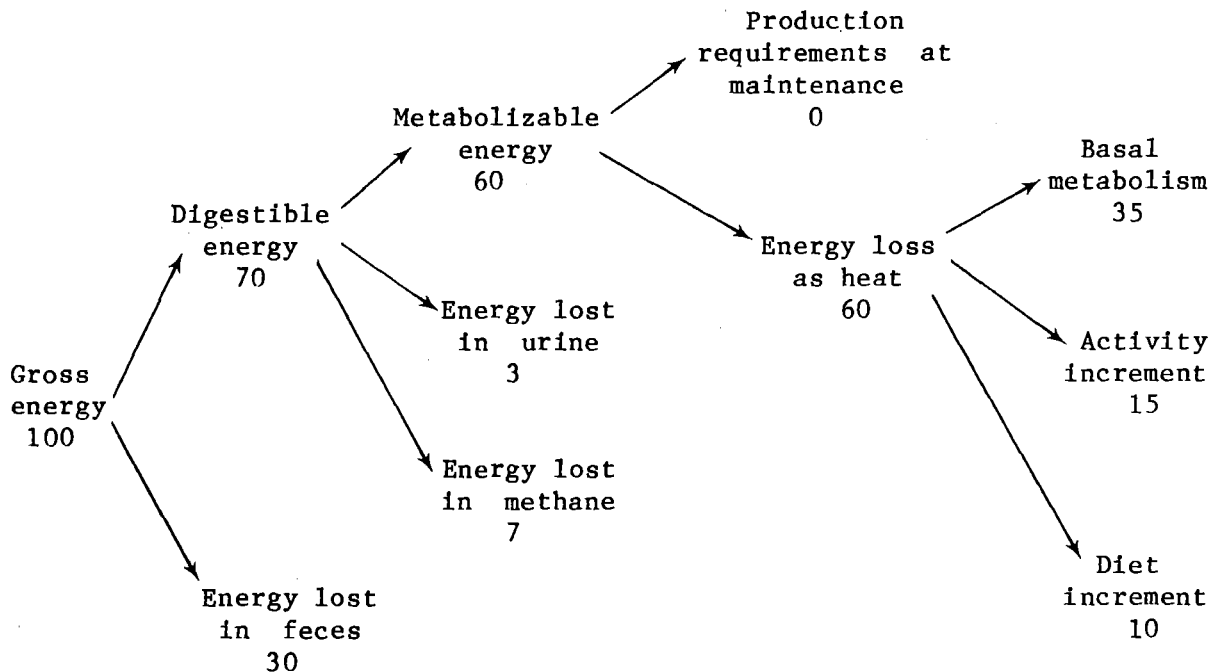


TOPIC 1. FACTORS AFFECTING ENERGY METABOLISM

Nothing is free. The maintenance of basic life processes, the completion of activities, and the production of new tissues are all energy-requiring processes. The energy costs of these processes can be estimated because the energy transfers involved are predictable processes. Equations can be derived that provide good first approximations of the costs of these processes in different ecological circumstances.

Each individual must meet its own requirements for the basic life functions--respiration, circulation, daily activities that provide food necessary to support these functions, maintenance of body tissues, production of new tissues to replace that metabolized--that combine to establish a maintenance requirement of each individual. Since metabolism is an energy-using process, the energy used must be replaced each day in order to sustain life. If the energy requirement is not being met, the animal is in a negative energy balance, and if the amount of energy in ingested nutrients exceeds the energy required, the animal is in a positive energy balance.

The energy flow through an organism includes several pathways of use and dissipation illustrated below. The numbers below each of the terms are relative values illustrating the efficiencies of an animal given by Crampton and Harris (1969:145) at each step.



The efficiencies of energy use have a direct bearing on the amounts of food required. Further, the nutritional requirements are constantly changing as a result of physiological and environmental variables. Since so little is known about the metabolic efficiencies and maintenance, activity, and productive functions of wild ruminants, it is difficult to assess the effects of the different variables in the lives of free-ranging animals in their natural environments. Nevertheless, some patterns may be recognized from data on both domestic animals and wild ruminants, providing insights into relationships between wild ruminants and their natural environments.

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UNIT 1.1: BIOLOGICAL FACTORS AFFECTING ENERGY METABOLISM

Some of the biological factors affecting energy metabolism are historically determined, and some are variables due to circumstances. The former include factors that are determined by genetic and by "programmed" physiological changes. The latter include interspecies and intraspecies relationships present due to current circumstances.

GENETIC

It is well known that animals exhibit individual variation due to genetic differences. The more obvious characteristics, such as coat color, body size, etc., are often the only characteristics considered by field biologists when studying particular populations. Since energy metabolism is so vital to the survival of the individual, genetic factors which affect the energetic efficiencies of animals may have a significant bearing on their survival, especially when conditions of stress begin to appear.

