A BIOLOGICAL BASIS
FOR THE CALCULATION
OF CARRYING CAPACITY

16-1 THE CONCEPTUAL DESIGN

How many boxes will fit into the one-inch-square box in Figure 16-1? The answer to that question is indeterminant because the sizes of the boxes to be fitted in are not known at this time. If a box to be fitted in is larger than the one illustrated, the number that will fit will be less than one. If boxes smaller than the one illustrated are selected, more than one will fit in. Further, nothing has been said about whether the boxes are the same size; they could all be different.

If the sizes of the boxes to be fitted in are known, it is possible to come up with an answer. Thus the box illustrated, exactly one-inch square, will hold 16 boxes exactly $\frac{1}{4}$-inch square. It will hold 13 boxes if 12 are $\frac{1}{4}$-inch square and the thirteenth is $\frac{1}{2}$-inch square. If the size of the holding box and the sizes of the inside boxes are determined, only one answer will satisfy the problem.

The example illustrates the kind of information needed to determine the number of animals that can be supported on a given area of land. Both the supply of resources on the range and the requirements of the animals must be known for an understanding of the relationship between the two. The numerical determination of carrying capacity is very complex since biological organisms, including both the animals and plants on the range, are dynamic assemblies of organic molecules that are highly organized into functional, living units whose "size" or requirements are changing continually.

There is an obvious need, then, for knowledge of the requirements of an animal for maintenance and productive purposes before a meaningful biological appraisal of carrying capacity can be made. The determination of the requirements of an
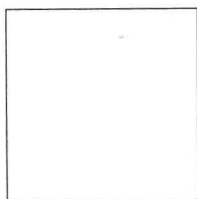
FIGURE 16-1. A box.

animal is a costly and time-consuming process consisting of feeding trials at different nutritional levels and the measurement of animal response, including weight, growth, and reproductive performance. These data are largely unavailable for wild ruminants. Data for domestic species can be used to make first approximations, and error analyses can be completed to find out how important variation in any one parameter is in the total animal-range relationship.

It is also necessary to know the quality of resources available to supply the requirements of the animal. These must be expressed in units that are biologically meaningful, such as the kilocalorie for energy and weight units for protein, with the relationship between animal and range analyzed through the use of *net* values.

16-2 PROTEIN REQUIREMENTS OF THE INDIVIDUAL ANIMAL

PROTEIN REQUIREMENTS FOR MAINTENANCE. Protein is necessary for the maintenance of basic life processes, including the synthesis of enzymes, the replacement of body tissue that is catabolized, and the replacement of tissue abraded from internal surfaces, such as the gastrointestinal tract, and from the skin.

Measurements of the protein requirements for these functions have been made for domestic cattle and sheep, and these experiments will form a base line for making first approximations for wild ruminants. Nitrogen requirements are calculated from protein requirements by dividing the latter by 6.25.

The nitrogen excreted in the urine that is of endogenous origin (EUN) is derived from the catabolism of body tissue, and this quantity is related to the metabolic weight of the animal according to Crampton and Harris (1969). They cite earlier work by Brody in assembling a table for the minimum daily requirements for protein, which can be expressed as endogenous urinary nitrogen in equation (16-1).

$$Q_{eun} = \frac{2 \times 70(W_{kg}^{0.75})}{1000} \tag{16-1}$$

where

Q_{eun} = endogenous urinary nitrogen in g day^{-1}
  2 = the ratio of N in mg to kcal in the equation for basal metabolism = $(N_{mg}/kcal)$
W_{kg} = animal weight in kg

Estimates of endogenous urinary nitrogen excretion, with weight expressed as $W_{kg}^{0.75}$, are presented in an Agricultural Research Council publication (1965) for

cattle and sheep. These estimates have been recalculated with weight expressed as $W_{kg}^{0.75}$, multiplied by 6.25, and shown as a protein requirement in Table 16-1. A comparison between the results using equation (16-1) and the ARC data shows that the endogenous urinary nitrogen calculated with equation (16-1) is slightly lower than the ARC data for the smaller animals within the weight range of deer and considerably higher for the larger animals.

