

METABOLIC RATIOS FOR ESTIMATING ENERGY METABOLISM IN MOOSE

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ABSTRACT: We have calculated metabolic ratios called multiple of base-line metabolism (MBLM) by dividing published data on daily energy costs of moose by a common denominator called base-line metabolism. Use of a common denominator makes all of these calculated ratios comparable on a mass-specific basis. We have used a tandem cosine algorithm to calculate the annual cycles of MBLM values for calves, cows, and bulls. Metabolic lows of mature cows and bulls are reached in mid-March to mid-April, and highs are reached when both milk production and antler growth reach a peak in mid-June. Calves, yearlings, barren cows, and immature bulls are expected to reach a peak in mid-July. Maximum MBLM values in early summer are about 3 times greater than the minimum values in late winter and early spring. The MBLM method can be used to estimate ecological energy metabolism throughout the annual cycle by interpolating between minimum and maximum values with the tandem cosine algorithm, and should be useful to modelers who want to incorporate energy costs as a continuous function throughout the year.

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Free-ranging cervids such as moose (*Alces alces*) in northern regions experience an annual cycle of high forage quality, quantity, and availability during the plant growing season in summer, and reduced forage quality, quantity, and availability during the plant dormant season in winter. Nutritional requirements for reproduction and its associated metabolic costs are synchronized with this cycle (Schwartz 1992). The temporal pattern of energy requirements of female moose over the annual cycle was first presented by Gasaway and Coady (1974) based on data for other ruminant species because no measurements of moose metabolism had been made at that time. Since then, metabolic rates of moose have been measured in chambers and stalls (Renecker *et al.* 1978, Regelin *et al.* 1985, Renecker and Hudson 1986, Welch *et al.* 1990), metabolizable energy intake has been determined in feeding trials (Schwartz *et al.*

1988), energy costs of moose have been calculated from telemetered heart rate data (Renecker and Hudson 1985, 1989), and metabolic rates and forage requirements of moose cows with 1 or 2 calves have been modeled (Moen *et al.* 1997). Reviews of physiological and nutritional energetics and adaptations document the synchrony of seasonal rhythms in both the physiological needs of moose and the quantity and quality of their food supply (Schwartz *et al.* 1987b, Schwartz 1992).

Physiologists have been measuring metabolizable energy, standard metabolism, basal metabolic rates (BMR), and fasting metabolic rates (FMR) of ruminants for over 75 years (Benedict and Ritzman 1923). BMR is defined as the minimum energy cost when the animal is in the post-absorptive condition in a thermoneutral environment and at rest (Brody 1945); FMR is the term used when the test animal is not at rest

and the results are not corrected for activity. Fasting metabolic rate is often used as a basis for calculating metabolic ratios because conditions for measuring BMR are logistically difficult to achieve. Estimates of FMR should account for the seasonal metabolic rhythm because a year-round average FMR is an inappropriate representation of the metabolic rhythm of moose (Schwartz *et al.* 1987b). Measured baseline values in summer and winter for moose "bedded dozing with the head tucked into the abdomen" were used by Renecker and Hudson (1989) to calculate metabolic ratios. The use of different denominators when calculating metabolic ratios does not allow for direct comparisons between studies on different species or for sex and age cohorts within a species.

Scaling metabolic costs in relation to body size with the interspecies BMR mean of $70 \cdot \text{body mass}^{0.75}$ proposed by Kleiber (1975) has been subject to debate as values other than 70 and 0.75 have been derived from different data sets. We use Kleiber's (1975) interspecific mean as a mass-specific mathematical baseline (Moen 1978), or common denominator called "baseline metabolism per day" (BLMD). While BLMD is equal to Kleiber's interspecific mean for basal metabolism, our use of this numerical expression as baseline metabolism does not verify it as an interspecific mean; it is simply used as a common denominator when calculating metabolic ratios.

The sum of the energy costs for maintenance, activity, and production of free-ranging animals was described by Moen (1973) as "ecological metabolism per day" (ELMD). Dividing ELMD by BLMD results in the metabolic ratio called "multiple of baseline metabolism" (MBLM) (Moen 1978). Since $\text{MBLM} = \text{ELMD} / \text{BLMD}$, it follows that ecological energy metabolism per day is calculated as $\text{ELMD} = \text{MBLM} \cdot$

BLMD. MBLM values were represented in previous publications by a sine wave approach that used phase corrections to generate an asymmetric pattern over the annual cycle for white-tailed deer (*Odocoileus virginianus*) (Moen 1978, 1985) and caribou (*Rangifer tarandus*) (Moen 1980). In this manuscript, MBLM values for moose are calculated over the annual cycle with a tandem cosine algorithm that represents the asymmetric slopes of the metabolic cycle better than the phase-corrected sine wave approach used earlier.