SEX

The two sexes have different metabolic rates at different times of the year; differences in metabolic rates of the sexes are related to their different biological roles. Males are very active during the breeding season, spending a lot of energy for activity. Females are very active during the lactation period, especially in foraging activity when they must supply nutrients for milk production.

AGE

It is well known that the metabolism per unit weight of young animals is higher than that of adults; the metabolic rate of an adult, relative to weight, is usually less than one-half that of a newborn. Lambs reach summit metabolism, the maximum heat production possible without voluntary muscular activity, within one-half hour after birth, and maximum values may be 15 times greater than fetal levels and 5 times greater than "basal" levels (Alexander 1962a). He noted that there was no increase after ingestion of milk, and heat production declined slowly with advancing age, prolonged exposure to cold, and continued fasting.

The physiological capabilities of newborn wild ruminants are quite well-developed as the young are active shortly after birth. Some species, such as caribou, goats, sheep, and muskox, sometimes give birth to young in rather severe weather conditions, and only well-developed offspring can survive. Newborn caribou are able to follow their dam within hours after birth, indicating a high level of physiological development, with survival very much dependent on the nutritional ties between the neonate and the dam.

HAIR CHARACTERISTICS

Since warm-blooded animals maintain a specific internal body temperature (with some variation of course), hair coats with lower insulation values may necessitate higher levels of heat production by the animal. If

two animals with equal surface areas were exposed to identical thermal environments, the one with the better insulation would lose less heat. If heat production were identical for the two animals, the one with the better coat would have a more positive heat balance. Brody (1954) attributed the ability of cattle to withstand temperatures to -40°F to their coat insulation and highly developed vascular control of the thermal conductivity of peripheral tissues. Wild ruminants are very dependent on hair characteristics for insulation from the cold, and have seasonal molts to accomodate seasonal changes in weather.

RELATION TO SURFACE AREA

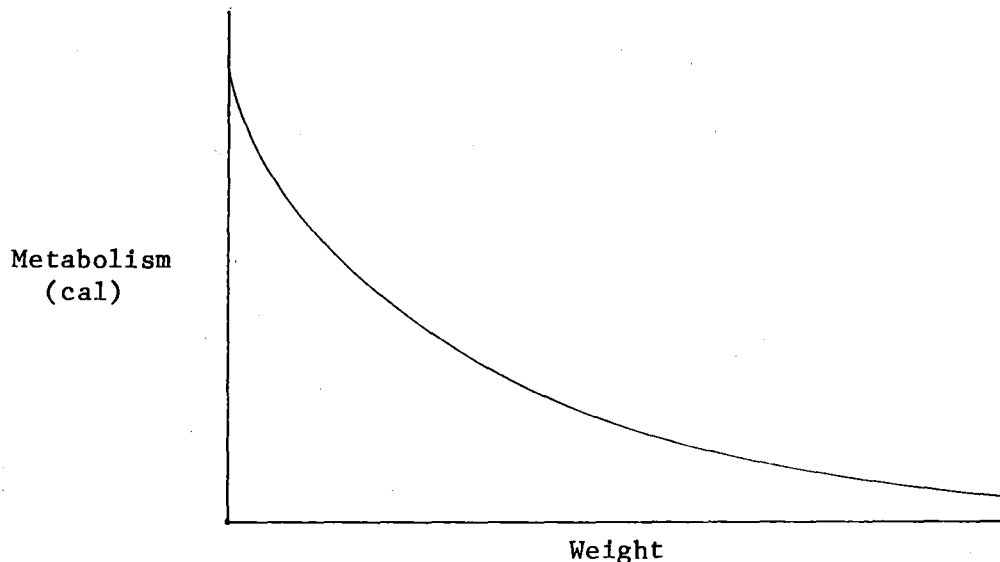
Interpretations of the basal metabolic rate have been made by physiologists for many years, and numerous disagreements have arisen over its relationship to surface area and body weight. The "surface area law" was formulated because it could be shown that heat loss from any object is proportional to surface area, and since heat production must be proportional to heat loss if homeothermy is to be maintained, it was concluded that heat production must be proportional to surface area. This was demonstrated for dogs and rabbits, and the concept was widely applied to other species as well (Brody 1964:356).

However, one factor in the relationship between surface area and heat production is the variability in the surface area of a single animal. A standing animal has a greater surface area than the same animal lying down and curled up. Thus the surface area of an individual is variable, and living organisms may be constantly changing their surface area, heat production, evaporative heat loss, muscular activity, diet, hair insulation through pilo-erection, and other characteristics to maintain a homeothermic condition. If one considers the complexity of heat exchange by radiation, conduction, convection, and evaporation, it becomes immediately obvious that surface area is only one of several important parameters operating in heat exchange. A simple relationship observed empirically between surface area and heat production can hardly be called a "law" in view of the many other associated variables.

