	Class Coefficients
Body weight (kg.)	0.40	0.36	
50-62			-285.91
63-65			-122.60
66-70			31.74
71-75			87.88
76-88			341.93
Sex	0.31	0.20	
Female			-117.45
Male			177.45
Date	0.17	0.53	
Sept.-Oct.			-93.23
Nov.-Feb.			-250.43
Mar.-Apr.			240.10
May-June			864.13
Exposure temperature	0.28	0.45	
-35 to -20			1470.00
-20 to -10			-28.90
-10 to 0			-28.24
0 to 10			-90.14
Adaptation temperature	0.03	0.23	
-35 to -10			45.38
-10 to +10			56.59
10 to 20			-359.57
Fasting	0.09	0.17	
Fed			45.45
Fasted			-237.37
Previous nutrition			
(kcal.kg^{-} 75.d^{-1})	0.04	0.27	
55-183			-128.78
183-220			-210.24
220-256			-53.62
256-330			202.10
330-515			223.64

R^2 complete model = 0.87 ($P < .001$)
Grand mean = 2631.87 kcal.d^{-1}

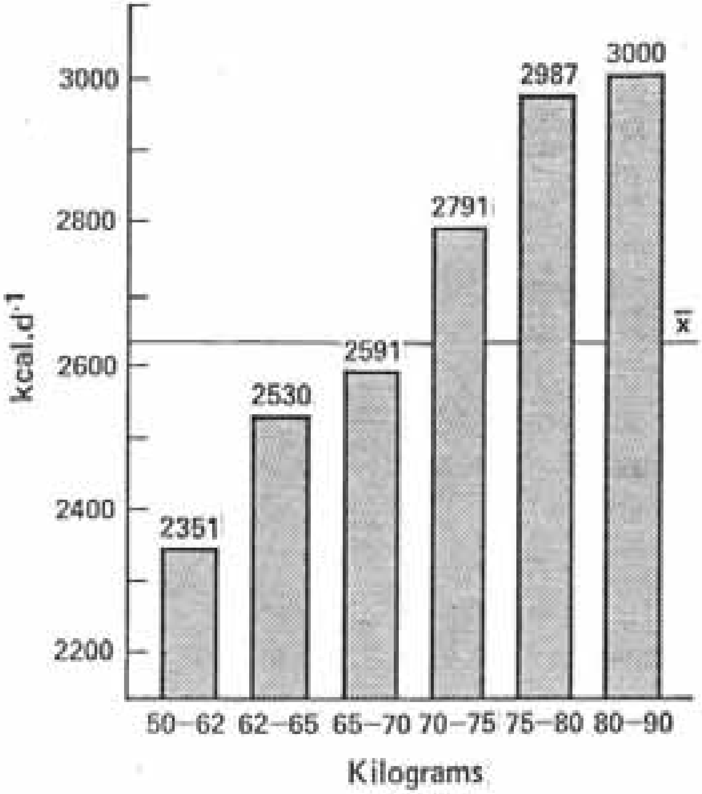

Fig. 1. Least squares means of metabolic rates in relation to body weight (kg). Grand mean metabolic rate denoted X.

Sex

Rams had metabolic rates which were 18% higher than those of ewes even when corrected for body weight differences (Figure 2). Although, in many species, the metabolic rate of males is higher than that of females, this apparently is not always the case with ruminants, perhaps because of the additional complexity of metabolic cycles. Silver et al. (1969) in a study on white-tailed deer did not find significant differences between does and bucks in summer coats. Wesley et al. (1970) found no obvious sex differences in pronghorn antelope. However, Graham (1968) reported that Merino rams had an FMR that was approximately 20% higher than wethers and ewes. Nordan et al. (1970) obtained similar results in black-tailed deer fawns.

Month

Month was an important predictor of metabolic rate when effects were fit jointly. Metabolic rates declined from fall to mid-winter, then rose to a peak in early summer (Figure 3). The amplitude of this oscillation was greater than 40%.

Because data were not collected for a complete seasonal cycle, it is difficult to compare these results with those reported for northern cervids. Silver et al. (1969, 1971) observed values in white-tailed deer which were greater than 50% higher in summer than in winter. Somewhat narrower contrasts were observed by McEwan and Whitehead (1970) in caribou. Weiner (1977) found seasonal variations in roe deer that amounted to less than 10%, while Brockway and Maloiy (1967) did not observe seasonal changes of metabolism in red deer. Differences among