TABLE 16-1   ESTIMATES OF ENDOGENOUS URINARY NITROGEN EXCRETION AND THE MINIMUM PROTEIN REQUIREMENT IN CATTLE AND SHEEP

| | | | *Calculated Protein‡ Requirement* | |
W_{kg}	$W_{kg}^{0.75}$	*Endogenous Urinary Nitrogen (g per day per $W_{kg}^{0.75}$)**	*Endogenous Urinary Nitrogen**	$[(2)(70)(W^{0.75})(6.25)]/1000$†
		Cattle		
50	18.80	.19	22.33	16.45
75	25.49	.17	27.08	22.30
100	31.62	.15	29.65	27.67
125	37.38	.14	32.71	32.71
150	42.86	.13	34.83	37.50
175	48.11	.12	36.09	42.10
200	53.18	.11 (200 kg+)	36.56	46.54
250	62.87		43.22	55.01
300	72.08		49.56	63.07
350	80.92		55.63	70.80
400	89.44		61.49	78.26
450	97.70		67.17	85.49
500	105.74		72.69	92.52
550	113.57		78.08	99.38
600	121.23		83.35	106.08
		Sheep		
2.5	1.99	.165	2.05	1.74
5	3.34	.16	3.34	2.93
10	5.62	.14	4.92	4.92
15	7.62	.13	6.19	6.67
20	9.46	.11	6.50	8.28
25	11.18	.09	6.29	9.78
30	12.82	.08 (30 kg+)	6.41	11.22
35	14.39		7.19	12.59
40	15.91		7.95	13.92
45	17.37		8.69	15.20
50	18.80		9.40	16.45
100	31.62		15.81	27.67

*Modified from Table 5.3, ARC 1965, p. 156.
†Crampton and Harris 1969.
‡Protein = N × 6.25.

The mechanical process of food passage through the gastrointestinal tract results in the abrasion of the epithelium lining the tract, resulting in a loss of protein. This loss, plus spent enzymes, bacterial residues, and other catabolized protein in the feces, is estimated to be 5 grams per kilogram of dry-matter intake per day for sheep and cattle on a forage diet, and 2.5 grams per kilogram of dry-matter intake for calves on a liquid diet (ARC 1965). Expressed mathematically for computational purposes,

$$Q_{mfn} = cF_{kg}/6.25 \qquad (16\text{-}2)$$

where

Q_{mfn} = metabolic fecal nitrogen in g day^{-1}

c = 5 for forage diets, 2.5 for milk diets, and $5 - (113.6 - 4.5 W_{kg})(2.5/100)$ for milk and forage diets for deer

F_{kg} = dry-matter intake in kg day^{-1}

PROTEIN REQUIREMENTS FOR PRODUCTION.   The deposition of new tissue during growth represents a protein requirement that is directly related to the amount of gain of different kinds of body tissue. For growth, the nitrogen retention has been estimated to be 2.4% to 3.5% of the gain, with variation according to species and weight (ARC 1965). Higher nitrogen requirements per unit gain in weight are expected in the younger animals that are depositing more protein tissue than fat. Lower nitrogen requirements are characteristic of the older animals that are depositing more fatty tissue and less protein in each unit gain in weight. The mathematical expression for the nitrogen in the gain, using 2.5% nitrogen fraction, is shown in equation (16-3):

$$Q_{ng} = 2.5 \, \Delta W_{kg}/100 = .025 \, \Delta W_{kg} \qquad (16\text{-}3)$$

where

Q_{ng} = quantity of nitrogen required for daily gain in g day^{-1}

ΔW_{kg} = gain in weight in kg day^{-1}

The production of hair requires protein, but the amount required by wild ruminants has not been measured. An estimate of the loss of nitrogen in hair and scurf of cattle has been made by Blaxter and reported in the ARC publication (1965). It can be calculated with equation (16-4):

$$Q_{nh} = 0.02 \, W_{kg}^{0.75} \qquad (16\text{-}4)$$

where

Q_{nh} = quantity of nitrogen required for hair growth in g day^{-1}

This estimate is a small portion of the total nitrogen requirement. It is included here to draw attention to the fact that the growth of hair does involve a nitrogen "cost."

