

7

ENERGY METABOLISM

All living organisms must utilize energy to maintain their life processes. Organisms are subject to the first law of thermodynamics, which states that energy can be neither created nor destroyed, but only changed in form. Not all of the energy that reaches the surface of an organism or is ingested by it is of direct benefit because some of it is in a form that is not directly useful to the organism. The amount of energy utilized compared with the amount actually available to an organism is an expression of the energetic efficiency of the organism.

The conversion of energy from one form to another in living organisms is called metabolism. These energy conversions or metabolic processes occur at different rates in different tissues within the body. The rate of metabolism in an active animal is high and in an inactive animal, low.

If cells accumulate more rapidly than they are destroyed, growth occurs. If cells are destroyed more rapidly, the animal loses weight. Growth results from the assimilation of the products of digestion and, in ruminants, rumen fermentation into new body tissue. Amino acids, for example, are synthesized into bacterial protein in the rumen. The bacteria are then broken down into amino acids for assimilation into body tissue in the ruminant. During catabolism, carbohydrate and fat molecules are broken down into simpler carbon dioxide and water molecules. Protein molecules are broken down into carbon dioxide, water, and the nitrogen compound urea, which is excreted in the urine. As a result of this process, energy stored in the large molecules is released and becomes available to the animal.

Metabolic energy is expressed in units called calories. One gram-calorie is approximately equal to the amount of heat required to raise the temperature of one gram of water from 14.5° to 15.5°C. A more useful unit in physiological work is the kilocalorie, which is one thousand times larger than the gram-calorie.

7-1 BASAL METABOLISM AND ASSOCIATED TERMINOLOGY

Basal metabolism has been defined as the minimal energy cost when an animal is at rest in a thermoneutral environment and in a post-absorptive condition (Brody 1945). The measurement does not represent the minimum rate of metabolism needed to support life. In humans, for example, measurements indicate that the metabolic rate is lower during sleep than during rest. The post-absorptive condition is necessary to reduce as much as possible any heat production that can be attributed to the heat of fermentation of food or the heat of nutrient metabolism.

The energy required to maintain life at the basal metabolic rate provides for circulation, excretion, secretion, respiration activities, and the maintenance of muscle tone. Crampton and Harris (1969) estimate that 75% of the energy of basal metabolism is spent in maintaining muscle tone and body temperature, with 25% being used in circulation, excretion, secretion, and respiration.

USES FOR MEASUREMENTS OF BASAL METABOLIC RATE. The basal metabolic rate (BMR) is useful as a base line with which comparisons may be made when the animal is physically active, on different diets, diseased, infected with parasites, pregnant, lactating, or in some condition that requires expenditure of energy. Thus it is useful in diagnostic work and for evaluating the effect of activity and production on the energy requirements of free-ranging animals.

CONDITIONS FOR MEASUREMENT. The standard conditions of thermoneutrality, post-absorptive digestion, a lying posture, and a calm psychological state are necessary for establishing a base line for energy metabolism because animals react physiologically to heat or cold stress, digestive processes, changes in activity, and psychological stress. Thermoneutral conditions are required because the metabolic rate increases when an animal is subject to either heat stress or cold stress. Air temperatures of 20° to 25°C are usually considered to be in the thermoneutral range of most large animals, although this range is dependent on physiological, behavioral, and environmental factors (Moen 1968). Air temperature is a useful index to the thermal conditions in a metabolism chamber, but in the field environment many other factors must also be considered. These are discussed in Chapters 6, 13, and 14.

A post-absorptive digestive state is necessary as a standard condition because the digestion of different diets affects the rate of heat production. Ritzman and Benedict (1931) found that sheep reach a post-absorptive state in 34 to 48 hours although foodstuffs may still remain in the intestinal tract. The level of feeding affects the amount of time that an elevated heat production persists; sheep that had been on a high level of feeding had a higher heat production for a seven-day

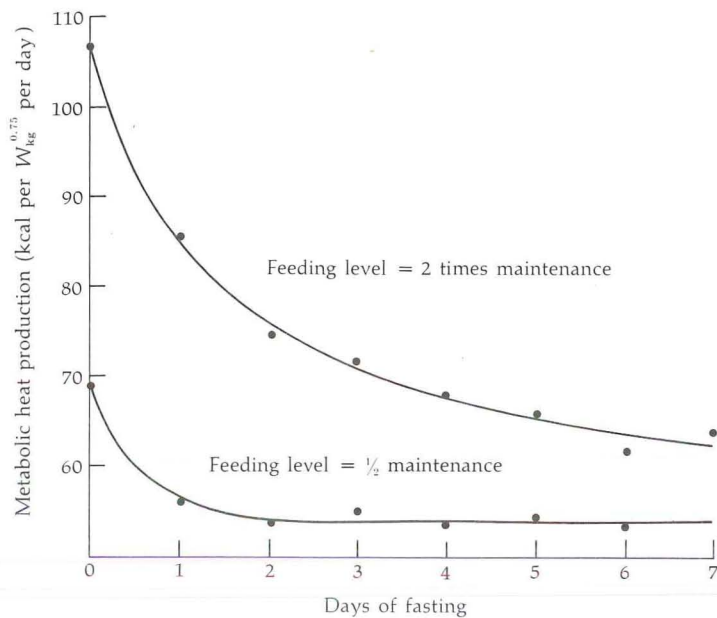


FIGURE 7-1. The relationship between heat production of sheep and the number of days of fasting. (Data from Marston 1948.)

fasting period than those that had been on a lower level of feeding (Figure 7-1).

The lying posture is an easy requirement to meet when working with humans, but domestic and wild animals lie down and stand up at their own discretion. The only practical way to solve this problem is by mathematically correcting the standing measurements to the comparable lying-posture level, eliminating the muscular effect of supporting the body during basal-metabolism measurements. The data may be left uncorrected and expressed as fasting metabolism, although variation in results will then be partly due to differences in the proportion of time spent standing and lying in the metabolism chamber.

A calm psychological state can be attained only after an animal has received the proper amount of training in the chamber. This may be accomplished in a few days or weeks for domestic animals. Wild ruminants generally require longer periods of training before they can be confined in a chamber. Even with training, as many sensory stimuli as possible should be excluded from the chamber environment. This reduces the psychological tension of the animal and may reduce the number of changes in posture.

The results of metabolic measurements are not uniform for all individuals within a species. There are inherent differences between individuals that contribute to this variation. There are also differences in the presumed standard conditions that can be attributed to experimental error. Metabolic measurements under standard conditions are actually somewhere between true basal metabolism and some upper limit.

The value of basal metabolic measurements and other physiological parameters will increase as wildlife research advances from a descriptive field phase to a more

basic diagnostic and experimental phase that includes the entire laboratory-pen-field spectrum. It is important to establish a base line so that the effect of experimental variables can be analyzed.

ASSOCIATED TERMINOLOGY. Heat production can increase in the absence of voluntary muscular activity. There may be a physiological response to cold or a psychological response to environmental stimuli. Hoar (1966) credits Giaja with the term "summit metabolism," which is the highest metabolic rate attainable at normal body temperature without voluntary muscle activity.

Since the term basal metabolism implies a sort of minimum, Brody (1945) used the term "resting metabolism" when the metabolism is not post-absorptive and "fasting metabolism" when the resting metabolism is approximately post-absorptive. Hoar (1966) suggests that the term "standard metabolism" should be a preferred term for use by comparative physiologists. Fasting heat production may be preferred for ruminants with the length of the fasting period specified, since it is difficult to determine just when they reach a post-absorptive state (Crampton and Harris 1969).

Standard metabolism or fasting heat production are perhaps better terms since they imply that the measurements were made under standard conditions or at a certain time after eating without attaching exact significance to the resulting level of measurement. The term basal, however, is so firmly established with reference to mammals that its replacement by a more appropriate term is highly unlikely.

