TOPIC 4. ESTIMATES OF THE ENERGY COSTS OF ACTIVITIES

Every activity that an animal participates in has an energy cost associated with it. The movement of any mass for any distance involves work, and this is as true of wild ruminants as it is of man-made machines. Work is also involved in maintaining posture; muscles develop a tonus that permits animals to hold their heads erect, their ears in an alert position, stand, and other postures. While the holding of these postures may not involve motion, work is still being performed as the body is held in place against the force of gravity.

The energy costs of activities such as bedding, standing, walking, foraging, and running can be quantified with the use of the principles of physics involving the movement of mass over distance, and they may be calculated from oxygen consumption measurements. There are differences in efficiencies at different rates of movement, but such details have been analyzed for only two species of wild ruminants.

The energy costs of five different activities are discussed in the units that follow, with worksheets for calculating the costs for use in time and energy budget calculations.

REFERENCES, TOPIC 4

ESTIMATES OF THE ENERGY COSTS OF ACTIVITIES

BOOKS

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UNIT 4.1: THE ENERGY COST OF BEDDING

The energy costs of bedding may be approximated with the measurements of resting metabolism in relation to basal metabolism. This ratio provides a first approximation that can be conveniently applied to any animal, especially when evaluated in relation to base-line metabolism. There are differences due to posture, such as an erect head posture or a curled-up posture, but these details have not yet been discerned by experimentation.

The energy cost of bedding is a part of basal metabolism measurements. Animals then are at rest, and in a post-absorptive state in thermoneutral conditions. The measured heat production under basal conditions includes no heat of fermentation or heat of nutrient metabolism due to digestive processes, or extra heat production due to thermogenesis.

Resting metabolism of reindeer (rata) has been measured by White and Yousef (1978). Resting metabolism of two reindeer used in walking experiments varied markedly. A group of four adult females taken from late summer grazing had a resting metabolism of 125 LWKG\(^{0.75}\) per day.

It is very important to realize that the resting metabolism of free-ranging animals also includes the costs of productive processes in progress. Thus the measured cost while resting is not the costs of resting alone.

Basal metabolism references and worksheets are given in UNIT 2.1, with WORKSHEET 4.1a in this UNIT illustrating how the activity costs of bedding can be calculated as a multiple of base-line metabolism.

LITERATURE CITED


REFERENCES, UNIT 4.1

THE ENERGY COST OF BEDDING

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JTBIA 49--2 345 362 mamm model, est metab, rest, ac wunder,ba 1975
CHAPTER 7, WORKSHEET 4.1a

Estimates of the energy cost of bedding

The energy cost of bedding may be considered equal to basal metabolism, because basal metabolism test results are expressed for animals at rest. The heat production of the free-ranging animal is expected to be higher, of course, since the heat of fermentation and heat of nutrient metabolism are present.

Calculations of the cost of bedding are easily made by multiplying base-line metabolism by the appropriate MBLM. If basal metabolism is considered equal to be the interspecific mean of 70 W0.75, then the energy cost of bedding per day (ECBD) is:

\[
ECBD = BMBL \times (70)^{0.75} \times IFW \times FTBD
\]

where ECBD = energy cost of bedding per day,
BMBL = bedded multiple of base-line metabolism,
IFWK = ingesta-free weight in kg, and
FTBD = fraction of time bedded per day.

If basal metabolism is greater than the interspecific mean, it is still convenient to express ECBD as a multiple of base-line metabolism. Using the average value of basal/base-line ratio for deer, MBLM = 80/70 = 1.1 (see CHAPTER 7, UNIT 2.1). The equation for seasonal rhythms in basal metabolism expressed as MBLM may also be used; this is given in CHAPTER 7, UNIT 6.1.

Note that the fraction of time bedded per day (FTBD) is given in the equation above. The initial MBLM calculation is for a 24-hour period so FTBD, based on time budgets discussed in PART II, is used to allocate the portion of the day spent in bedded activity.
The energy costs of standing have been measured for several species, both ruminants and non-ruminants. The cost of standing above lying is about 9% in man, cattle, and sheep (Crampton and Harris 1969:151). An increase of 9.7% in oxygen consumption was observed in a reindeer when standing compared to lying (White and Yousef 1978). Elk calves had standing metabolic rates of 137 to 161 LWKg$^{-0.75}$ per day (Robbins et al. 1979). These are more than 9% higher than the expected basal rate, but it must be emphasized that the energy costs measured while standing also include the costs of productive processes. The total measured cost while standing is not only the cost of standing.