PROTEIN REQUIREMENTS FOR GESTATION.   The fetus, placenta, uterus, and the fluids surrounding the fetus increase in weight as pregnancy progresses. The nitrogen

retained also increases; the amount of nitrogen and its protein equivalent that is retained per day in fetal tissue is shown in Table 16-2 for cattle and sheep. The amount retained per day increases in a logarithmic manner (Figure 16-2). An estimation of the protein requirement for pregnancy of wild ruminants can be made as follows:

1. The protein requirements per day from Table 16-2 are expressed in a linear regression equation with a log transformation of Y, where $Y =$ the protein required per day and $X =$ time pregnant in days (t_d) (Table 16-3).

2. The protein requirements calculated with the equations in Table 16-3 are total daily requirements for pregnancy in cattle and sheep.

3. The calculated protein requirement per day during gestation is divided by the weight of the fetus at term, resulting in the expression of protein requirements per day per kilogram of fetus weight at term.

4. The gestation periods for cattle, sheep, and wild ruminants are different, so conversion factors that express the gestation periods on an equivalent physiological time scale are calculated (Table 16-4). The young of moose, elk, and bison are larger than lambs at birth, so the cattle data are used as a base for calculation. The young of other wild ruminants are more like lambs in size at birth, and sheep data (single lambs) are used as a base.

TABLE 16-2   RETENTION OF NITROGEN AND PROTEIN BY COWS
AND EWES IN THE FETUS, PLACENTA, UTERUS,
AND FLUIDS

Gestation Time		Retention of	Protein Equivalent
Month	Days	Nitrogen (g day^{-1})	(N × 6.25)
Cows: calf, 45 kg at birth			
5th–6th	185	1.7	10.63
7th	220	5.1	31.88
8th	250	12.0	75.00
9th	280	29.0	181.25
Ewes: single lamb, 5.9 kg at birth			
2nd	56	0.18	1.13
3rd	84	0.34	2.13
4th	112	1.45	9.06
5th	140	4.96	31.00
Ewes: twin lambs, 10.0 kg at birth			
2nd	56	0.24	1.50
3rd	84	0.96	6.00
4th	112	3.07	19.19
5th	140	7.40	46.25