7-2 MEASUREMENTS OF BASAL METABOLIC RATE

DIRECT METHODS. Direct measurements of the metabolic rate involve the measurement of the actual heat production by the animal. Lavoisier, in the latter part of the eighteenth century, discovered a relationship between heat energy given off by an animal and energy in the ingested food (Hoar 1966). This was done by placing a guinea pig in a closed box surrounded by ice and recording the amount of ice that melted in a specified period of time. Knowing that about 80 calories of energy are required to melt one gram of ice, he then calculated the amount of heat energy released by the animal, and this was found to be related to the energy in the food.

The early direct methods of Lavoisier have been refined in calorimetry chambers. Professor Armsby built one early in the twentieth century at The Pennsylvania State University using the same basic principle as the crude icebox calorimeter, but circulating water removed the heat energy from the chamber. Calculations were based on the flow rate, temperature changes, and other thermal characteristics of the water and chamber.

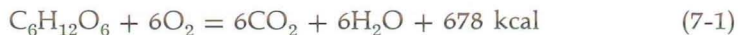
INDIRECT METHODS. Indirect measurements of heat production in use today are simpler and less expensive than the direct methods used by the earlier investigators. These indirect methods are used to measure the amount of oxygen con-

sumed and the amount of carbon dioxide produced by the animal. Heat production is calculated from the measured oxygen and carbon dioxide volumes and their relationships to exothermic metabolic processes.

The use of a mask through which the oxygen intake can be monitored is one of the most inexpensive methods. The advantage of this is that the animal need not be confined in a small chamber; domestic animals usually become quite at ease, once accustomed to wearing the mask. Hammel (1962) and Hart et al. (1961) used this method in their studies of reindeer and caribou, respectively.

A respiration chamber designed for indirect calorimetry for deer is currently in use at the University of New Hampshire (Figure 7-2). The oxygen and carbon dioxide content of the air leaving the chamber is measured and is compared with that of air entering the chamber. The differences are attributed to the metabolic processes of the experimental animal. The chamber is equipped with temperature controls, so experiments on metabolic responses to changes in chamber temperature can be measured.

CALCULATION OF HEAT PRODUCTION. The calculation of heat production using indirect calorimetry is illustrated by equation (7-1) from Brody (1945).



This equation shows that the oxidation of one mole of hexose ($\text{C}_6\text{H}_{12}\text{O}_6$: 180 g) requires 6 moles (134.4 liters) of oxygen (O_2). Six moles (134.4 liters) of carbon dioxide (CO_2) and 6 moles of water (H_2O) are produced, plus 678 kcal of heat. The heat production per liter of oxygen consumed is determined by dividing the heat production (678 kcal) by the liters of oxygen consumed (134.4 liters), resulting in 5.047 kcal per liter of oxygen consumed. The heat production per liter of carbon

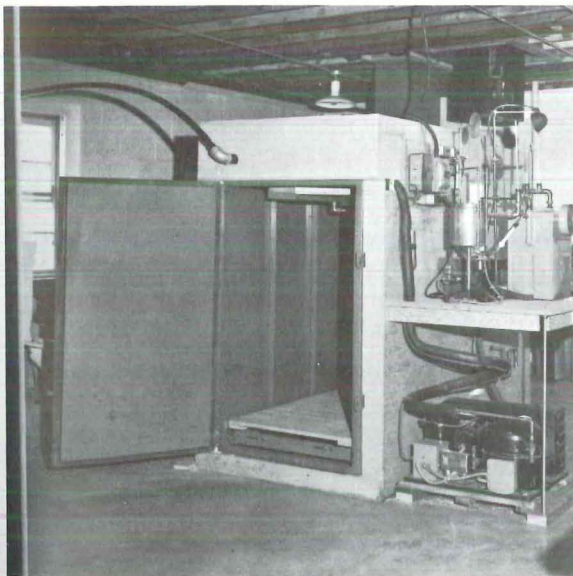


FIGURE 7-2. The respiration chamber for deer in the Ritzman Laboratory at the University of New Hampshire, Durham. (Photograph courtesy of Helenette Silver.)

dioxide produced can be found in the same way; 5.047 kcal of heat are produced for each liter of CO_2 produced. This value is for carbohydrate oxidation only. The oxidation of mixed fat results in the release of 4.69 kcal per liter of oxygen consumed, and 6.6 kcal per liter of carbon dioxide produced. For the oxidation of mixed protein, 4.82 kcal are released per liter of oxygen consumed, and 5.88 kcal per liter of carbon dioxide produced.

The above figures show that the numbers of calories produced by oxidation vary with the carbohydrate, fat, and protein content of the food. The proportion of carbohydrate, fat, and protein in a food must be known or estimated before an accurate calculation can be made of the heat production from either oxygen consumption or carbon dioxide production.

The amount of protein oxidized is determined by dividing 100 by the percentage of nitrogen in the protein. Most animal proteins contain about 16% nitrogen, so the amount of protein can be estimated by multiplying the nitrogen content by 6.25, calculated from $100/16$. Cereal proteins contain 17%–18% nitrogen, so the conversion factors are $100/17 = 5.9$ and $100/18 = 5.6$. In practice, however, the assumption that protein contains 16% nitrogen is sufficient at this time.

The relative amounts of fat and carbohydrate in a food that are oxidized can be determined from the nonprotein respiratory quotient (R.Q.). The R.Q. is the ratio of moles or volumes of CO_2 produced to moles or volumes of O_2 consumed. In equation (7-1) the R.Q. is equal to 1 ($6\text{CO}_2/6\text{O}_2 = 1.00$), indicating that carbohydrates had been consumed. If the nonprotein R.Q. were less than 1.00, it would indicate that some fats had been consumed. The R.Q. for mixed fats is 0.71. These are averages only, since fatty acids vary in their R.Q. (short-chain fatty acids have an R.Q. nearer to 0.8) and each protein and amino acid has its distinctive R.Q. (Brody 1945). The amount of heat produced by the oxidation of different mixtures of carbohydrates and fats can be computed from the R.Q. (Table 7-1).

The calories per liter of oxygen consumed range from 4.686 to 5.047. The mean value is about 4.86, and this occurs at an R.Q. of 0.85. The R.Q. of protein is about 0.82, so if an approximation is sufficient, the rate of heat production can be calculated by multiplying the liters of oxygen by 4.82 to 4.85 without correcting for protein metabolism. This method is often used by comparative physiologists (Hoar 1966).

The R.Q. is not always as simple as is implied in the preceding discussion. In ruminants, large quantities of CO_2 are produced by the rumen bacteria. This cannot be distinguished from the CO_2 originating in cellular respiration.

The calculation of heat production from oxygen consumption using an approximation of 0.85 for the R.Q. results in a good estimate of the energy expenditure of unrestrained animals. Measurement of oxygen consumption by unrestrained animals is difficult, however. Ventilation masks prohibit feeding, and the air must be sampled for gas analysis. If an implantable oxygen measurement transducer were available for placement in the trachea of an animal, the continuous measurement and wireless telemetry of this parameter would provide more precise measurements of the energy expenditures of free-ranging animals.

TABLE 7-1 THERMAL EQUIVALENTS OF O₂ AND CO₂ AND THE CORRESPONDING PERCENTAGES OF FAT AND CARBOHYDRATES OXIDIZED FOR DIFFERENT RESPIRATORY QUOTIENTS

R.Q.	O ₂ (kcal liter ⁻¹)	CO ₂		% O ₂ Consumed by		% Heat Produced by Oxidation of	
		(kcal liter ⁻¹)	(kcal g ⁻¹)	Carbo- hydrates	Fat	Carbo- hydrates	Fat
0.70	4.686	6.694	3.408	0	100	0	100
0.75	4.729	6.319	3.217	14.7	85.3	15.6	84.4
0.80	4.801	6.001	3.055	31.7	68.3	33.4	66.6
0.85	4.863	5.721	2.912	48.8	51.2	50.7	49.3
0.90	4.924	5.471	2.785	65.9	34.1	67.5	32.5
0.95	4.985	5.247	2.671	82.9	17.1	84.0	16.0
1.00	5.047	5.047	2.569	100	0	100	0

SOURCE: Data from Brody 1945.