METHODS

We calculated MBLM values by dividing published daily energy values for moose by BLMD. The formula for BLMD when the units are kcal per day is: $\text{BLMD} = 70 \cdot \text{body mass}_{\text{kg}}^{0.75}$. When results were given in Joules, we converted Joules to kcal by dividing by 4.184.

A tandem cosine algorithm with 2 successive half-waves, each with their own period length, is used to represent rhythmic changes in amplitude over the annual cycle. Periods of unequal length result in an asymmetric wave with no discontinuity because the slope of a line tangent to the end-points of each half-wave is zero. The basic components of the 2 half-wave formulas are:

$$\text{MBLM}_{\text{ascend}} = \text{MBLM}_{\text{midpt}} + \cos(\text{days}_{\text{ascend}}) \cdot \text{deviation} \quad (1)$$

$$\text{MBLM}_{\text{descend}} = \text{MBLM}_{\text{midpt}} + \cos(\text{days}_{\text{descend}}) \cdot \text{deviation} \quad (2)$$

where $\text{MBLM}_{\text{ascend}}$ = MBLM value during the half-wave period of increasing metabolic rate, $\text{MBLM}_{\text{midpt}}$ = midpoint value between maximum and minimum MBLM, $\text{days}_{\text{ascend}}$ = days into ascending half-wave period, and deviation = the difference between maximum and minimum MBLM divided by 2. $\text{MBLM}_{\text{descend}}$ = MBLM during the half-wave period of decreasing metabolic rate, $\text{MBLM}_{\text{midpt}}$ = midpoint value be-

tween maximum and minimum MBLM, and $\text{days}_{\text{descend}} = \text{days into descending half-wave period}$.

The tandem cosine algorithm interpolates between maximum and minimum values. It is a pattern-generating procedure rather than a curve-fitting procedure, creating an asymmetric cosine curve when the period lengths from minimum to maximum and from maximum to minimum are of unequal length. Transitions in MBLM values are gradual as the algorithm interpolates between the end points of each half-wave. The asymmetric ascending and descending half-waves between minimum and maximum MBLM values are obvious in the figures that follow.

The algorithm requires only 4 inputs—maximum and minimum MBLM values and the Julian days when each occurs—to calculate MBLM values over the annual cycle. The ascending half-wave begins with the minimum MBLM value and is applied to the time period in days up to the maximum value. The descending half-wave is applied to the time period from maximum to minimum MBLM. It is necessary to do a phase shift to set the maximum day to 0°, to convert days (365) to degrees (360) by multiplying the number of days into the time

period by 360/365, and to select the appropriate half-wave to represent the sequence of Julian days when maximum and minimum values occur with "if-then" decisions when programming the algorithm.

RESULTS

The discussions, measurements, and calculations of energy metabolism in the literature show clearly that there is a pattern of MBLM values for moose over the annual cycle, reaching a maximum during the most costly productive period during the year—lactation and antler growth—and a minimum in the winter. We have normalized published estimates for moose and used supporting evidence from other wild and domestic ruminants when estimating the ranges of minimum and maximum MBLM values and the Julian days when they are expected to occur for the 4 cohorts of moose in Table 1.

The rhythmic pattern of MBLM for calves, yearlings, barren cows and immature bulls in Fig. 1 has been calculated with the tandem cosine algorithm and the MBLM values and Julian days in the first cohort in Table 1. Data from Renecker and Hudson (1989) for two 24-month old barren cows have been used in our estimates of the

Table 1. Ranges of MBLM values that represent published data for 4 cohorts of moose and the dates when minimum and maximum values occur. MBLM patterns over the annual cycle are plotted in Figs. 1, 2, and 3.

		Range	Date	Julian Day
Calves, yearlings, barren cows, and immature bulls	Min MBLM	1.3-1.6	Apr 15	105
	Max MBLM	2.8-3.8	Jul 15	196
Mature bulls	Min MBLM	1.5-1.8	Apr 15	105
	Max MBLM	3.5-4.5	Jun 14	165
Cows with 1 calf	Min MBLM	1.5-1.8	Mar 16	75
	Max MBLM	3.2-4.2	Jun 14	165
Cows with 2 calves	Min MBLM	1.5-1.8	Mar 16	75
	Max MBLM	3.5-4.5	Jun 14	165

timing and of the maximum and minimum MBLM values in Fig. 1. While their results show a distinct seasonal rhythm, values from their cow data are lower than the MBLM values we calculated in 5 of the 7 months.