If, however, one considers two animals of the same species with identical thermal characteristics of the coats and equal rates of heat production per unit of metabolic tissue, the larger animal with its more favorable surface area:weight ratio should be able to withstand more cold stress than a smaller one. It is possible to calculate the critical surface area (Moen 1968) of an animal. The critical surface area is the surface area:weight relationship which is just sufficient to result in a net thermal exchange of zero. Larger animals have relatively less surface area than smaller ones, and they also have more metabolic tissue and greater metabolic potentials. Heavier lambs were able to maintain homeothermy under conditions of higher heat loss than lighter ones (Alexander 1962b), and this may be due not only to their more favorable size and surface area ratio but also their larger amounts of metabolic resources.

RELATION TO BODY WEIGHT

A large animal has a higher absolute metabolism than a small one. The heat production per unit weight of a small animal is greater than the heat production per unit weight of a large animal, however. The relationship is illustrated below.



Benedict's mouse to elephant curve (Benedict 1938; see also Dukes 1955:625 and Moen 1973:116), widely known in physiological circles, is a quantified display of this relationship; variations between species were found to be quite low and the smooth and logical shape of the entire graph striking. Deviations from the curve may be real or they may be artifacts, and perhaps are a combination of the two.

The total mass of an animal includes some tissue that is not actively participating in the metabolic processes but is the final product of metabolic processes. The hair, horns, and antlers, once growth is completed, are examples. Ingesta in the gastro-intestinal tract is another example; it adds to body weight but is not part of the animal's metabolic tissue.

There has been considerable discussion of the mathematical relationship between heat production and body weight. The formula for this relationship is:

$$Q = k W^b$$

where Q is the heat production in calories per day, k is a constant, W is the weight in kilograms, and b is an exponent that has generated most of the controversy. Physiologists have been searching for an exponent which will result in a constant value of k . If this could be found, the basal heat production of any animal could be determined by simple multiplication after measuring the weight of the animal.

Published values of b have ranged from 0.66 to 0.75. Much of the controversy is in the rounding off of the value. Brody (1945) suggests that b should be 0.7 and Kleiber (1961) uses 0.75. The National Research Council (1966) adopted the exponent $b = 0.75$. Fasting homeotherms under standard conditions produce about 70 kcal of heat per $\text{kg}^{0.75}$ (Kleiber 1961). Measurements of four deer in winter coat resulted in an average of 75.6 Kcal per $\text{kg}^{0.75}$ per 24 hours, and measurements of three deer in summer coat had an average of 84.4 Kcal per $\text{kg}^{0.75}$ (recalculated from Silver 1968; see Moen 1973:117). Since winter and summer differences are part of the rhythmic seasonal variations in metabolism of deer, I no longer calculate an average basal metabolism for deer, choosing rather to use $70W_{\text{kg}}^{0.75}$ as a mathematical base-line and representing ecological metabolism with time-dependent equations.

REPRODUCTIVE CONDITION

Three stages in the reproductive cycle--breeding, gestation, and lactation--have definite effects on the energy metabolism. It is well known that male wild ruminants expend large amounts of energy in increased activity during the breeding season and lose considerable weight. During gestation, the female must expend additional energy to maintain the uterus, to meet increased demands on the circulatory, respiratory, and excretory systems, to handle the endocrine influences on her own metabolism, and provide for fetal growth (Brody 1945). The energy metabolism per unit weight is not higher for pregnant females until the last 1/3 of pregnancy when fetal growth is much accelerated, however (Morrison 1948). During rapid fetal growth, elevated metabolism is expected since growth demands additional energy for synthesis of fetal tissue. The high rate of fetal metabolism is followed by a declining but still high neonate metabolism, after which metabolic rates decline to more stable and rhythmic adult levels.

Lactation places a high physiological demand on the female as milk is synthesized from the nutrients in ingested food. The heat production of cattle during heavy lactation is approximately 100% above the non-lactating level, with the increase directly proportional to milk production. The higher metabolic rate is associated with the higher food consumption and milk production rather than with muscular activity (Brody 1945:820). Calculations of the cost of lactation for white-tailed deer indicate that it is the most costly sustained biological process there is (Moen 1973 and Robbins and Moen 1975).

PATHOGENS AND PARASITES

Whenever one organism supports the life processes of another organism living upon or within it, the energy requirements of the host animal must go up unless the two species exhibit a kind of mutualism (Odum 1959) in which the growth and survival of both populations is benefited. The relationship between a ruminant and the rumen flora and fauna is an example of mutualism. Pathogens and parasites, however, increase the catabolic mechanisms of an animal (Jones 1963 in Thayer), resulting in increased energy demands.

HEAT INCREMENTS

Heat production increases when an animal becomes more active since muscle contractions are exothermic. Digestion of food in the gastrointestinal tract also results in an increment in heat production of an animal. It is defined as an extra heat increment incident to the total nutritive process, including the energy cost of excretion of the end products (Brody 1945:59). It is sometimes called an energy waste associated with the use of food, but the extra heat energy may be of value during cold weather as it helps keep the animal warm.