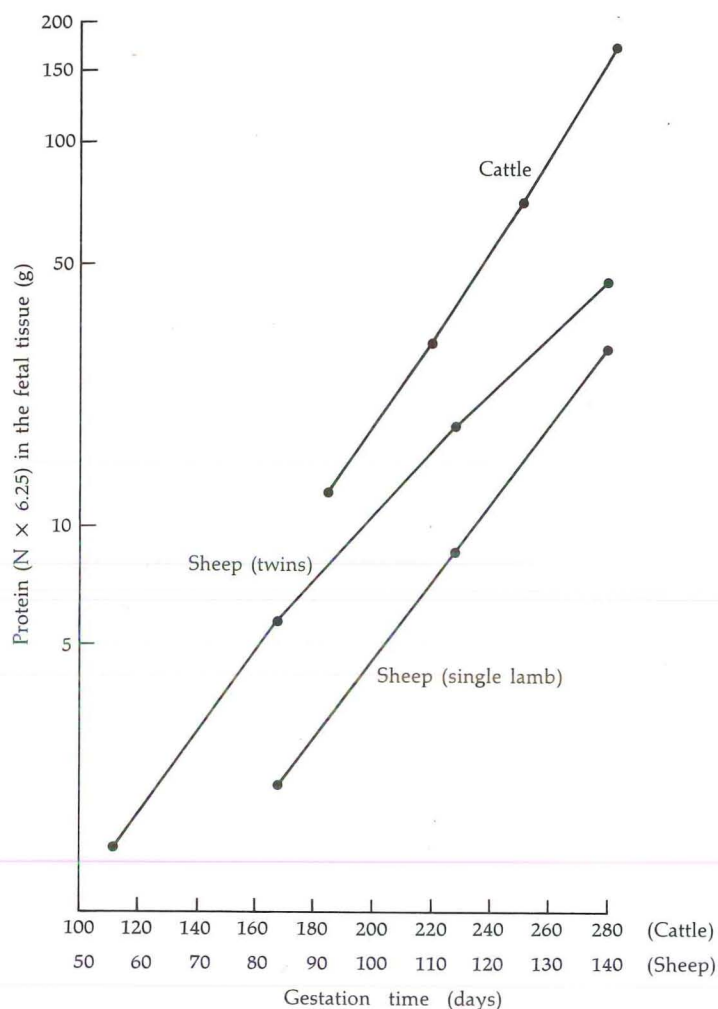SOURCE: Data from ARC 1965, pp. 163–165.

FIGURE 16-2. The protein retained per day in the fetus, placenta, uterus, and fluids in cattle and sheep. Note that the Y axis is a log scale.

TABLE 16-3 PROTEIN REQUIREMENTS FOR GESTATION (calculated from data in Table 16-2)

Species	Equation	Weight of Fetus at Term (kg)
Cattle	$Y_g = e^{(-3.1206 + 0.0298\ t_d)}$	45.0
Sheep (single lamb)	$Y_g = e^{(-2.3623 + 0.0407\ t_d)}$	5.9
Sheep (twins)	$Y_g = e^{(-1.7605 + 0.0409\ t_d)}$	10.0

TABLE 16-4 CONVERSION FACTORS FOR EXPRESSING
EQUIVALENT TIMES IN THE GESTATION PERIODS
OF DOMESTIC AND WILD RUMINANTS

Species	Gestation Period	Conversion Factor
Domestic cattle	280	—
Moose	245	0.87500
Elk	260	0.92857
Bison	290	1.03571
Domestic sheep	140	—
Mule deer	200	1.42857
White-tailed deer	200	1.42857
Pronghorn	240	1.71429
Bighorn sheep	150	1.07143
Mountain goat	180	1.28571
Caribou	220	1.57143

The protein requirement for pregnancy of any wild ruminant, expressed as the protein required at time t (days) in gestation per kilogram of fetus weight at birth, can then be calculated by equation (16-5):

$$Q_{pp} = [e^{a+b(t_d/c)}]/W_{kg} \qquad (16\text{-}5)$$

where

Q_{pp} = quantity of protein required for pregnancy (grams per day per kg fetus weight at birth)

a and b = constants (see Table 16-5)

t_d = days pregnant

c = conversion factor for gestation periods (see Table 16-4)

W_{kg} = weight of fetus at term for cattle or sheep, depending on the base selected (see No. 4)

The numerical equations for calculating the protein requirements for pregnancy in wild ruminants are shown in Table 16-5. These protein requirements, expressed as grams per day per kilogram of fetus weight at term, are plotted through the entire gestation period in Figures 16-3 and 16-4. Absolute protein requirements are easily calculated by multiplying the grams per kilogram of fetus weight by the birth weight of the infant animal.

The equations for calculating the protein or nitrogen (dividing protein by 6.25) requirements can be stored in the memory of an electronic computing system, and the protein or nitrogen requirement for pregnancy can be calculated by entering the gestation time and the fetus weight at full term. An average birth weight for each species can also be stored, leaving the gestation time in days as the only variable to enter for a solution. This procedure is used in Chapter 17 for calculations of carrying capacity.