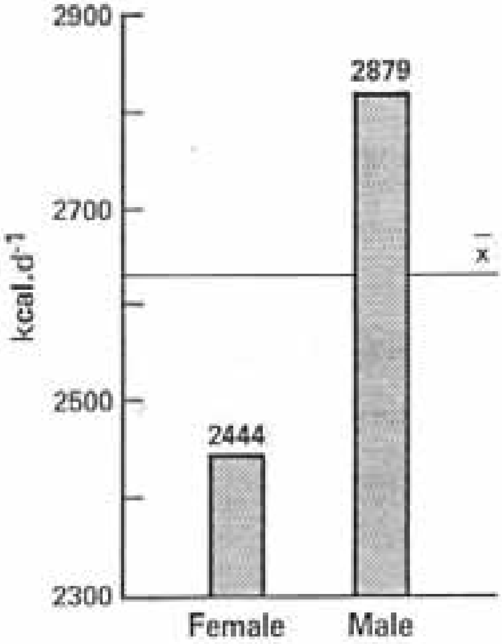

Fig. 2. Least squares means of metabolic rates of ewes and rams.

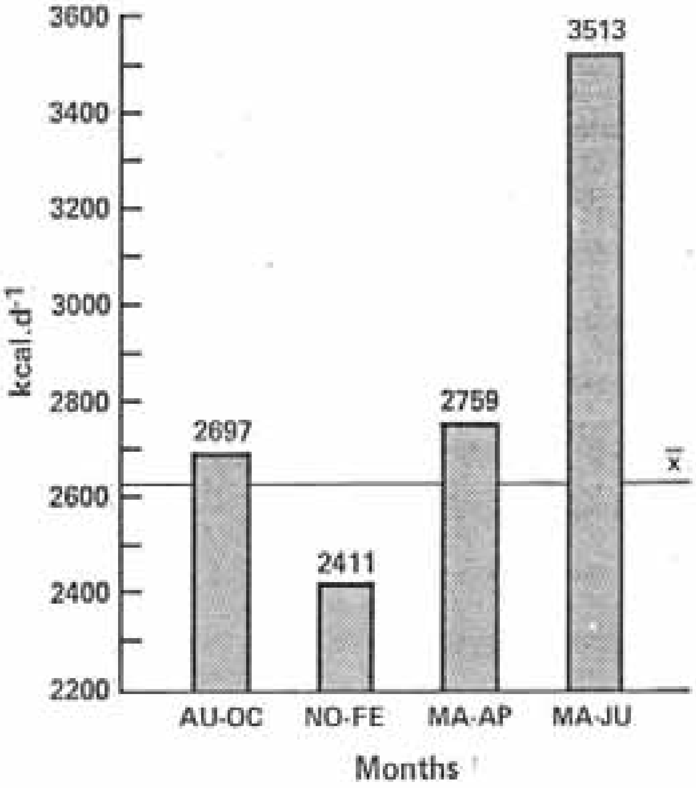

Fig. 3. Least squares means of metabolic rates in relation to dates of measurement.

these studies may be related to the environmental conditions under which animals were held. Photoperiod appears to be a dominant factor regulating seasonal metabolic cycles in wild ruminants (McEwan, 1975).

Exposure Temperature

The range of exposure temperatures used in this study included those which invoked a strong thermoregulatory response. The metabolic response to cold is shown in Figure 4. Temperatures as low as -20°C were within the thermoneutral zone but, between -20° and -30°C, metabolic rates rose sharply. Chappel (1978) has reported controlled experiments on the independent and combined effects of ambient temperature and wind on Rocky Mountain bighorn sheep.

Critical temperatures of bighorn sheep appear considerably lower than those of a number of other species of similar size. In winter coat, the lower critical temperature of roe deer, one of the smallest northern cervids, is about 0°C (Weiner 1977). Holter *et al.* (1975) estimated the comfort zone for white-tailed deer in winter to be between 5°C and 20°C. Wesley *et al.* (1973) found the critical temperature for fasting pronghorn antelope to be near 0°C and for fed animals to be between -12°C and -23°C. The superior cold tolerance of bighorn sheep, in comparison with deer, may be related to their habitat preferences. Bighorn sheep select open windswept slopes during winter, whereas white-tailed and roe deer seek forest cover where the opportunities to select favorable micro climates exist. Pronghorn antelope live in open country but do not match the northerly distribution of Rocky Mountain bighorn sheep.