7-3 METABOLIC RATES OF RUMINANTS

RELATIONSHIPS TO BODY WEIGHT. The relationship between heat production and body weight has been determined for a variety of species, and Benedict's "mouse to elephant" curve (Benedict 1938) is widely known among physiologists (Figure 7-3). The variation among species is quite low. The shape of the curve illustrates that the heat production per unit weight of a small animal is far greater than the heat production per unit weight of a large animal. Deviations from the mean may be attributed to species differences, to experimental error, or to variations in the proportions of metabolically active to metabolically inert tissue.

The body of an animal includes metabolically active tissue such as muscles, blood, fat, and other tissue that is being continually replaced or removed. Metabolically inert tissue is present also, including hair and antlers after both have reached maximum dimensions. Inert residues are also found in the gastrointestinal tract when an animal is on feed. Thus body weight does not truly represent the amount of metabolic tissue in an animal at the time of weighing, but if several measurements are made on different animals the error is reduced.

There has been considerable discussion of the mathematical relationship between heat production and body weight, which is expressed in equation (7-2).

$$Q_{mb} = c W_{kg}^b \quad (7-2)$$

where

Q_{mb} = energy expenditure for basal metabolism

c = constant

W_{kg} = weight of the animal in kg

b = an exponent that has been the focal point of most of the controversy $\cong 0.75$

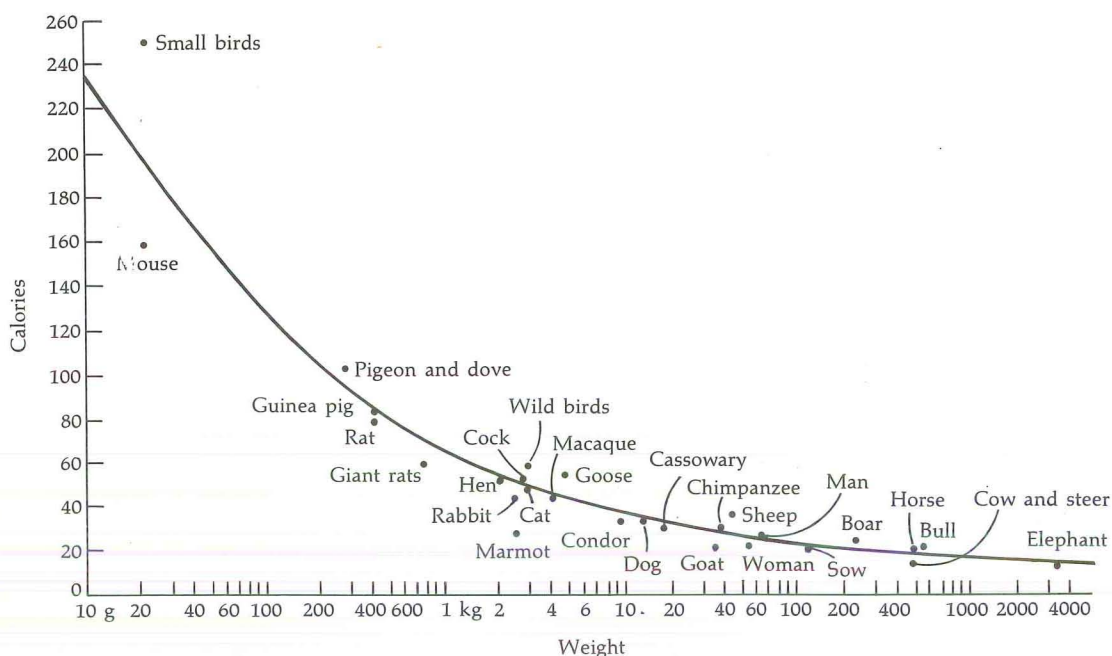


FIGURE 7-3. Semilogarithmic chart showing the trend of the average heat production per kilogram of average body weight of each animal species. Weights range from 20 g to 4000 kg. (From Benedict 1938. Courtesy of Carnegie Institution.)

Physiologists have been searching for an exponent that will result in a constant value of c . If this were found, the basal heat production of any animal could be determined by simple multiplication after weighing the animal.

Reported values of the exponent b have ranged from 0.66 to 0.75. Kleiber (1961, p. 212) summarizes the results of metabolic rate measurements on a variety of mammals and concludes: "For all practical purposes, one may assume that the mean standard metabolic rate of mammals is seventy times the three-fourth power of their body weight (in kg) per day, or about three times the three-fourth power of their body weight (in kg) per hour." The results of several experiments may be found in "Nutrient Requirements of Farm Livestock," Number 2-Ruminants (1965), a publication sponsored by the Agricultural Research Council, and in Blaxter (1967). The general conclusion from these data is that the basal heat production approximates $70 W_{\text{kg}}^{0.75}$ kcal per day. The National Research Council (1966) has adopted the exponent $b = 0.75$.

METABOLIC RATES OF WILD RUMINANTS. Several measurements of the basal metabolic rates of wild ruminants have been made. Helenette Silver of the New Hampshire Fish and Game Department has made several measurements of white-tailed deer at different times of the year. Six series of measurements of four deer in winter coat resulted in an average of $75.7 \text{ kcal per } W_{\text{kg}}^{0.75}$ per 24 hours, and three series of measurements of three deer in summer coat yielded an average

of 84.4 kcal per $W_{\text{kg}}^{0.75}$ per 24 hours (Table 7-2). The data indicate that there are consistent differences between individual deer since male no. 101 had a higher heat production than the other three deer measured in winter coat; in summer coat it was also higher than that of two others. The males generally had a higher heat production per kg and per $W_{\text{kg}}^{0.75}$, but with only two females and four males in the sample it is impossible to draw any definite conclusions.

The fasting metabolic rates of white-tailed deer have been measured by Silver et al. (1969) and are shown in Table 7-3. Again, there is considerable variation between individual deer. The females in winter coat vary from 64 to 128 kcal per $W_{\text{kg}}^{0.75}$ per day.

The resting heat production of young black-tailed deer weighing from 5 to 25 kg and ranging in age from 28 to 166 days is about two times the basal rate for adults (Table 7-4). The fawns being measured had been fed, however, so their heat production was higher owing to the effects of heat of fermentation and heat of nutrient metabolism.

A few measurements of metabolic rates of other wild ruminants have been reported in the literature. Krog and Monson (1954) measured a ^{mountain} goat (*Oreamnos americanus*). The heat production was calculated to be 1027 kcal per 24 hours when the animal was confined in a chamber at temperatures from 20° to -20°C. The animal's heat production was 1.3 times higher at -30°C and 2.3 times higher at -50°C (Table 7-5).

TABLE 7-2 BASAL METABOLIC RATES OF WHITE-TAILED DEER

Deer I.D.		Sex	Age	Weight (kg)	Coat	Avg. Chamber Temperature (°C)	H.P.		H.P. (kcal per $W_{\text{kg}}^{0.75}$ per 24 hr)	Avg. H.P. (kcal per $W_{\text{kg}}^{0.75}$ per 24 hr)
No.							(kcal per 24 hr)	(kcal per $W_{\text{kg}}^{0.75}$ per 24 hr)		
101	M		9 mo	32.9	W	19.2	1173	35.7	85.4	82.0
101	M		9 mo	31.3	W	16.0	1038	33.2	78.6	
102	M		9 mo	30.2	W	18.8	971	32.2	75.4	
102	M		9 mo	27.9	W	16.0	814	29.2	67.1	71.3
101	M		1 yr 4 mo	68.6	W	17.7	1988	29.0	83.4	85.3
101	M		1 yr 4 mo	68.2	W	18.4	2069	30.3	87.2	
101	M		1 yr 8 mo	49.4	W	18.2	1481	30.0	79.5	79.5
1	M		1 yr 8 mo	61.8	W	-0.4	1534	24.8	69.6	69.6
1	F		1 yr 8 mo	51.8	W	-3.9	1272	24.6	65.9	65.9
Average for winter coat = 75.6										
101	M		1 yr	35.7	S	18.7	1499	42.0	102.6	111.0
101	M		1 yr	36.5	S	19.7	1771	48.5	119.3	
2	M		2 yr	51.1	S	21.2	1327	26.0	69.4	69.4
2	F		2 yr	40.0	S	21.5	1160	29.0	72.9	72.9
Average for summer coat = 84.4										

SOURCE: Recalculated from Silver 1968.