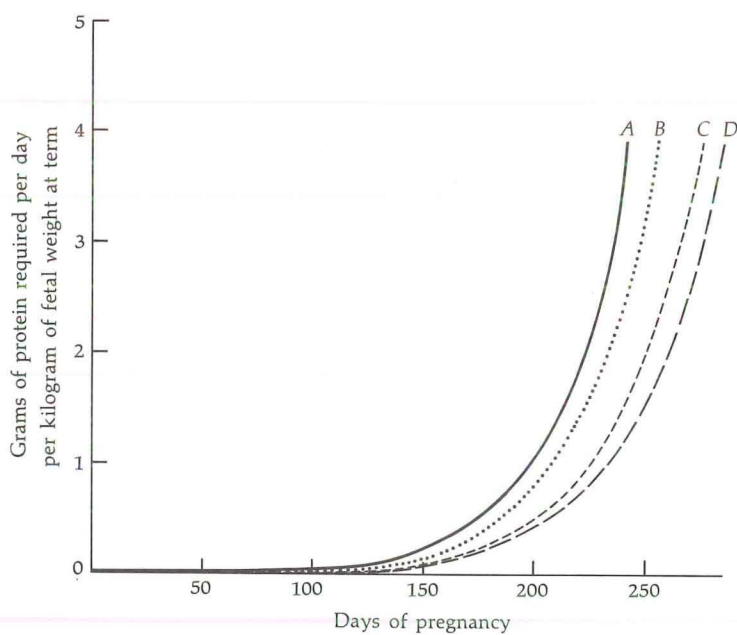**TABLE 16-5** PROTEIN REQUIREMENTS FOR GESTATION IN GRAMS PER DAY PER KILOGRAM OF FETAL WEIGHT AT TERM

Species using cattle requirements as a base

Cattle	$Y_g = [e^{(-3.1206 + 0.0298\ t_d/1)}]/45$
Elk	$Y_g = [e^{(-3.1206 + 0.0298\ t_d/.92857)}]/45$
Moose	$Y_g = [e^{(-3.1206 + 0.0298\ t_d/0.875)}]/45$
Bison	$Y_g = [e^{(-3.1206 + 0.0298\ t_d/1.03571)}]/45$

Species using sheep requirements as a base

Domestic sheep (singles)	$Y_g = [e^{(-2.3623 + 0.0407\ t_d/1)}]/5.9$
Deer	$Y_g = [e^{(-2.3623 + 0.0407\ t_d/1.42857)}]/5.9$
Pronghorn	$Y_g = [e^{(-2.3623 + 0.0407\ t_d/1.71429)}]/5.9$
Mountain goat	$Y_g = [e^{(-2.3623 + 0.0407\ t_d/1.28571)}]/5.9$
Bighorn sheep	$Y_g = [e^{(-2.3623 + 0.0407\ t_d/1.07143)}]/5.9$
Caribou	$Y_g = [e^{(-2.3623 + 0.0407\ t_d/1.57143)}]/5.9$
Domestic sheep (twins)	$Y_g = [e^{(-1.7605 + 0.0409\ t_d/1)}]/10$