What heat increments are characteristic of animals on different diets? Blaxter (1962:141) presents a table showing the differences in heat production of sheep and steers on fasting, maintenance, and full-feed diets. For sheep the ratio of the maintenance to the fasting diet is 1.47/1, and of the full feed diet to the fasting diet 1.88/1. The ratio for steers on a maintenance diet compared to a fasting diet was 1.38/1. Such increments are of interest to the field biologist when analyzing the energy balances of animals on ranges with different food supplies, topographies, and weather conditions.

ACTIVITY

Activity, or the movement of mass through distance, is work. Every animal must expend energy when moving its mass horizontally and vertically for whatever distances are involved. Range and wildlife managers ought to be interested in the amounts of energy required for these movements since topographic relief, distances to water and other range characteristics may have effects on the efficiencies of the animals and on population ecology.

The speed with which an animal moves also has an effect on the energy cost of movement. In sheep, the energy cost of horizontal locomotion increased but the cost of ascending vertical gradients decreased with increasing speed (Clapperton 1961). It is interesting to speculate on the energy costs involved in rapid bursts of speed exhibited by wild ruminants during escape behavior.

SOCIAL AND PSYCHOLOGICAL EFFECTS

Numerous sociological and psychological stressors influence energy requirements. Pfander (1963:117) lists such things as confinement vs. natural range, herd vs. individual response, numbers per group, space per animal, noise level, and other disturbances as factors that affect energy requirements of domestic species.

One unknown factor in basal metabolism measurements is the effect of confinement on the psychology and metabolism of the animal. Well-trained animals appear more calm, of course, but visible signs of excitement need not be present to have elevated metabolism. A male white-tailed deer that was rescued from an ice-covered lake (Moen 1967) showed body temperature variations that were not accompanied by visible signs of excitement when resting in the garage at the laboratory. The deer showed a steady increase

in body temperature from a low of 26.4°C to a high of 39.5°C as it was warmed up, after which it returned to 38°C. My presence in the room, however, caused the temperature to rise quickly to 38.5°C, but the animal showed no signs of fear. When I left the room, body temperature declined to 38°C again. The docile nature of the deer when in the garage changed instantly when it saw the trees through the open garage door as we prepared to release him. After thrashing around in its nylon mesh cage, the deer was finally released and ran directly into the woods.

RHYTHMIC CHANGES IN THE BASAL METABOLIC RATE

Marked changes in the rates of metabolism during daily and seasonal periods have been observed. Nocturnal animals have a lower BMR during the daytime (Benedict 1938), and times of muscular activity and metabolic rates are related (Brody 1945). Seasonal variations also occur. A depressed winter metabolism in white-tailed deer was first reported by Silver (In Siegler 1968:191), but the number of deer studied was not sufficient to warrant a definite conclusion about seasonal lability. Several years of research at the Wildlife Ecology Laboratory have shown definite seasonal metabolic rhythms in ecological metabolism (Moen 1978).

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BIOLOGICAL FACTORS AFFECTING ENERGY METABOLISM

SERIALS

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
JWMAA	34--4	863	869	odvi	diges metab ener mich does ullrey,de; youat/		1970
JWMAA	42--4	715	738	odvi	seas chan, heart rate, act moen,an		1978
JWMAA	42--4	776	790	odvi	diet prot, engy effct fawn seal,us; verme,1/		1978

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
CJZOA	48--2	275	282	odhe	feed intake, heat producti nordan,hc; cowan/		1970
JWMAA	35--3	461	468	odhe	radioiodine uptake, retent gist,cs; whicker,		1971

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
SZSLA	21---	101	108	ceel	physiol of diges and metab maloiy,gmo; kay,/		1968

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

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

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
JWMAA	34--4	908	912	anam	ener flux, water kinet, yo wesley,de; knox,/		1970
JWMAA	37--4	563	573	anam	energy metabolism, prongho wesley,de; knox,/		1973

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

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

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

oram

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

AJAEA 11--1	85	96	dosh seas var wool gr, heat tol	wodzicka,m	1960
AJAEA 13--1	82	99	dosh temp reg, metab, newborn l	alexander,g	1962
AJAEA 13--1	144	164	dosh energ metab, starved newbo	alexander,g	1962
AJAEA 15--6	969	973	dosh ener cost, expend, feed ac	graham,nmcc	1964
BJNUA 16--4	615	626	dosh fasting metab, adult wethe	blaxter,kl	1962
COVEA 57--1	43	53	dosh erythrocyte loss, restitut	georgi,jr; whitlo	1967
PAANA 5---1	138	140	dosh effect lactat, wool growth	corbett,jl	1964
PNSUA 20- xxxi	xxxii		dosh energy expenditur, walking	clapperton,jl	1961
SCIEA 145--	1318		dosh hematocr val, hemoglo type	evans,jv; whitloc	1964