MBLM values for mature bulls range from low values of 1.5 to 1.8 in mid-March, calculated from Gasaway and Coady (1974), to high values of 3.5 to 4.5 in mid-June (Fig. 2). The phenological pattern of antler growth in moose (Van Ballenberghe 1982) and a simulation model of energy requirements during antler growth (Moen and Pastor 1998) were used to estimate the amplitude and timing of these MBLM values. Variable and possibly higher short-term costs due to breeding activity in early autumn are not represented on a daily basis with this algorithm; the cosine curve smoothes these daily costs out.

MBLM values for cows with 1 calf (Fig. 3A) and for cows with 2 calves (Fig. 3B) vary from minimums of 1.5 to 1.8 in mid-March to maximums at peak lactation

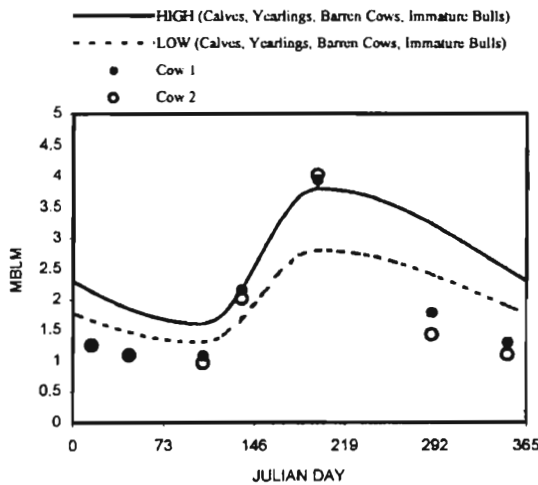


Fig. 1. The MBLM pattern for calves, yearlings, barren cows (data points from Renecker and Hudson 1989), and immature bulls over the annual cycle. The “high” line represents the upper end and the “low” line the lower end of the Min and Max MBLM range in Table 1.

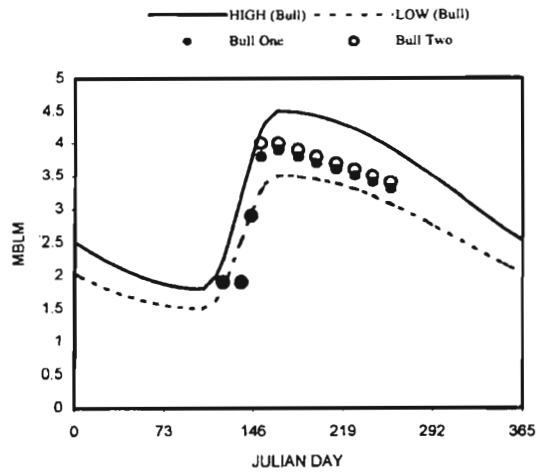


Fig. 2. The MBLM pattern for 2 mature bulls over the annual cycle, with data points from Moen and Pastor (1998). The “high” line represents the upper end and the “low” line the lower end of the Min and Max MBLM range in Table 1.

(Reese and Robbins 1994) in mid-June. The data points are from a simulation model of energy requirements during reproduction (Moen and Pastor 1998). Cows regain body condition after lactation, depositing fat and protein, but this is not as energetically costly as lactogenesis so MBLM declines after peak lactation.

DISCUSSION

We have converted measured and calculated estimates of energy metabolism for 4 cohorts of moose to MBLM values that may be compared directly because we used BLMD as a common denominator in each calculation. The MBLM method is useful when there are no data sets available that provide enough data to curve-fit throughout the annual cycle. Even if specific data were available, the MBLM approach may be useful because of its simplicity and generality. Curve-fitting yields coefficients that are specific to a data set, while the MBLM method provides flexibility both in the amplitude and timing of metabolic highs and