FIGURE 16-3.   Protein requirements of wild ruminants for gestation, using cattle data as a base for the calculations: *A*, moose; *B*, elk; *C*, cattle; *D*, bison.
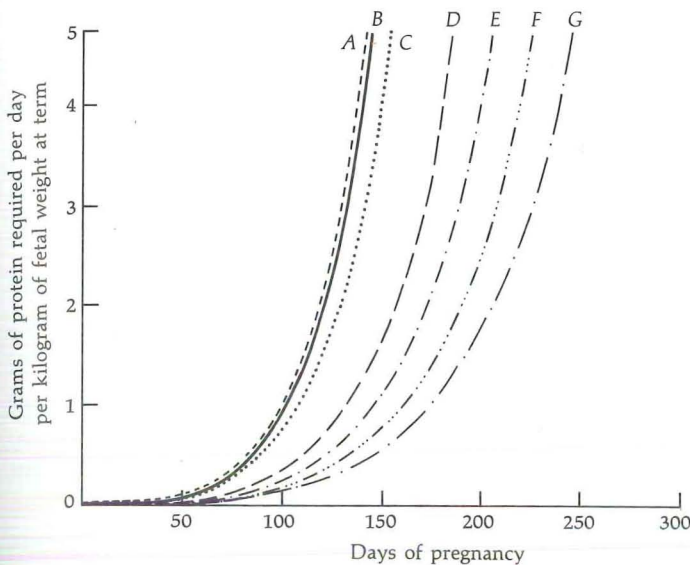
FIGURE 16-4. Protein requirements of wild ruminants for gesta-
tion, using sheep data as a base for the calculations: *A*, sheep
(twins); *B*, sheep (singles); *C*, bighorn sheep; *D*, mountain goat;
E, white-tailed and mule deer; *F*, caribou; *G*, pronghorn.

MILK PRODUCTION.   The protein cost of milk production is an important consid-
eration when determining the total protein requirements of an animal. The milk
production of a wild ruminant has never been measured in a realistic way,
however, so a method must be found to estimate it. Lactation has been studied
extensively in dairy cattle, and some basic knowledge of the biological efficiency
of this production process is available.

One necessary assumption for the calculation of milk production of a wild
ruminant is that the nutritional requirements of the nursing ruminant are met
by the milk and forage consumed. It can also be assumed that the milk production
of a wild animal is in balance with the requirements of the nursing offspring.
This is a reasonable assumption because the amount of milk produced is partly
dependent on the demand, and it would be difficult to explain a significant
imbalance in this mother-young relationship after many years of natural evolution.

The biological relationships included in the calculation of the milk production
of a lactating female to meet both the protein and energy needs of the nursing
young are shown in Figure 16-5. The concept is clear; the next step is the numerical
representation of these relationships so that a mathematical expression can be
formulated.

The protein and energy requirements of the young are necessary for the
calculation of the milk production of a wild ruminant. Knowledge of rumen
development is also necessary for the calculation of the percentage of their protein
and energy requirements that are derived from milk.

Two criteria may be used for the development of the rumen. One, the proportional capacities of the rumen + reticulum and the omasum + abomasum change as the animal matures. The two divisions of the stomach are about equal when the fawn weighs 6–7 kg and is about one month old. This was discussed in detail in Chapter 8 for white-tailed deer. Two, the length of the papillae lining the rumen increases with rumen development. They are about 2 mm long at the age of one month, which is 50% of their length when the animal is 4 months old (see Table 8-3). These two changes indicate that the rumen is about half developed between one and two months of age when the fawn weighs 6–7 kg.

The relationship between rumen development and diet is a useful tool for calculating the amount of energy and protein that is derived from milk as growth occurs and the diet changes. The data in Chapter 8 on rumen development of deer can be used to express a rumen-development–nutrient-absorption ratio (Table 16-6). Since milk is very digestible and forage much less so, a coefficient expressing this ratio is applied to the rumen-development–nutrient-absorption curve. The value used is 10:6, where 10:6 ≅ 97:58, with 97 being the estimate of the digestibility of milk and 58 the digestibility of forage. This coefficient expresses the relative proportions of ingested milk and forage that are used to meet the energy and protein requirements. The application of this ratio to the rumen-development–nutrient-absorption data in Table 16-6 results in the percentage of rumen digestion shown in the table. The final step is the calculation of a regression equation representing the amount of milk required to meet the nutrient requirements supplied by milk. Regression equation (16-6) has been calculated for 100% milk utilization at birth (3 kg) to no utilization at 25.2 kg, or weaning.