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

AJPHA 219-4	1104	1107	scali, energ cost, running	taylor,cr; schmi/	1970
AMNTA 99---	373	376	nat mort, reprod, min meta	wilson,ta	1965
AMZOA 8---1	71	81	thermodynam consid, nutrit	wiegert,rg	1968
ATRLA 24-12	125	136	metab, body size, homeothe	poczopko,p	1979

continued on the next page

CODEN	VO-NU	BEP	ANIM	KEY WORDS	AUTHORS	YEAR
CIWPA	503--	1	215	vital energ: comp bas meta	benedict,fg	1938
FEPRA	29--	4	1524	1532	ener metab, bod size, scal	schmidt-nielsen,k 1970
JANSA	43--	3	692	704	fasting heat prod, body wt	thonney,ml; touc/ 1976
JCCPA	31---		281	291	oxyge consump, basal condi	morrison,pr 1948
NUMEB	21--	1	88	104	energet fat metabo, growth	van es,ajh 1977
OJSCA	74--	6	370	380	energetics of endotherms	mcnab,bk 1974
PECTD	1---	2	85	101	bioenerg params, wild rumi	drozdz,a; weiner/ 1975
PHREA	27--	4	511	541	body size, metabolic rate	kleiber,m 1947

OTHER PUBLICATIONS

Davydov, A. F. On the processes of muscular activity in reindeer during procurement of feeds from under the snow. Russian original from Sbornik "opyt izucheniya regulyatsii fiziologicheskikh funkstii v estestvennykh uslovyakh sushchestvovaniya organizmov," Vol. 6:35-40. 1963. Translation available from U.S. Dept. Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Va.

CHAPTER 7, WORKSHEET 1.1a

Resting heat production of black-tailed deer

Measurements of the resting heat production of male and female black-tailed deer fawns have been made by Nordan et al. (1970). The weight and heat production measurements reported in TABLE II (p. 278) make it possible to calculate multiples of base-line metabolism (MBLM) at each weight. The data and calculations are given below.

	<u>LWKG</u>	<u>REHP</u>	<u>LWKG^{0.75}</u>	<u>BLM</u>	<u>MBLM</u>
Males:	5	382	3.34	234	1.63
	10	880	5.62	394	2.24
	15	1180	7.62	534	2.21
	20	1460	9.46	662	2.21
	25	1722	11.18	783	2.20
Females:	5	498	3.34	234	2.13
	10	837	5.62	394	2.12
	15	1076	7.62	534	2.01
	20	1408	9.46	662	2.13
	25	1669	11.18	783	2.13

Note how similar the MBLM values are throughout this range of body weights.

Keep in mind these are resting heat production values, and will be different from ecological metabolism. The MBLM for the ecological metabolism of a growing fawn will be higher (see CHAPTER 7, Page 2. and also TOPIC 6).

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Nordan, H. C., I. McT. Cowan, and A. J. Wood. 1970. The feed intake and heat production of the young black-tailed deer (Odocoileus hemionus columbianus). Can. J. Zool. 48(2):275-282.

CHAPTER 7, WORKSHEET 1.1b

Energy metabolism of pronghorn

The total heat production and fasting heat production of female pronghorns from 2 months to 18 months are given by Wesley et al. (1973). Calculations of MBLM are easily made from the age, weight, and heat production data presented in Table 2 (p. 567). The following table is derived from their data.

<u>Month of Year</u>	<u>Age Class (months)</u>	<u>LWKG</u>	<u>MEWK*</u>	<u>Total Heat Production</u>	<u>MBLM</u>	<u>Fasting Heat Production</u>	<u>MBLM</u>
July	2.0	8.9	5.15	783	2.17	603	1.67
January	7.5	26.1	11.55	1316	1.63	843	1.04
May	12.0	26.8	11.78	1425	1.73	884	1.07
November	18.0	37.8	15.24	1707	1.60	1220	1.14

*MEWK = metabolic weight in kg = $LWKG^{0.75}$

Note how MBLM for total heat production varies from 1.60 to 2.17. Variations after the age of 2.0 months may be a reflection of a seasonal rhythm, but there are too few data through the annual cycle to confirm that.

Evaluate these MBLMS in relation to the seasonal rhythms of white-tailed deer discussed in TOPIC 6.

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CHAPTER 7, WORKSHEET 1.1c

Behavioral effects on the energy expenditures of white-tailed deer

The effects of different amounts of physical activity in six different behavioral regimes on energy metabolism have been demonstrated in a sequence of calculations in Moen (1976). The least activity, with 75% of the time spent bedded, 10% standing, 10% foraging, 5% walking, and no running, resulted in graphed values of energy expenditure as low as 1700 kcal per day for a 60-kg deer. The most activity, with 25% of the time spent bedded, 30% standing, 12% walking, 30% foraging, and 3% running, resulted in graphed values approaching 3000 kcal per day for a 10-kg deer. These two expenses, and various combinations of effects between them, are plotted in Figure 3, page 198 of Moen (1976).