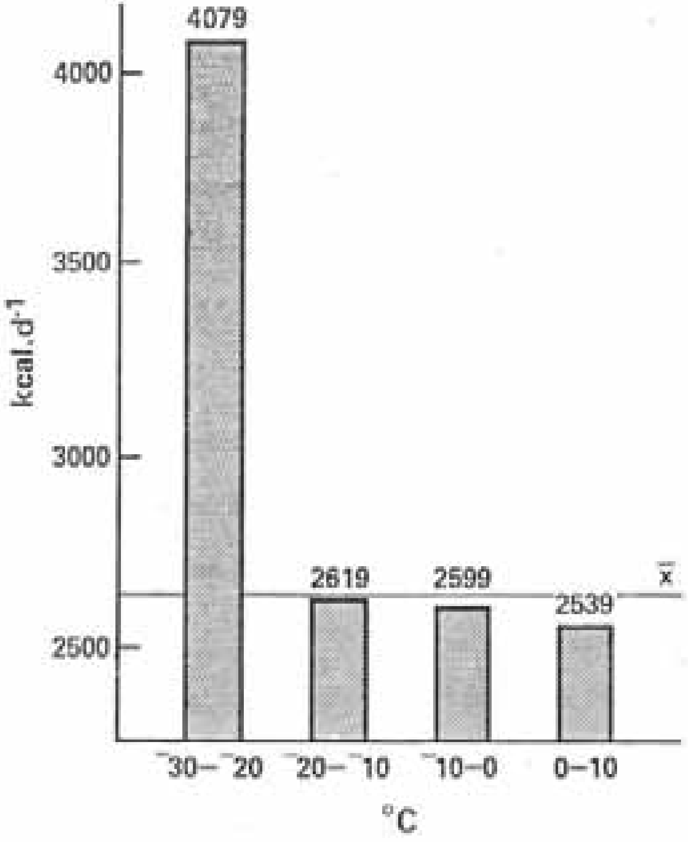

Fig. 4. Least squares means of metabolic rates in relation to exposure temperature.

Adaptation Temperature

Prolonged exposure to low ambient temperatures induced an upward adjustment of metabolic rate (Figure 5). Although mean ambient temperatures at 1 day, 3 days, 1 week, 2 weeks and 1 month prior to metabolic trials were examined, the best improvement of fit of the model was obtained with mean ambient temperatures for 3 days prior to measurement.

This factor has received little attention in studies on wild ruminants. However, gradual increases in thermoneutral metabolic rate have been found in domestic sheep (Webster *et al*. 1969) and cattle (Young, 1975) exposed to winter weather.

Fasting

In this study, bighorn sheep were fasted either 8 hours (fed group) or 72 hours (fasted group). The extent of the fast accounted for a relatively small proportion of variance, but mean differences of about 13% were observed (Figure 6).

Weiner (1977) found the resting metabolism of non-fasted roe deer exceeded values for fasting metabolism by 25-30%. McEwan (1970) estimated the difference in reindeer to be almost 20% whereas Wesley *et al*. (1973) reported the difference in antelope to be over 50%. In comparing these values, it is important to recognize that metabolic rate declines rapidly following feeding (Chappel 1978) so that differences may be due entirely to the exact time since the last meal.

Previous Nutrition

The mean intake of gross energy (kcal.kg^{-} 75) during the previous 2 week interval generally increased energy expenditures of bighorn sheep

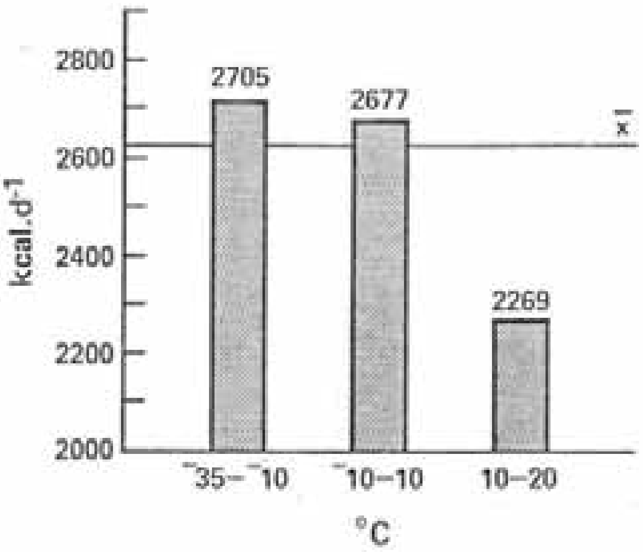

Fig. 5. Least squares means of metabolic rates in relation to mean ambient temperatures for 3 days prior to measurement.

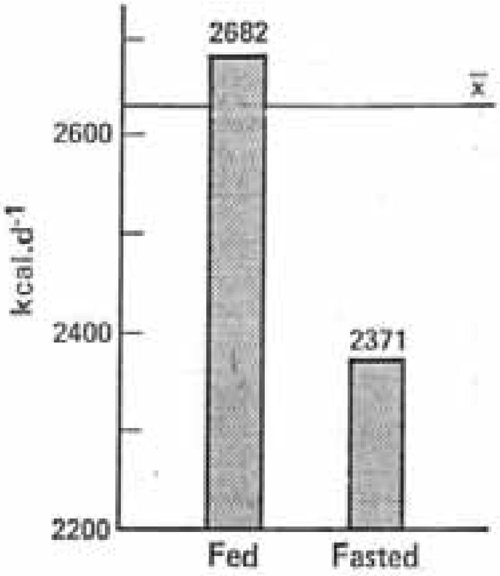

Fig. 6. Least squares means of metabolic rates of animals fasted 8 hours (fed) or 72 hours (fasted).