TABLE 7-3 FASTING METABOLISM OF WHITE-TAILED DEER

		Heat Production per 24 Hours		
Weight (kg)	Month of Measurement	Total Kcal	Kcal per Kg	Kcal per $W_{kg}^{0.75}$
Adult males, winter coat				
82.0	Dec	2596	31.7	95.3
80.0	Apr	3192	39.9	119.3
80.0	Jan	2880	36.0	107.7
69.0	Jan	2318	33.6	96.8
68.6	Oct	2339	34.1	98.1
68.2	Oct	2434	35.7	102.6
66.5	Nov	2042	30.7	87.7
64.5	Jan	1737	26.9	76.3
63.8	Jan	2286	35.8	101.3
60.1	Mar	1750	29.1	81.1
58.4	Feb	1758	30.1	83.2
52.0	Jan	1620	31.2	83.7
49.4	Feb	1742	35.3	93.5
44.0	Mar	1908	43.4	111.7
		Averages =	33.8	95.6
Adult females, winter coat				
70.0	Dec	1548	22.1	64.0
69.5	Sept	3078	44.3	127.9
64.4	Sept	2290	35.6	100.7
		Averages =	34.0	97.5
Fawns, winter coat				
32.9	Feb	1380	41.9	100.5
31.3	Feb	1221	39.0	92.3
30.2	Feb	1142	37.8	88.6
27.9	Feb	958	34.3	78.9
		Averages =	38.3	90.1
Adult males, summer coat				
77.1	Aug	4150	53.8	159.5
54.6	July	2543	46.6	126.6
50.1	June	2789	55.7	148.1
47.9	May	2393	50.0	131.4
		Averages =	51.5	141.4
Adult females, summer coat				
66.0	June	2945	44.6	127.2
60.6	Aug	3268	53.9	150.5
58.8	July	3675	62.5	173.1
57.6	June	3134	54.4	149.9
54.6	June	2632	48.2	131.0
		Averages =	52.7	146.3
Yearlings, summer coat				
36.5	June	2084	57.1	140.3
35.7	May	1764	49.4	120.8
		Averages =	53.3	130.6

SOURCE: Recalculated from data in Silver et al. 1969.

TABLE 7-4 RESTING HEAT PRODUCTION OF BLACK-TAILED DEER FAWNS IN A THERMONEUTRAL ENVIRONMENT BUT NOT IN THE POST-ABSORPTIVE STATE

Body Weight (kg)*	$W_{kg}^{0.75}$	Age in Days*		Resting Heat Production* (kcal per day)		H.P. per $W_{kg}^{0.75}$ (kcal per day)		Multiple of BMR†	
		M	F	M	F	M	F	M	F
5	3.34	28	30	382	498	114.4	149.1	1.6	2.1
10	5.62	67	70	880	837	156.6	148.9	2.2	2.1
15	7.62	98	106	1180	1076	154.9	141.2	2.2	2.0
20	9.46	126	137	1460	1408	154.3	148.8	2.2	2.1
25	11.18	153	166	1722	1669	154.0	149.0	2.2	2.1

* Data from Nordan, Cowan, and Wood 1970.

† BMR = $Q_{mb} = 70 W_{kg}^{0.75}$

Hammel (1962) computed the heat production of a reindeer (*Rangifer tarandus*) from the measured oxygen consumption both when the animal was standing quietly and when it was pulling a loaded sled (Table 7-6). At rest, reindeer heat production was similar to that reported for other species. It rose to about eight times the resting rate when exercising. The rectal temperature during rest ranged from 38.1° to 38.3°C, rising to a range of 38.8° to 39.2°C during exercise.

The metabolic rates of eight caribou calves were measured by Hart et al. (1961) (Table 7-7). These calves showed a response to the thermal conditions during the test as the metabolic rate rose to over ten times the basal metabolic rate for adult homeotherms. Several measurements of metabolic rates of female caribou during fasting and at maintenance have been reported by McEwan (1970) (Table 7-8). The results indicate that the metabolic rates are somewhat higher than 70 $W_{kg}^{0.75}$.

Brockway and Maloiy (1967) measured the metabolic rates of two red deer (*Cervus elaphus*) during fasting. The average of three measurements was 90 $W_{kg}^{0.75}$ kcal per day. The fasting metabolism of the wildebeest (*Connochaetes taurinus*) and eland (*Taurotragus oryx*) was 104.3 and 111.2 $W_{kg}^{0.73}$ kcal per day, respectively (Rogerson 1968).

TABLE 7-5 METABOLISM OF A MOUNTAIN GOAT (*Oreamnos americanus*)

Sex	Age	Weight (kg)	Dates Measured	Ambient Temperature (°C)	Total H.P. (kcal per 24 hr)	Kcal per $W_{kg}^{0.75}$	Multiple of BMR
M	1½ yr	32 ± 1.5	Feb 3-Mar 14	20 to -20	1027	76.3	1.09
				-30	1304	96.9	1.38
				-50	2362	175.6	2.51

SOURCE: Data from Krog and Monson 1954.

TABLE 7-6 METABOLISM OF A REINDEER (*Rangifer tarandus*)

Sex	Age	Weight (kg)	Date	Ambient	Heat Production		
			Measured	Temperature (°C)	Kcal per Hr	Kcal per 24 Hr	Kcal per W _{kg} ^{0.75}
Metabolism while standing quietly:							
M	5-6 yr	100	Feb 26	-16	157	3768	119.2
			Feb 27	-12	177	4248	134.3
			Feb 27	-12	192	4608	145.7
			Mar 1	-16	179	4296	135.9
			Mar 2	- 7	173	4152	131.3
			Mar 7	+ 3	172	4128	130.5
						Averages:	175
							Multiple of BMR = 1.90
Metabolism while pulling a loaded sled:							
			Feb 26	-16	739	17736	560.9
			Feb 27	-12	605	14520	459.2
			Feb 29	-21	699	16776	530.5
			Mar 7	+ 4	712	17088	540.4
			Mar 7	+ 4	752	18048	570.7
			Mar 8	(+) 4	705	16920	535.1
			Mar 8	+ 4	605	14520	459.2
			Averages:		688	522.3	
							Multiple of BMR = 7.46

SOURCE: Data from Hammel 1962.

FASTING METABOLISM OF DOMESTIC RUMINANTS. The number of metabolism experiments completed on domestic cattle and sheep is far greater than the number on wild ruminants.

The basal heat production of subadult sheep has been measured by Ritzman and Benedict (1930). The metabolic increment (I_m) over the basal metabolic rate varies from nearly 3 at one week of age to 1.4 at 16 weeks of age. The decline in heat production with age is essentially linear (Figure 7-4). The relationship between I_m and the weight of lambs is also linear (Figure 7-5), indicating that heat production decreases per unit metabolic weight as the lambs grow.

7-4 METABOLIC RATES OF OTHER ANIMALS

Several investigators have measured oxygen consumption or heat production of wild animals under laboratory conditions. The values are interesting for comparative purposes, but the analytical ecologist must recognize that the results under laboratory conditions are not directly applicable to the wild. The results discussed below are included mainly to call attention to the existence of data on several species. Additional data may be found in the biological handbook *Metabolism* (Altman and Dittmer 1968).