Determine multiples of base-line metabolism for the energy expenditures given in the paragraph above with the following formula:

$$\text{MBLM} = \text{Energy expenditure}/(70)(\text{MEWK})$$

where MBLM is the multiple of base-line metabolism, and MEWK is metabolic weight in kg, and (70)(MEWK) is base-line metabolism. Both of these are discussed on Chapter 7 - Page 2.

Other values of MBLM may be determined from Figure 3 in Moen (1976) also. Note that the 1976 publication includes discussions of multiples of basal metabolism rather than base-line metabolism. This change in terminology is due to clarification of concepts as a result of analyses described in Moen (1978).

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UNIT 1.2: ENVIRONMENTAL FACTORS AFFECTING ENERGY METABOLISM

The concept of thermoneutrality--the thermal range in which an animal does not need to respond physiologically to maintain normal body temperature --is well known. The terms "upper critical temperature" and "lower critical temperature," deeply entrenched in the literature, are meant to represent the limits of the thermoneutral range on a thermometric scale. Many more parameters are involved in heat exchange in the natural world than temperature alone, however. Further, temperature measurements are on an ordinal scale, and do not represent the actual amount of energy exchanged in a particular system. I have suggested that the concept of a critical thermal environment (Moen 1968) replace the "critical temperature" idea used previously. Critical thermal environment is a much more appropriate term in view of the many factors involved in heat exchange.

A critical temperature may be determined if all thermal parameters except temperature are held constant in a particular system. In the same manner, however, a critical wind velocity can be determined if temperature and all other thermal parameters are held constant. Similarly, critical values for body weights, evaporation rates, postures, heat production, and many other parameters can also be calculated.

The concept of thermal neutrality is physiologically sound. The term critical thermal environment is comprehensive and applies to the concept of thermoneutrality.

Another environmental factor affecting energy metabolism is snow. The depth and density characteristics of snow can have a major effect on energy metabolism as animals of different sizes and weights sink to different depths.

Surface characteristics also affect the metabolic cost of walking. Less energy expenditure was measured on reindeer walking on roads than on tundra (White and Yousef 1978), indicating that the more firm road surface was easier to walk on than the softer tundra surface.

The topography affects energy metabolism as the cost of walking on the level is less than the cost of walking upslope. The cost of walking downslope is less than the cost on an upslope (Robbins et al. 1977), but the compensation is not equal to the upslope costs.

Environmental stimuli, such as mechanical noises, wind, predators, and other stimuli, may get the attention of an animal and increase the energy metabolism. Many of these transients are of short duration, such as a jet plane passing overhead, and may contribute little to the total daily cost of living. Others, such as a predator, may demand a high rate of energy metabolism for escape. Heart rate increases are discussed in Moen and Chevalier (1977); corresponding changes in energy metabolism are unknown, however.

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ENVIRONMENTAL FACTORS AFFECTING ENERGY METABOLISM

SERIALS

CODEN	VO-NU	BEP	ANIM	KEY WORDS-----	AUTHORS-----	YEAR
BISNA	18-11	1041	1043	odvi critical thermal environme	moen,an	1968
CJZOA	53--6	679	685	odvi ambien temp effect, physio	holter,jb; urban/	1975
CJZOA	56--5	1207	1210	odvi heart rates w-t-d wolf how	moen,an; dellaf/	1978
ECOLA	57--1	192	198	odvi energy conservat in winter	moen,an	1976
JOMAA	48--4	655	656	odvi hypotherm, water-chill	dee moen,an	1967
CODEN	VO-NU	BEP	ANIM	KEY WORDS-----	AUTHORS-----	YEAR
JWMAA	33--3	482	490	odvi diges ener, win, mich	does ullrey,de; youat/	1969
JWMAA	34--4	863	869	odvi diges metab ener mich	does ullrey,de; youat/	1970
JWMAA	35--1	37	46	odvi effect falli temp, heat pr	silver,h; holter/	1971
JWMAA	42--4	715	738	odvi seas chan, heart rate, act	moen,an	1978
CODEN	VO-NU	BEP	ANIM	KEY WORDS-----	AUTHORS-----	YEAR
CJZOA	48--2	275	282	odhe feed intake, heat producti	nordan,hc; cowan/	1970
ECMOA	2---1	1	46	odhe seasonal migration, mule d	russel,cp	1932
JWMAA	43--1	162	169	odhe energ requi, fawns, winter	baker,dl; johnso/	1979

CODEN	VO-NU	BEP	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
CBPAB	60A-3	251	256	ceel	energ, nitr metab, cold en simpson,am; webs/		1978

CODEN	VO-NU	BEP	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
JOMAA	50--2	302	310	alal	od, structur adaptat, snow kelsall,jp		1969
QSFRA	3----	51	73	alal	influence of snow on behav des meules,p		1964