(Figure 7). The lowest category was made up largely of rams in rut. This may explain the deviation from a direct linear relationship.

The importance of nutritional status has been well established in work on domestic animals. Marston (1948) found differences between domestic sheep fed either at ½ or 2 times maintenance requirements which were evident up to 7 days of fasting. Graham et al. (1968) also found a direct effect of previous energy intake on metabolic rates of domestic sheep.

Application of the Statistical Model

To predict the metabolic rate of bighorn sheep within the range of conditions used in the construction of this model, the appropriate class coefficients (Table 1) are summed and added to the grand mean. The BMR of an animal weighing 66 - 70 kg. can be estimated by summing those coefficients which define the measurement (date of lowest metabolic rate, thermoneutral exposure temperature, thermoneutral adaptation temperature, fasted state and lowest level of previous nutrition). For males, the predicted value was 1714 kcal.d^{-1}, and for females 1480 kcal.d^{-1}. Using the mid-point weight, this was equivalent to 77 kcal.kg^{-} 75.d^{-1} and 63 kcal.kg^{-} 75.d^{-1} for males and females, respectively. This is in agreement with the accepted interspecies mean of 70 kcal.kg^{-} 75.d^{-1}. Approximate energy budgets of free-ranging bighorn sheep can be estimated by choosing the coefficients relevant to prevailing environmental conditions. Where certain variables cannot be measured in the field (e.g., level of forage intake), a value of zero can be substituted as a best estimate since the coefficients are simply added to the overall mean. Since the

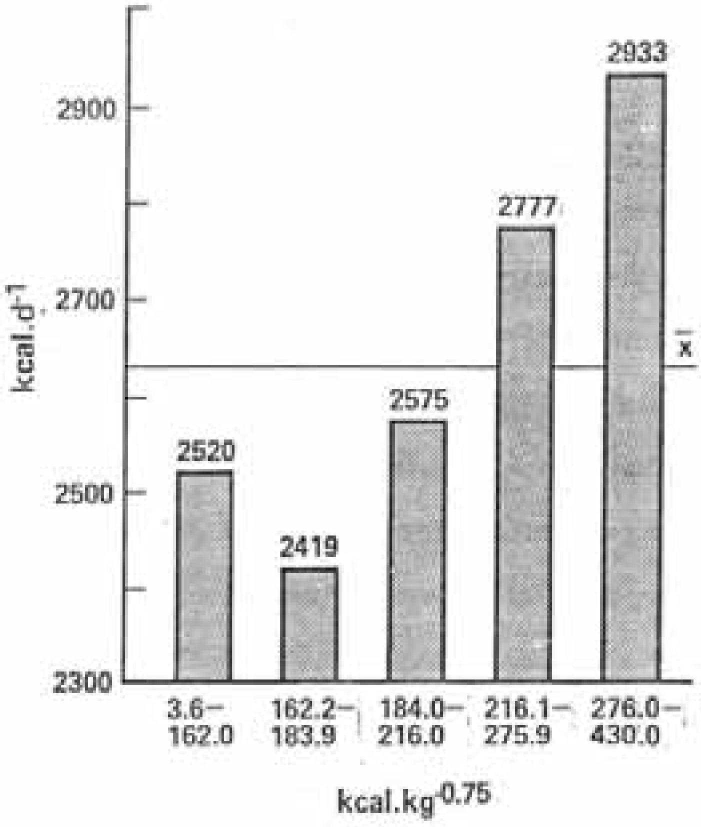

Fig. 7. Least squares means of metabolic rates in relation to mean gross energy intakes during two weeks prior to measurement.

model predicts only resting metabolic rate, costs of feeding and locomotion must be added. Chappel (1978) estimated the cost of feeding to be approximately 32% of resting metabolic rate. The energy expenditure of bedding animals was 18.9%. Since this model predicts expenditures of animals which were standing, this increment is subtracted to obtain the appropriate value for bedding animals. In our studies, the energy cost of locomotion of bighorn sheep has not been determined. However, activity increments measured in a wide variety of species, including elk which we have studied on treadmills, suggest a value of 0.5 $kcal.kg^{-1}.km^{-1}$. This could be used as an approximation until specific information on bighorn sheep becomes available.

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