The energy costs of standing may be expressed as multiples of baseline metabolism. The multiple for man, cattle, and sheep (9% increase) would be 1.1. The costs of standing for domestic ruminants under controlled experimental conditions may be less than the costs for wild ruminants since standing by the latter may be accompanied by a state of alertness that contributes to the metabolic cost while standing. Some of the cost estimates for standing discussed by Robbins et al. (1979:451-452) seem unreasonably high; increase of more than 60% must be due to some experimental effects. The cost of standing should be considered as a physical cost, separate from the costs of alertness while standing.

LITERATURE CITED


Chapter 7 - Page 54
Estimating the energy cost of or while standing

Estimates of the energy cost of standing may be made by using MBLM for standing as the measure of the cost of standing. If this MBLM is applied to free-ranging animals, it should either contain concomitant costs of production, or the value of MBLM should be supplemented by additional costs of production. The important point is that a distinction must be made when calculating the costs of standing or while standing.

The costs of standing may be expressed with MBLM = 1.1 or slightly higher. The costs while standing, based on measurements of wild ruminants on ad libitum diets, were as high as 2.3, based on data (161/70 = 2.3) in Robbins et al. (1979:447). If the former is used, production costs are to be added. If the latter, they are a part of the direct measurement.

Another necessary parameter when calculating the cost of standing is the fraction of time spent standing each day (FTSD). This is necessary because the base-line metabolism approach is on a 24-hour basis. Thus, the formula for determining the energy cost of standing per day is:

\[ \text{ECSD} = (\text{SMBL})(70)(\text{IFWK}^{0.75})(\text{FTSD}) \]

where ECSD = energy cost of standing per day,
SMBL = standing multiple of base-line,
IFWK = ingesta-free weight in kg, and
FTSD = fraction of time standing per day.

Since there are variables in the formula dependent on the species, weights, time of year, and other factors unique to the situation being evaluated, equations are left for you, the user, to derive. An unlabeled grid is provided for plotting results.
LITERATURE CITED

UNIT 4.3: THE ENERGY COST OF WALKING

Walking, defined as locomotion resulting when no more than two of the hooves are off the ground at one time, involves the movement of mass over distance at a fairly slow rate of speed. Walking on the level is composed of movement in one plane (the horizontal), and walking uphill involves movement in two planes (horizontal and vertical).

**Horizontal.** The energy cost of walking may be calculated if the mass of the animal and the distance traveled are known. Equations for different species were evaluated and summarized in Moen (1973: 356). More recently, direct measurements of oxygen consumption by adult reindeer and elk calves have been made by White and Yousef (1978) and Robbins et al. (1979), respectively. Oxygen consumption of reindeer walking on the horizontal was 14% higher than estimated for several smaller mammals by Taylor et al. (1970). Energy expenditures of elk calves were also higher than that predicted with equations in Taylor et al. (1970). The Taylor estimates should not be considered an interspecies mean, however, since too few animals and species were represented. Robbins also reported that the energy expenditure was a direct linear function of the speed of travel, as was oxygen consumption by adult female reindeer (White and Yousef 1978).

**Vertical.** The vertical component of the topography adds greatly to the cost of locomotion. Measurements have not been made on species which live on rugged topography, such as mountain goats, and those which live on more level terrain, such as pronghorn. The reindeer and elk experiments mentioned above also included measurements on different gradients. The energy cost of climbing was determined for reindeer by measuring oxygen consumption on the incline and subtracting the consumption measured on the horizontal. The energy cost of descent was determined in the same way, resulting in an estimate of locomotion downhill that was less than that on the horizontal. A similar relationship was observed for the elk calves.