TABLE 7-7 METABOLISM OF INFANT CARIBOU

Calf No.	Weight		Wind (mi per hr)	Fur	Location	T_a (°C)	T_{br}^* (°C)	Heat Production per $W_{kg}^{0.75}$		Multiple of BMR
	(lb)	(kg)						Kcal per Hr	Kcal per 24 Hr	
1	11.7	5.3	0	dry	lab	20	40.0	4.11	98.64	1.4
2	11.3	5.1	0	dry	lab	22	40.2	9.04	216.96	3.1
3	11.7	5.3	0	dry	lab	19	39.0	6.42	154.08	2.2
3	12.8	5.8	0	dry	lab	20	40.0	9.64	231.36	3.3
5	12.0	5.5	0	dry	lab	14	39.2	12.07	289.68	4.1
7	13.4	6.1	0	dry	†	10	39.2	8.80	211.20	3.0
8	11.4	5.2	0	dry	†	10	38.8	6.60	158.40	2.3
1	11.6	5.3	0	dry	tent	4	40.5	12.23	293.52	4.2
2	11.0	5.0	0	dry	tent	4	39.2	12.86	308.64	4.4
4	11.4	5.2	0	dry	†	-3	39.2	15.02	360.48	5.1
6	12.0	5.5	0	dry	†	0	39.1	17.37	416.88	6.0
7	12.5	5.7	0	dry	†	0	38.8	12.20	292.80	4.2
5	14.5	6.6	0	dry	†	0	38.8	14.68	352.32	5.0
3	11.7	5.3	2	dry	†	0	39.0	16.01	384.24	5.5
1	11.8	5.4	15	dry	exposed	-1	38.1	19.20	460.80	6.6
1	11.6	5.3	14	dry	exposed	3	39.7	21.17	508.08	7.3
2	11.0	5.0	12	dry	exposed	6	39.0	14.20	340.80	4.9
3	12.8	5.8	14	dry	exposed	-5	41.0	21.61	518.64	7.4
2	11.6	5.3	14	dry	exposed	-5	41.0	22.94	550.56	7.9
7	19.7	9.0	21½	dry	exposed	3	39.0	20.69	496.56	7.1
6	12.0	5.5	18	damp	exposed	-1	38.5	28.65	687.60	9.8
7	10.6	4.8	15	damp	exposed	-0.5	39.2	20.88	501.12	7.2
5	12.0	5.5	15	wet	exposed	-1	38.5	26.28	630.72	9.0
6	13.4	6.1	17	wet	exposed	0	39.0	31.47	755.28	10.8
5	16.1	7.3	15	wet	exposed	-0.5	38.8	23.51	564.24	8.1
7	19.7	9.0	28	wet	exposed	3	38.3	29.69	712.56	10.2

SOURCE: Data from Hart et al. 1961.
 * Rectal temperature.
 † Location not given.

TABLE 7-8 ENERGY METABOLISM OF FEMALE BARREN-GROUND CARIBOU (*Rangifer tarandus*)

Age	Weight (kg)	Activity and Diet	Heat Production		
			Total Kcal per Day	Kcal per $W_{kg}^{0.75}$	Kcal per $W_{kg}^{0.75*}$
21 mo	80.0	Resting at maintenance	3215	124.5 ± 1.94	120.2
21 mo	90.0	Resting at maintenance	3575	107.0 ± 3.04	122.3
9 mo	57.3	3rd day of fasting	2400	115.4	115.2
9 mo	56.0	6th day of fasting	2100	102.5	102.6
3 yr	94.0	21st day of fasting	2750	91.0	91.1

SOURCE: Data from McEwan 1970.
 * Calculations made by the author.

Beck and Anthony (1971) calculated the mean standard metabolic rates of the long-tailed vole (*Microtus longicaudus*), concluding that the values were 60% to 70% higher than those predicted based on body weight. He cites other investigators who also found that microtine rodents had higher standard metabolic rates than those predicted based on body weight.

Packard (1968) found the standard metabolic rates of montane voles (*Microtus montanus*) to be 75% higher than those predicted from the empirical relationship of metabolism to body weight. Grodzinski and Gorecki (1967) summarize the data on daily energy budgets of small rodents in the temperate zone of central Europe. They state that "the well-known dependence of metabolism on body size (Kleiber 1961) definitely holds true among the discussed rodent species." The species studied ranged in weight from 8 to 37 g.

The metabolic rates of different species of birds have been expressed in a single equation by King and Farner (1961):

$$\log m = \log 74.3 + 0.744 \log W \pm 0.074 \quad (7-3)$$

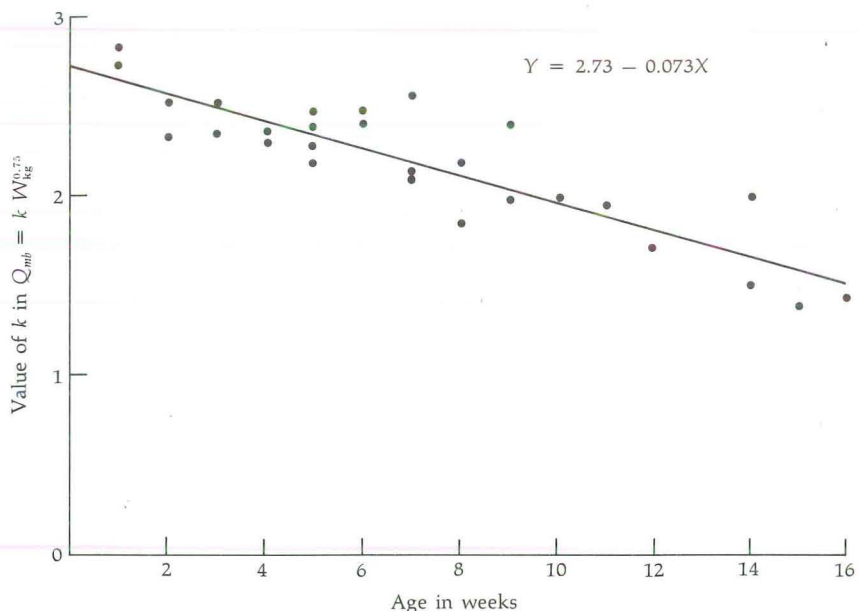
where

m = metabolic rate (kcal per 24 hrs)

W = body weight in kg

This equation is apparently satisfactory for birds whose body weights range from 0.125 to 10 kg. It is nearly the same as an equation by Kleiber in 1947 [see King and Farner (1961)], indicating that the base line equation describing the metabo-

FIGURE 7-4. The relationship between heat production and age of lambs. (Data from Ritzman and Benedict 1930.)