CODEN	VO-NU	BEP	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
APSCA	105-3	268	273	rata	spitzberg, wint-dorman ung ringberg,t		1979
CJZOA	39--7	845	856	rata	clima, metab, therm, infan hart,js; heroux,/		1961
CJZOA	48--2	391	392	rata	energy metab, barren groun mcewan,eh		1970
IJBMA	12--1	21	27	rata	act wint cari, snow, alask henshaw,j		1968
PHZOA	30--2	93	105	rata	melt points, anim fat, col irving,l; schmid/		1957

CODEN	VO-NU	BEP	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
JWMAA	31--1	159	164	anam	mort, severe wint, montana martinka,cj		1967
JWMAA	37--4	563	573	anam	energy metabolism, prongho wesley,de; knox,/		1973

CODEN	VO-NU	BEP	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
bibi							

CODEN	VO-NU	BEP	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
CJZOA	56-11	2388	2393	ovca	winter bioenerget, rocky m chappel,rw; hudso		1978
JWMAA	35--3	488	494	ovca	variat of rectal temperatu franzmann,aw; heb		1971

CODEN	VO-NU	BEP	ENPA	ANIM	KEY WORDS	AUTHORS	YEAR
ovda							

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

obmo

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

oram

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

JASIA 44--1 5 66 doca wint nutr depres, grow, re joubert,dm 1954

JASIA 58--1 109 120 doca sig extremities, therm reg whitton,gc 1962

RSPYA 4---3 353 362 doca oxy cost, therm- hyperven hales,jrs; findla 1968

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

AJAEA 11--3 402 407 dosh regula bod temp, hot envir brook,ah; short,b 1960

AJAEA 13--1 82 99 dosh wind, h2o, metab rate, lam alexander,g 1961

AJAEA 13--1 122 143 dosh heat excha, lamb.hot envir alexander,g; will 1962

AJAEA 13--1 144 164 dosh energ metab, starv newborn alexander,g 1962

AJAEA 15--6 982 988 dosh ambi temp, heat prod, preg graham,nm 1964

BJNUA 21--3 769 785 dosh conti meas, heart ra, ener webster,ajf 1967

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

CNJNA 43--1 39 46 dosh low envir temp, phys respo hess,ea 1963

JASIA 52--1 13 24 dosh ener metab, clos clipped s graham,nm; wainm/ 1959

JPHYA 198-2 251 276 dosh shiv, nonshiv thermogenesi alexander,g; will 1968

SCIEA 145-- 1318 1318 dosh hematocr val, hemoglo type evans,jv; whitloc 1964

CODEN	VO-NU	BEP	ANIM	KEY WORDS-----	AUTHORS-----	YEAR
ANYAA	53--3	600	607	mamm role, piliary sys, therm e	herrington,lp	1951
BISNA	18-11	1041	1043	critical thermal environme	moen,an	1968
FEPR	28--3	1053	1058	intersp diff, cold adaptat	jansky,l; bartun/	1969
FEPR	29--4	1541	1552	many rhythmic var in ener metab	aschoff,jj; pohl/	1970
JAPYA	7---4	355	364	skin temp, arcti, heat reg	irving,l; krog,j	1955
NATUA	234--	483	484	many hier watr, eng, desrt	macfarlane,wv; h/	1971
NUMEB	21--1	88	104	energet fat metabo, growth	van es,ajh	1977
SSEBA	18---	31	48	many insulat, metab adapt, cold	hart,js	1964
ZOBIA	2---	887	899	calor val equiv, bod wt ch	dargol'ts,vg	1973

OTHER PUBLICATIONS

Davydov, A. F. On the processes of muscular activity in reindeer during procurement of feeds from under the snow. Russian original from Sbornik "opyt izucheniya regulyatsii fiziologicheskikh funkstii v estestvennykh uslovyakh sushchestvovaniya organizmov," Vol. 6:35-40. 1963. Translation available from U.S. Dept. Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Va.

CHAPTER 7, WORKSHEET 1.2a

Chamber temperature effects on MBLM of the white-tailed deer

The energy expenditure values for white-tailed deer in a temperature-controlled chamber given by Holter et al. (1975) may be converted to MBLM by dividing the y-axis values in Figure 3 (p. 682) by 70. In the summer, MBLM was about 3.0 as the ambient temperature in the chamber was lowered to near 0°C. This is a very high relative rate of metabolism as a response to cold; productive processes require MBLM's of 2.5 to 4.0 (Moen 1978). In the winter, MBLM reached a low of about 1.3 at about 10°C, and a high of about 1.8 at about -20°C. These values are within the range of values for the winter period in the annual metabolic cycle discussed in Moen (1978). No indications of a rise in energy metabolism have been observed in the deer at Cornell's Wildlife Ecology Laboratory when air temperatures have dropped from about 10°C to -20°C. These animals have been free to choose their options in response to natural weather patterns.