The costs of locomotion at different speeds and on different gradients is of ecological interest because of potential energy costs associated with activities on different topographies. Patterns of energy conservation are discussed for white-tailed deer in Moen (1976). The extent of such differences may be estimated by calculating the costs of movements of different speeds and distances by species on different topographies, and by quantifying the behavior patterns of the species and calculating the daily costs of all activities. While the cost of movement may be more costly on rugged topography, it may be compensated for by adjustments in the time spent in different activities.

**LITERATURE CITED**


REFERENCES, UNIT 4.3

THE ENERGY COST OF WALKING

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JWMAA 42--4 715 738 odvi seas chan, heart rate, act moen,an 1978

CODEN VO-NU BEPA ENPA ANIM KEY WORDS------------------------ AUTHORS---------- YEAR

dohe

CODEN VO-NU BEPA ENPA ANIM KEY WORDS------------------------ AUTHORS---------- YEAR

ATRLA 23-22 365 370 ceel energy cost of locomotion gates,c; hudson,r 1978
CBPAB 61A-1 43 48 ceel oxy util, horiz, vert loco cohen,y; robbins/ 1978
JWMAA 43--2 445 453 ceel energy expendi, elk calves robbins,ct; cohe/ 1979
JWMAA 43--2 564 567 ceel postur, activ, metab, cold gates,c; hudson,r 1979
QJEPA 62--4 333 340 ceel ener cost locom level, gra brockway,jm; ges/ 1977

CODEN VO-NU BEPA ENPA ANIM KEY WORDS------------------------ AUTHORS---------- YEAR

CJZOA 57-11 2153 2159 alal morph param affec loco,sno telfer,es; kelsa/ 1979

Chapter 7 - Page 56
Chapter 7 - Page 57
Chapter 7 - Page 58
Estimates of the energy cost of walking based on weight and gradient

Estimates of the energy cost of walking may be made based on data for domestic sheep, where the costs are calculated as a function of weight, distance, and height. Equations given in Moen (1973:356), modified with different symbols here, are:

\[
ECWL = (0.59)(LWKG)(DSTK)
\]

\[
ECVA = (6.45)(LWKG)(HGTK)
\]

where \( ECWL \) = energy cost of walking on the level,
\( LWKG \) = live weight in kg,
\( DSTK \) = distance in kilometers,
\( ECVA \) = energy cost of vertical ascent and,
\( HGTK \) = height ascended in kilometers.

Suppose an animal weighed 60 kg and walked a distance of 4 horizontal km at 4 km per hour on a 10% gradient as indicated in the drawing below.

![Diagram showing a steep incline with dimensions 4 km and 0.4 km.]

The equations are:

\[
ECWL = (0.59)(60)(4.0) = 141.60
\]

\[
ECVA = (6.45)(60)(0.4) = 154.8,
\]

and the total cost is 296.4 kcal.

How does this relate to MBLM? Multiply 296.4 by 24 to get the cost on a daily basis. The answer is 7113.6 kcal per day. Divide by base-line metabolism: 7113.6/(70)(600.75) = 4.71 = MBLM. This is a rather high cost, and could not be sustained for long. If the rate of speed were cut in half (2 hours rather than 1 hour of walking time), then 148.2 kcal per hour 3556.8 and MBLM = 2.36. A further reduction in speed of travel at 1 km per hour would reduce the cost to 74.1 kcal per hour. Base-line metabolism is
62.9 kcal per hour, so the cost of walking 1 km per hour and ascending vertically a total of 10% of the horizontal distance plus the cost of base-line metabolism (or basal if you wish) is, in this case $74.1 + 62.9 = 137$ kcal, $137/70 = 1.96 = MBLM$.

Note how the example on the previous page allows for differences in the rate of speed. Variations in vertical ascent were not evaluated. New variables may be used and different combinations evaluated. The calculation of MBLM is always a good idea because of the large amount of evidence for upper limits to ecological metabolism as discussed in UNIT 6.1 of this CHAPTER.