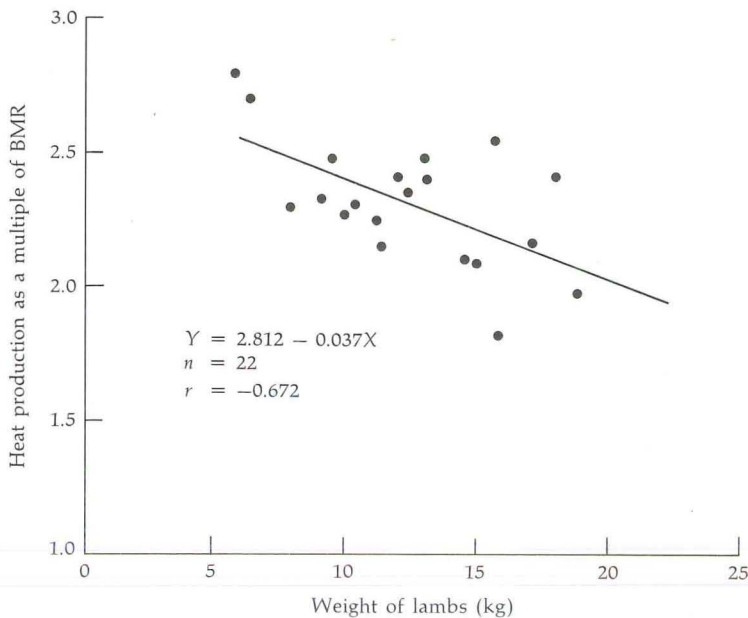


FIGURE 7-5. The relationship between heat production and weight of lambs. (Data from Ritzman and Benedict 1930.)

lism of birds and mammals may, for practical purposes, be combined. Such equations are only base lines, of course; it is necessary to consider the metabolic rates of free-ranging birds participating in different activities and various productive functions in order to analyze the energetics of animals in their natural habitats. Mullen (1963) has pointed out that the relationship between metabolic rate and body weight varies, and that the effect of any parameter on metabolic rate cannot be fully evaluated until changes in body weight are considered. This makes it imperative that data on metabolic rates be accompanied by weight data, with changes in weight if possible. Many species exhibit cyclic weight changes, and these are important considerations when applying metabolic rates to the analysis of energetics of free-ranging animals in natural habitats. It appears that metabolic-rate variation due to natural functions may be considerably greater than variations in rates determined under "standard" conditions, and the analytical ecologist needs to relate these functions to the free-ranging animal if ecological considerations are to be made.

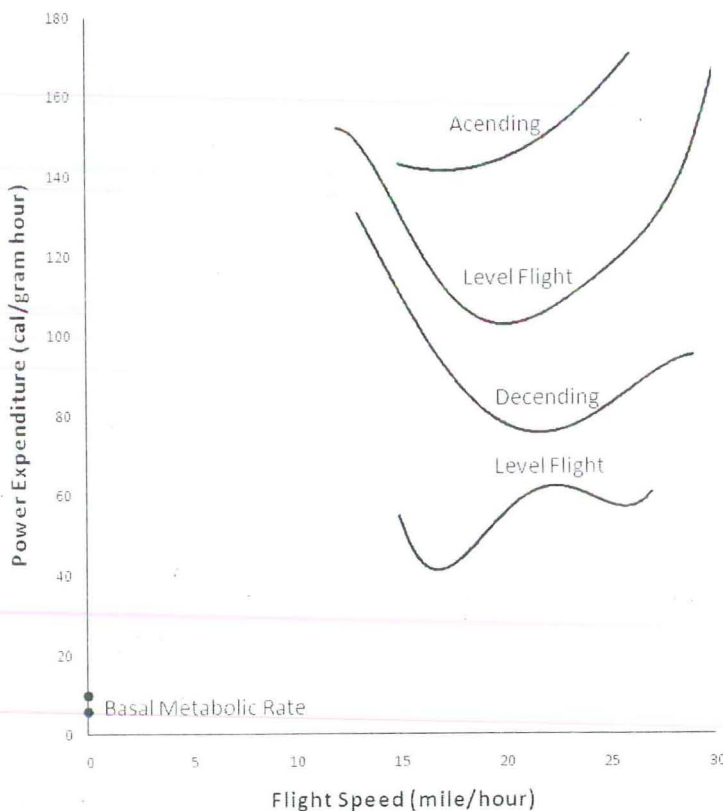
7-5 FACTORS INFLUENCING ENERGY METABOLISM AND HEAT PRODUCTION

The energy metabolism and heat production of free-ranging animals is highly variable, depending on the activity of the animal, its diet, thermoregulatory functions, sex, reproductive condition, time of day and year (daily and seasonal rhythms occur), hair or feather characteristics, weather factors, parasites and pathogens, and various social and psychological effects. A free-ranging animal

has an *ecological metabolic rate* that is an expression of the energy "cost of living" for the conduction of daily activities and other life support processes. This ecological metabolism varies from one activity to another; the cost of actively escaping from a predator is different from the cost of resting. Further, the cost of escaping from one type of predator may be different than the cost of escaping from another type. To illustrate, a rabbit may run from a fox, but hide under a log to escape from an avian predator.

There is considerable difficulty in measuring the energy cost of the different activities in the life of a free-ranging animal. Tucker (1969) has published results of experiments on birds flying in a wind tunnel, showing rather marked differences in the metabolic cost in relation to ascending, descending, and level flight at different wind velocities (Figure 7-6). While flying, budgerigars (the common parakeet) and laughing gulls expend energy at eleven to twenty times the rate at which they metabolize while at rest. He has compared the cost of flying (birds and insects) with other transport costs, including walking and running (man and several domestic and wild mammals), swimming (a fish), and mechanical modes of transport (Figure 7-7). The cost of transport by swimming for a salmon is less than the cost of transport for any other animal or machine considered by Tucker.

FIGURE 7-6. Energetic cost of flight for gulls and budgerigars. When flying, these birds expend energy at eleven to twenty times the resting metabolic rate. (Adapted from: "The Energetic of Bird Flight" by Vance A. Tucker.)



Comparing Body Weight and Cost of Transport

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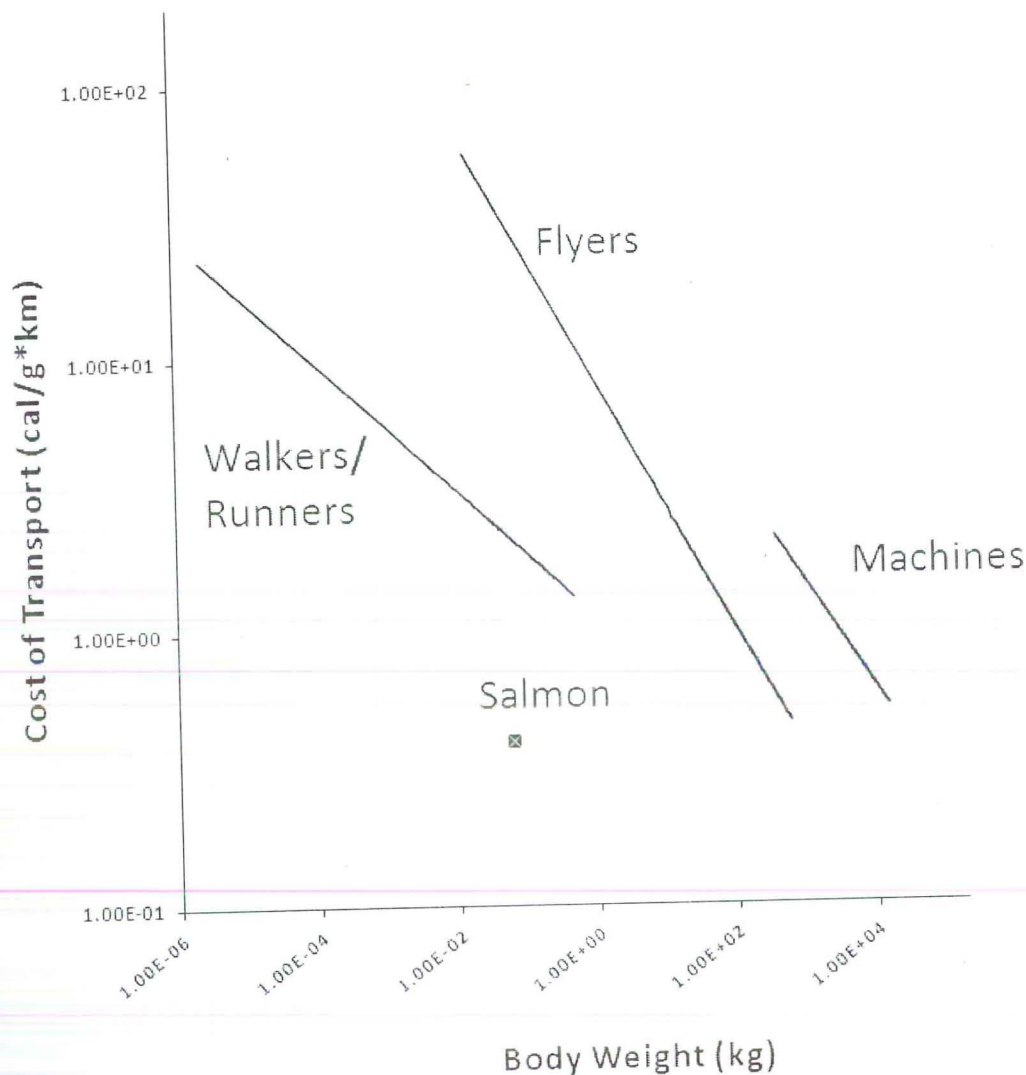


FIGURE 7-7. Bird flight, compared with other kinds of animal locomotion, is generally more economical than walking or running. Large flying birds travel farther for each calorie per unit of weight than a light plane or jet fighter. The young salmon's performance shows, however, that a fish can travel more economically than gulls, pigeons, horses, or any other kind of animal. (Adapted from "The Energetics of Bird Flight" by Vance A. Tucker.)