Air temperatures to -20°C and cooler have always been accompanied by further reductions in heart rates and energy conservation behavioral responses by these deer. Different results in the New Hampshire chamber are likely due to the fact that the number of options are very limited in a chamber, and that the freedom to select and move to locations of the deer's choice cannot be exercised.

Equations for energy expenditures during different seasons are not given in Holter et al. (1975), but values may be estimated from plotted data using a grid overlay. Complete the estimations and compare MBLM's determined with the seasonal rhythms in Moen (1978).

LITERATURE CITED

- Holter, J. B., W. E. Urban, Jr., H. H. Hayes, H. Silver, and H. R. Skutt. 1975. Ambient temperature effects on physiological traits of white-tailed deer. *Can. J. Zool.* 53(6):679-685.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism and forage intake of white-tailed deer. *J. Wildl. Manage.* 42(4):715-738.

CHAPTER 7, WORKSHEET 1.2b

The effects of walking speed, percent slope, and snow depths
on the energy expenditures of white-tailed deer

The effects of various combinations of walking speed, percent slope, and snow depths on energy expenditures have been graphed in Moen (1976, Figure 3, p. 194). The energy costs of different combinations may be read on the y-axis and MBLM determined for a 60-kg deer. For example, a deer in Behavioral Regime 6, walking 90 cm per second on a 0% slope in about 18 cm of snow is predicted to have an energy expenditure of 2400 kcal per day. The multiple of base-line metabolism is:

$$\text{MBLM} = 2400 / (70)(60^{0.75}) = 1.59$$

Determine the energy costs of different combinations and summarize in the space below. Note that the multiples of basal metabolism given in Moen (1976) are considered in this book to be multiples of base-line metabolism (see WORKSHEET 1.1c, Chapter 7 - Page 18c).

LITERATURE CITED

Moen, A. N. 1976. Energy conservation by white-tailed deer in the winter. Ecology 57(1):192-198.

CHAPTER 7, WORKSHEET 1.2c

Energy exchanges of red deer (ceel) at three chamber temperatures

Energy exchanges of young red deer at three air temperatures and three levels of feeding are given in Table 4 (p. 253) of Simpson et al. (1978). The values are presented in MJ per day, which can be converted to kcal with the following equation:

$$\text{kcal per day} = (\text{MJ}/4.184)1000$$

Multiples of base metabolism are determined by dividing kcal per day by (70)(MEWK). Using these equations, the following MBLMs have been determined:

	<u>Level of Feeding</u>		
	<u>Low</u>	<u>Medium</u>	<u>High</u>
Metabolizable energy intake (MBLM)	1.10	1.84	2.33
Heat production (MBLM) at 16°	1.57	1.58	1.70
8°	2.05	2.35	2.49
4°	1.86	2.38	2.20

These multiples indicate a rise in heat production at each level of feeding as the temperature dropped from 16 to 8°, and at only one level of feeding as the temperature dropped from 8 to 4°.

The MBLM calculations are illustrated here to call attention to the utility of MBLM as a parameter for comparisons between levels of feeding, chamber conditions, weights, and species. Verify these calculations based on the original data in Simpson et al. (1978) in order to become thoroughly familiar with the patterns of MBLM in different situations.

LITERATURE CITED

- Simpson, A. M., A. J. F. Webster, J. S. Smith, and C. A. Simpson. 1978. Energy and nitrogen metabolism of red deer (Cervus elaphus) in cold environments: a comparison with cattle and sheep. Comp. Biochem. Physiol. 60:251-256.

CHAPTER 7, WORKSHEET 1.2d

Effects of weather on energy metabolism of infant caribou

The effects of different combinations of air temperature, wind and precipitation on the metabolism of infant-caribou was studied by Hart et al. (1961). Results are presented in Table III (p. 850), including a column for heat production in kcal per hour/kg^{0.75}. These data may be converted to MBLMs by simply multiplying the HP value by 24 and dividing by 70. Values of MBLM range from about 1.4 for a dry calf in the lab at 0°C to over 10 for a calf exposed to wind and precipitation.

Complete the calculations of MBLM for each of the test conditions given in the published paper and evaluate them in relation to the experimental variables. Examples are MBLM in relation to air temperature (the first five results in Table III) and MBLM in relation to wind velocity (the last six results in Table III). Multiple regression analyses may be useful here too, except that the effects of wind on MBLM may not be linear. This is discussed further in PART V.

Note that Hart et al. indicate that 25 kcal per hour/kg^{0.75} is a "lethal level." This is $(25)(24)/70 = 8.6 = \text{MBLM}$, which is a higher rate of metabolism than that of very high producing dairy cows! Infant caribou can hardly be expected to maintain such a metabolic level for very long.

LITERATURE CITED

- Hart, J. S., O. Heroux, W. H. Cattle and C. A. Mills. 1961. The influence of climate on metabolic and thermal responses of infant caribou. Can. J. Zool. 39(7):845-856.