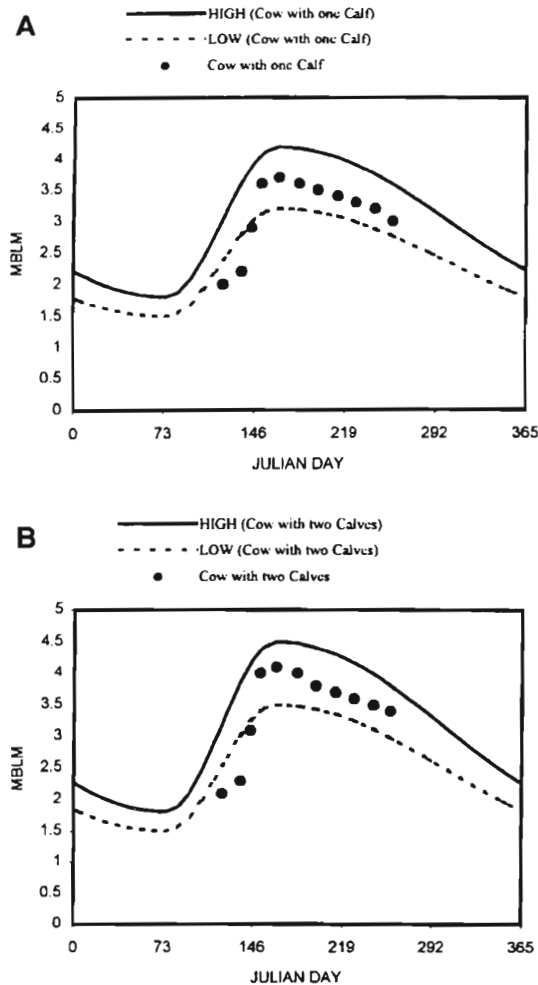


Fig. 3. The MBLM pattern for cows with 1 calf (3A) and for cows with 2 calves (3B) over the annual cycle, with data points from Moen and Pastor (1998). The “high” lines represent the upper end and the “low” lines the lower end of the Min and Max MBLM ranges in Table 1 for cows with 1 and 2 calves.

lows. Our suggested MBLM values and the Julian days when maximum and minimum values are reached can be replaced by more locally specific values and days if available.

We have used available seasonal data for total daily energy costs to derive our estimates of the MBLM values in Table 1. The temporal pattern described by Gasaway and Coady (1974) provided a good starting

point, but in the absence of any data on moose they underestimated the cost of lactation. The calculations of Renecker and Hudson (1989), who used telemetered heart rates as the basis for calculating estimates of energy expenditure, provided strong evidence for seasonal rhythms in energy expenditures of barren cows. Their low estimates in the winter may be due to a physiological adaptation for energy conservation; heart rate-to-metabolism conversion values had a seasonal rhythm in white-tailed deer (Moen 1978).

The MBLM values calculated by the Moen and Pastor (1998) model are lower at the end of gestation than the MBLM pattern shows. While this may be an artifact of the cosine function that interpolates between the minimum and maximum MBLM values, the energy cost of gestation in moose has not been measured. A better understanding of the energy cost of gestation and lactation is needed because the cost of reproduction is high and it has significant effects on population dynamics. Since reproduction has been thoroughly studied in domestic ruminants, simulation modeling of gestation in moose would provide a vital understanding of energy costs from the late winter metabolic low to the peak lactation high.

While chamber measurements provide strong evidence for seasonal rhythms in metabolism, MBLM values from a moose confined to a chamber cannot be applied to free-ranging moose for obvious reasons. MBLM values calculated from fasting metabolic rates of yearling moose infected by ticks (Welch *et al.* 1990) ranged from less than 1.0 to over 3.0, with no detectable effects of hair loss on metabolic rates. Metabolic values for 2 bull calves 5-8 months old in a wind tunnel ranged from 1.5 to 3.3 (Renecker *et al.* 1978). The higher short-term values would not be maintained over a 24-hour period by free-ranging moose.

Ecological energy metabolism is calcu-

lated by multiplying the MBLM values in Figs. 1, 2, and 3 for a specific day by BLMD. Since BLMD is a function of body mass, which varies over the annual cycle (Schwartz *et al.* 1987a), moose body mass should be represented by seasonal rhythms when calculating BLMD and ecological energy metabolism. The tandem cosine algorithm can be used to calculate moose body mass by representing annual maxima for different ages by a growth curve and the amplitude of seasonal variations by expressing minimum weights as a fraction of the maximum, as for white-tailed deer (Moen and Severinghaus 1981).

We have presented the logic and evidence for using MBLM to calculate ecological energy metabolism because it is central to energy-based modeling. Moose survival in early spring depends on the growth of high quality forage at a time when metabolic costs are biologically programmed to increase in order to meet energy costs in late gestation and lactation. We suggest that the MBLM method is a sound way to incorporate meaningful estimates of energy metabolism over the annual cycle for moose, and can help predict energy balance in late winter and early spring in relation to the duration of snow and the timing of green-up. It need not be the only method used in a model, but we do suggest that results from direct measurements or other model calculations be compared to the patterns for specific cohorts using the tandem cosine algorithm to calculate MBLM values over the annual cycle. Ultimately, the seasonal changes in energy metabolism should be of interest to researchers and managers when evaluating carrying capacity as a dynamic animal-range relationship over time.

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