However, the range in the cost of transport for the animals considered is wide. The cost for machines in comparison with that of some of the animals is low.

The efficiency of energy use has a direct effect on the physiology and behavior of an animal in the field. This results in constantly changing nutritional requirements, and differences between the energy required for daily life activities and

the amount ingested are reflected in weight gains or losses as body tissue is used to ameliorate the differences.

The metabolism of blue-winged teal (*Anas discors*) carrying heart-rate transmitters was measured with birds in metabolism cages and in 1200-m² enclosures (Owen 1969). The relationship between heart rate and metabolism was determined in the chambers and applied to the birds in the enclosures. The results showed a 30% increase in heart rate when the birds were preening and a 60% increase when they swam rapidly. These increases may not be in direct proportion to metabolism, however, since stroke volume, oxygen transport, respiration efficiency, and so forth may also change.

Research currently in progress at the BioThermal Laboratory has provided us with many significant insights into physiological responses of white-tailed deer. These will be published upon completion of the current experiments. The extensive literature describing the effect of some important factors on domestic animals provides additional insight into mechanisms that may be important in the environment of free-ranging animals.

THE RELATIONSHIP BETWEEN HEAT PRODUCTION AND SURFACE AREA. In the nineteenth century great interest developed in the relationship between the heat production of an animal and its surface area. The "surface area law" was formulated because heat loss from any object is proportional to surface area. In a homeothermic animal, heat production must be proportional to heat loss if homeothermy is to be maintained. Thus it was concluded that heat production must be proportional to surface area.

In considering the many modes of heat exchange (radiation, conduction, convection, and evaporation), it becomes obvious that surface area is only one of several parameters that must be considered in the calculation of heat loss. Thermal insulation values of hair coats, for example, are variable over different areas of an animal, between species, and seasonally for many species. This insulation represents a barrier to heat loss from the animal. If two animals with equal surface areas are exposed to identical thermal conditions, the one with the higher-quality insulation will lose less heat, and less heat will be necessary to maintain a given body temperature.

Another factor entering into the relationship between surface area and heat production is the variability in the surface area participating in heat exchange between an animal and its environment. A greater surface area is exposed when an animal is standing than when it is lying down. A living animal changes not only its surface area but also its heat production, evaporative heat loss, muscular activity, diet, hair insulation through piloerection, and other characteristics to maintain homeothermy.

If all of the characteristics of the thermal energy regime were known, it would be possible to calculate the critical surface area for an individual animal (Moen 1968). This critical surface area would be determined by the relationship of surface area to weight that is just sufficient to result in a net thermal exchange of zero. The dynamic characteristics of thermal exchange make the calculations virtually impossible, but the concept is easily understood. It is clear that the relationship

observed between surface area and heat production is far more complex than it appeared to early investigators.

HEAT INCREMENTS DUE TO DIET. An animal on feed has a greater heat production than it does in a post-absorptive state. The difference between heat production on feed and on fast is called the heat increment. This heat increment results from the release of heat during fermentation in the gastrointestinal tract and from the heat of nutrient metabolism in the assimilation of body tissue. This heat energy is of value to the animal during colder weather since it helps maintain a balance between heat production and heat loss. When other metabolic processes are sufficient to maintain this balance, the heat increment represents a quantity of heat that must be dissipated to prevent a rise in body temperature.

How do variations in diet affect these heat increments? Dukes (1955) cites work by Benedict and Ritzman who found that steers on timothy hay produced heat at a rate 50% greater than the fasting metabolic rate, while steers on an alfalfa diet produced heat at a rate 60% greater than the fasting rate. Blaxter (1967) presents a table showing the differences in heat production between sheep and steers on fasting, maintenance, and full-feed diets. For sheep the ratio of the maintenance to the fasting diet was 1.47:1, and of the full-feed diet to the fasting diet, 1.88:1. Ritzman and Benedict (1931) determined a ratio of 1.26:1 for sheep 0-4 hours after feeding compared with 48-52 hours after feeding.

The effect of diet on metabolism may not be limited to the individual animal alone, but may also carry over into newly born offspring. Alexander (1962) suggests that a low summit metabolism in lambs may be associated with poor prenatal nutrition. This may cause mortality since the lamb must increase heat production if it is to survive cold weather shortly after birth. Adult sheep have been observed to be so underfed that their body temperatures fell 4°C when the surrounding temperature dropped from 35°C to 20°C (Graham 1964). This shows clearly that food can be important in the maintenance of homeothermy.

HEAT INCREMENTS DUE TO ACTIVITY. Heat production increases when an animal is active. Benedict and Ritzman (1923) stated that the activity of steers in the stall increased heat production by 15% over basal rates. Ritzman and Benedict (1931) consider the heat produced while standing compared with lying to be 15% greater for sheep and 17% greater for cattle. Dukes (1955) cites Hall and Brody who found an energy increment of standing over lying of 9% for cattle, with a 13% increment for one very fat steer.

Crampton and Harris (1969) suggest that the energy requirements for maintenance can be estimated by multiplying the basal metabolic rate by 1.33. This increment is applicable on a daily basis, with activities such as walking or running costing much more and standing or bedding somewhat less. Analyses of the energy cost of the daily activity of wild ruminants are given in Chapter 16.

NONSHIVERING THERMOGENESIS. Homeotherms have the physiological capability of increasing their heat production without overt activity. Summit metabolism is one example of this; newborn lambs can increase their heat production up to

five times the basal rate without muscular activity. Postnatal tissue is the initial source of the energy. This is followed by the lamb's increasing dependence on milk and forage for energy.

SEX DIFFERENCES. The few data on wild ruminants do not indicate that there are differences between male and female when both are in the same physiological and psychological condition. When the effects of gestation and lactation are considered, observed differences in energy requirements can be attributed to these reproductive processes.

REPRODUCTIVE CONDITION. Each of the three stages in the reproductive cycle—breeding, gestation, and lactation—has a definite effect on energy metabolism. Male ruminants expend a large amount of energy during the breeding season, and this activity is accompanied by a reduction in forage intake and a marked weight loss. The increase in energy expenditure is most likely due to the increase in the overt activity of the animal rather than to changes in the rate of tissue metabolism per se.

The female must expend additional energy during gestation to maintain the uterus, for fetal growth, for the increased demands on the circulatory, respiratory, and excretory systems, and to handle the endocrine influences on her own metabolism (Brody 1945). Ritzman and Benedict (1931) reported a slight decrease in the metabolism of cows during the first three months of pregnancy, and it is generally accepted that the energy metabolism on a per weight basis is no higher for pregnant females until the last one-third of pregnancy when fetal growth is accelerated (Morrison 1948). Any small changes in the metabolic rate during the first two-thirds of pregnancy can be considered by expressing metabolism on a metabolic body-weight basis. During the stage of rapid fetal growth, elevated metabolism may result when the growth processes demand additional energy for synthesis of fetal tissue.