LITERATURE CITED

Estimates of energy expenditure of elk calves at different speeds on different upslopes

Measurements of the energy expenditure of elk calves at different speeds on three different slopes were made by Robbins et al. (1979). The energy expenditures per kg per hour on three different slopes were graphed in Figure 1, but no equations were presented for these results. A single equation may be derived for locomotion upslope by first determining linear regression equations for each of the slopes (11.7, 4.2, 0°). The a and b values in these equations are then expressed with equations. The a values are best fit with exponential regression equations, and the b values with linear regression equations. The final, overall equations are:

\[ ECWU = 3.28599 \cdot e^{0.01660 \cdot \text{SLPD}} + [0.97296 + 0.05722 \cdot \text{SLPD}] \cdot \text{SPKH} \]

\[ ECWD = 3.18453 \cdot e^{0.01741 \cdot \text{SLPD}} + [0.96953 + 0.02381 \cdot \text{SLPD}] \cdot \text{SPKH} \]

where ECWU = energy cost of walking upslope in kcal per kg per hour,
SLPD = slope in degrees,
SPKH = speed in km per hour and,
ECWD = energy cost of walking downslope in kcal per kg per hour.

Calculate several combinations of speed and slope and plot below. Different slopes may be conveniently represented as a family of curves.

LITERATURE CITED

The energy cost of walking for reindeer (rata)

Measurements of oxygen and consumption by reindeer walking on roads or on tundra have been made by White and Yousef (1978). Their results are expressed as equations for oxygen consumption Table 1, p. 217. Using the energy equivalent of oxygen consumed in relation to the respiratory quotient (see CHAPTER 7, UNIT 2.2, WORKSHEET 2.2a, p. 32a), a respiratory quotient of 0.85 may be used if a specific REQO is not available, calculate the energy cost for each of the several experimental conditions. Body weights are also given in Table 1, so MBLM may be calculated.

Complete the calculations and compare these costs of walking calculated in WORKSHEETS 4.3a and 4.3b. Keep in mind that these direct measurements are for all of the metabolic processes of reindeer while walking.

LITERATURE CITED

UNIT 4.4: THE ENERGY COST OF FORAGING

The costs of foraging are quite variable due to the differences in the styles of foraging and in the terrain inhabited by different wild ruminants. Pronghorn, for example, live in a rather sparsely vegetated habitat and cover large land areas as their home range. Forage density is much less than one finds on white-tailed deer range in the northeastern states where deciduous forests are interspersed with farms. Sheep and goats live in rugged areas with rather sparse forage densities too, and foraging for these species may be more costly than for pronghorn or deer.

Measurements of the energy costs of foraging have not been made for free-ranging ruminants. The use of oxygen consumption masks, as for the measurements on reindeer and elk discussed in the two previous units, prohibits foraging, of course. Tracheal cannulae have apparently not been tried on wild ruminants.

A single value, for the cost of foraging, based on data for grazing domestic sheep and expressed as a multiple of base-line metabolism, is given in Moen (1973:356). Such approximations are often necessary because of the lack of measured data on free-ranging wild ruminants due to the technical difficulties involved in the measurements. A WORKSHEET provides opportunities to estimate the energy cost of foraging.

LITERATURE CITED


REFERENCES, UNIT 4.4

THE ENERGY COST OF FORAGING

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JWMAA 34--2 431 439 odvi wint feed patterns, penned ozoga,jj; verme,l 1970
JWMAA 42--4 715 738 odvi seas chan, heart rate, act moen,an 1978

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odhe

Chapter 7 - Page 59
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ala

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anam

CODEN VO-NU BEPA ENPA ANIM KEY WORDS--------------------- AUTHORS--------- YEAR

bibi

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ATRLA 23-21 359 363 ovca energ costs feedin, roc mt chappel, rw; hudso 1978

CODEN VO-NU BEPA ENPA ANIM KEY WORDS--------------------- AUTHORS--------- YEAR

ovda

CODEN VO-NU BEPA ENPA ANIM KEY WORDS--------------------- AUTHORS--------- YEAR

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AJAEA 15--6 969 973  dosh energ cost, feed act, graz graham, nc 1964
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JRMGA 27--6 437 443  rumi physiol, ener expen, pastu osuji, po 1974

Chapter 7 - Page 61
Estimating the energy cost of foraging

The energy cost of foraging may be estimated with a simple mathematical relationship given in Moen (1973:356). The equation given is \((0.54)(Wkg)\) the rate per hour. Multiplying by 24 to convert to a 24-hour period and using 4-letter symbols, the equation is:

\[
ECFD = (12.96)(LWKG)(FTFD)
\]

where \(ECFD\) = energy cost of foraging per day,
\(LWKG\) = live weight in kg, and
\(FTFD\) = fraction of time foraging per day.