There is an obvious physiological demand on the female during lactation since milk must be produced. The heat production of cattle during peak lactation is approximately 100% above the nonlactating level and is associated with the higher food consumption and milk production rather than with muscular activity. The increase is directly proportional to milk production (Brody 1945). Lactating ewes consumed about two times as much feed but grew only 84% as much wool as those ewes whose lambs were removed at birth (Corbett 1964). When feed intake was held constant, wool growth during lactation ceased. Dolge (1963) reports that dairy cattle fed at a high grain level (challenge feeding) showed a marked increase in milk production but lost an average of 61 pounds of body weight during the 70-day test period. This indicates the high cost of lactation as body reserves were mobilized to meet the demands for energy and other nutrients. Calculations for white-tailed deer, discussed in Chapters 16 and 17, indicate a similar high cost for these wild ruminants.

Egg production by female birds has the same effect on the annual cycle of energy costs as gestation and lactation in mammals. West (1968) has studied the

bioenergetics of willow ptarmigan (*Lagopus lagopus*) throughout the year, finding that egg-laying females had a higher energy requirement than nonlaying but molting females and males. The extensive literature on domestic poultry provides a good foundation for these kinds of considerations in wild birds.

RHYTHMIC CHANGES IN THE BASAL METABOLIC RATE. Marked changes occur in the rate of metabolism during a 24-hour period. Nocturnal animals have a low BMR during the daytime (Benedict 1938). Muscular-activity rhythms and basal-metabolic rhythms follow similar time patterns according to Brody (1945). He points out that the diurnal variations in metabolism exceed the effect of the heat increment of food in rats. Thus the diurnal variation is an important consideration when interpreting variations in the metabolic rates, both within and between species, since the time of day at which the measurement was made is a source of variation.

Seasonal variations may occur also. Early studies on cattle indicate a seasonal lability (Ritzman and Benedict 1930; Benedict 1938), but additional research has shown that this conclusion was based on experimental artifacts. Helenette Silver and her associates at the University of New Hampshire, however, have an indication of depressed fasting metabolism in white-tailed deer in the winter (Silver et al. 1969). The number of deer studied, however, is not sufficient to warrant a definite conclusion about seasonal lability, but current research at the Bio-Thermal Laboratory indicates that it is a definite physiological rhythm. Additional studies by Patrick Karns of the Minnesota Department of Natural Resources also indicate seasonal changes in physiological parameters (personal communication).

INSULATION CHARACTERISTICS. Warm-blooded animals maintain a fairly constant body temperature, so it is reasonable to assume that a decrease in the insulation value of the coat will cause an increase in the heat production of the animal if the heat loss is sufficient to cause the animal to have a negative thermal balance. The effectiveness of the coat on white-tailed deer has been demonstrated by Silver et al. (1969); they sheared a deer and then noted a marked increase in its heat production while it was in the cold respiration chamber. The same effect has been observed when sheared sheep are released in a cold environment; the lack of insulation can cause heat losses great enough to cause mortality. Shearing increases the heat tolerance of sheep exposed to high thermal energy environments (Wodzicka 1960).

Lambs with hairy coats have been observed to conserve heat more effectively than lambs with fine coats (Alexander 1962), and this results in a lower metabolic requirement for those with hairy coats. Brody (1945) attributed the ability of cattle to withstand temperatures of -40°F to their coat insulation and to highly developed vascular control of peripheral tissues.

Mallard and black ducks (*Anas platyrhynchos* and *Anas rubripes*) with oil on their feathers show higher metabolic rates as the oil concentrations are increased (Hartung 1967). The metabolic rates return to normal levels several days after the

oil has been removed. This can be attributed to a reduction of the insulating capability of the feathers, since oil causes derangement of the feather barbs.

WEATHER. Complete consideration of all the weather factors that affect the thermal balance of an animal is an enormous task. The concept of thermoneutrality has been discussed for many years. The complexity of the concept has not always been recognized, however. Identification of the many physiological, behavioral, and thermal factors that affect thermoneutrality helps to provide a broader understanding of the concept. Factors affecting the upper limit (*critical hyperthermal environment*) and lower limit (*critical hypothermal environment*) of the thermoneutral range are discussed in a paper by the author (Moen 1968) and are considered further in Chapters 6, 13, and 15.

PATHOGENS AND PARASITES. Whenever an organism must support the life processes of another organism living upon or within it, the energy requirements of the host must increase. The growth and survival of both species may be benefited, however. These beneficial interactions, called *mutualism* by Odum (1959), can be characterized by the relationship between a ruminant and the rumen flora and fauna. Pathogens and parasites, however, increase the cost of metabolism by the host organism, especially when their numbers exceed the normal complement of associated organisms that are either beneficial to or without effect on the host.

VanVolkenburg and Nicholson (1943) found eleven kinds of parasites in the nasal passage, skin, abomasum, and small intestine of dead deer on the Edwards Plateau, Texas. They concluded that infestations of parasites are apparently *unimportant among deer on ranges with sufficient food*. This is logical, perhaps, but it is important that variability between both the ability of individual deer to withstand the effect of parasites and the effect of different species of parasites on their host be recognized. Georgi and Whitlock (1967), for example, established a direct relationship between the exposure of sheep to infection by *Haemonchus contortus* and the onset of erythrocyte loss. They show clearly that the rate of iron loss in sheep infected with *H. contortus* was greater than that for noninfected sheep. The loss of iron promotes loss of erythrocytes, resulting in a reduction in the efficiency of the oxygen transport system, which in turn may depress the rate of tissue metabolism.

Evans and Whitlock (1964) conclude that ". . . other things being equal, an animal (sheep) with a low erythrocyte volume has a smaller chance of surviving a natural challenge with this parasite than an animal having a greater erythrocyte volume." The experimental evidence in sheep suggests that there is a need for basic research on the *reaction* of wild ruminants to pathogens and parasites rather than the mere identification and counting of them.

7-6 SOCIAL AND PSYCHOLOGICAL EFFECTS ON HEAT PRODUCTION

Numerous sociological and psychological interactions influence heat production. Pfander (1963) lists such things as confinement versus natural range, herd versus individual response, numbers per group, space per animal, noise level, and other

disturbances as factors that affect the heat production of domestic animals. Voles (*Clethrionomys glareolus*), kept in groups of two to four animals, lowered their daily metabolism rate by 13.3% (Gorecki 1968). Group reductions by different species are expected to occur owing to thermal factors or social factors, depending on the thermal regime, population density, endocrine levels, and so forth.

Noise from cars, tractors, snowmobiles, and other sources definitely affects the heat production of deer at the BioThermal Laboratory, although not to the same extent at all times during the day or year. Newborn fawns are quite sensitive; even "well-trained" adults exhibit excitement from rather common and frequent noises.

The effect of confinement on the psychology of the animal is very difficult to quantify. Well-trained wild animals appear to be more calm, but the real cause of any variability between animals is hard to identify. Elevation of the metabolic rates of wild ruminants over the rates of domestic ones should not be considered an inherent difference in cell metabolism between these two groups, since elevated cellular metabolism can occur without visible signs of excitement in the animal. I have observed this in a male white-tailed deer that was rescued from icy water (Moen 1967). The deer showed a steady increase in rectal temperature during the warming process from a low of 26° to a high of 39.5°C, after which it stabilized at 38°C. My presence in the room caused the rectal temperature to rise within five minutes to 38.5°C, but the animal did not show any overt signs of fear. It decreased to 38°C when I left the room. The increase in the rectal temperature indicates that heat production was increased by the fear response. The rapidity of this change is surprising, considering the animal's size. Similar changes are being observed in the physiological telemetry experiments in progress on white-tailed deer at the BioThermal Laboratory.

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