The result does not include maintenance costs; \(ECFD\) is for the cost of foraging alone and not the other concomitant productive processes.

Note that the fraction of time spent foraging per day is part of the calculation. These fractions were discussed in PART II, and need to be considered again here.

Convert the estimates to MBLMs again. Note that foraging costs less than walking at the rate of 1 km per hour. Foraging is intermittent standing and walking.

LITERATURE CITED

UNIT 4.5: THE ENERGY COST OF RUNNING

Running is a highly variable cost due to the different velocities possible, but a small contributor to the daily energy expenditure of wild ruminants because only a small fraction of each day is spent running. The cost of running may be determined from estimates, or calculated with the heart rates or respiration rates and converted to estimates of metabolism, and expressed as multiples of base-line metabolism. Since muscle artifacts often interfere with the telemetered ECG signal, heart rates of running animals are difficult to obtain. It may be that multiples from 6 to 20 times base-line metabolism have to be chosen as estimates simply because measured values are unavailable.

REFERENCES, UNIT 4.5

THE ENERGY COST OF RUNNING

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<td>ECOLA 57--1 192 198 odvi energy conservation, winter moen, an 1976</td>
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<td>JWMAA 42--4 715 738 odvi seas chan, heart rate, act moen, an 1978</td>
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<td>CBPAB 61A-1 43 48 ceel oxy util, horiz, vert loco cohen, y; robbins/ 1978</td>
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<tr>
<td>JWMAA 43--2 445 453 ceel energy expendi, elk calves robbins, ct; cohe/ 1979</td>
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<tr>
<td>JWMAA 43--2 564 567 ceel postur, activ, metab, cold gates, c: hudson, r 1979</td>
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<tr>
<td>QJEPA 62--4 333 340 ceel ener cost locom level, gra brockway, jm; ges/ 1977</td>
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<td>CJZOA 57-11 2153 2159 alal morph param affe loco, sno telfer, es; kelsa/ 1979</td>
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CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS-------- YEAR

CJZOA 56--2 215 223 rata energy expend, walk, tundr white, rg; yousef, 1978

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anam

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CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS-------- YEAR

ovca

CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS-------- YEAR

ovda

CODEN VO-NU BEPA ENPA ANIM KEY WORDS---------------- AUTHORS-------- YEAR

obmo

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oram

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AJPHA 219-4 1104 1107 mamm energy cost run, body size taylor, cr; schmi/ 1970

CBPAB 34A-4 841 846 many energetic cost, locomotion tucker, va 1970

SCIEA 178-- 1096 1097 runni up, down hills: size taylor, cr; caldw/ 1972

Chapter 7 - Page 64
Estimates of the energy costs of running

The cost of running is quite variable, depending on the speed. The cost of locomotion of elk calves at 12 km per hour on 0° slope (Robbins et al. 1979) has an MBLM of 13 to 14. The range of multiples--6 to 20--given on page 63 indicates wide possibilities for errors. Actual errors on a daily cost basis are small, however, since running can take up only a very small fraction of each day. Thus the suggested formula is:

$$ECRD = (RMBL)(70)(IFWK^{0.75})(FTRD)$$

where $ECRD$ = energy cost of running per day,
$RMBL$ = running multiple of base-line metabolism,
$IFWK$ = ingesta-free weight in kg, and
$FTRD$ = fraction of time spent running each day.

A running time of 10 minutes per day is less than 1% of the daily time budget, so larger variations in MBLM are offset by small possibilities for error in FTRD.

Complete calculations of $ECRD$ for different combinations of $RMBL$ and $FTRD$. Use data in PART II on time budgets to establish realistic limits to $FTRD$ and evaluate the possible errors of estimation. Once the costs of all activities are added up, errors in $ECRD$ will be found to be small.

LITERATURE CITED