$$\%MD = 113.6 - 4.5\ W_{kg} \tag{16-6}$$

where

$\%MD$ = % of nutrients met by milk

W_{kg} = weight of the fawn

FIGURE 16-5. Steps in the calculation of milk production necessary to meet the needs of the growing fawn.
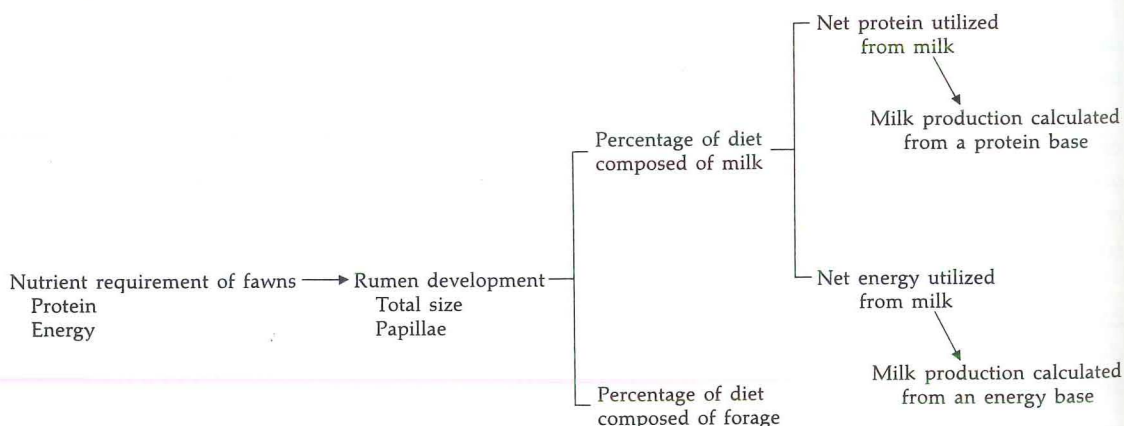
TABLE 16-6 RUMEN-DEVELOPMENT–NUTRIENT-ABSORPTION RATIOS FOR WHITE-TAILED DEER

Weight of Fawn (kg)	% Nutrients Absorbed from Milk	% Rumen Digestion Composed of Milk
3	100	100
4	90	94
5	81	88
7	66	76
10	48	60
15	28	39
20	17	25
25	10	16
25	0	0

The protein requirement for lactation includes the protein that is in the milk and the additional protein requirement associated with the production of milk. The total requirement due to lactation can be expressed by equation (16-7):

$$Q_{nl} = \frac{(Q_{mp})(N\%)(I_{mp})}{100} \qquad (16\text{-}7)$$

where

Q_{nl} = grams of nitrogen required for lactation

Q_{mp} = quantity of milk produced in g day^{-1}

N% = percent nitrogen in milk = 1.76 [see Silver (1961)]

I_{mp} = metabolic increment for milk production

Weight increments of up to $\frac{1}{2}$ pound per day were recorded for white-tailed fawns receiving 2.1 grams of crude protein per day (calculated from data in Long et al. 1961). Using this information, the protein requirements can be estimated to range from 1.5 to 3 grams of crude protein per pound per day or 3.3 to 6.6 grams per kilogram per day during the nursing period. The milk production necessary to meet the protein needs of a white-tailed deer fawn can be calculated with equation (16-8):

$$Q_{mp} = \frac{(W_{kg})(MD)(Q_{pf}/6.25)}{(.0176)(.85)} \qquad (16\text{-}8)$$

where

Q_{mp} = quantity of milk produced (g) based on protein requirements

W_{kg} = weight of the fawn

MD = milk dependence = $(113.6 - 4.5W_{kg})/100$

Q_{pf} = quantity of protein required by the fawn in g kg^{-1} day^{-1}

6.25 = protein:nitrogen ratio for body tissue

.0176 = nitrogen fraction in deer milk

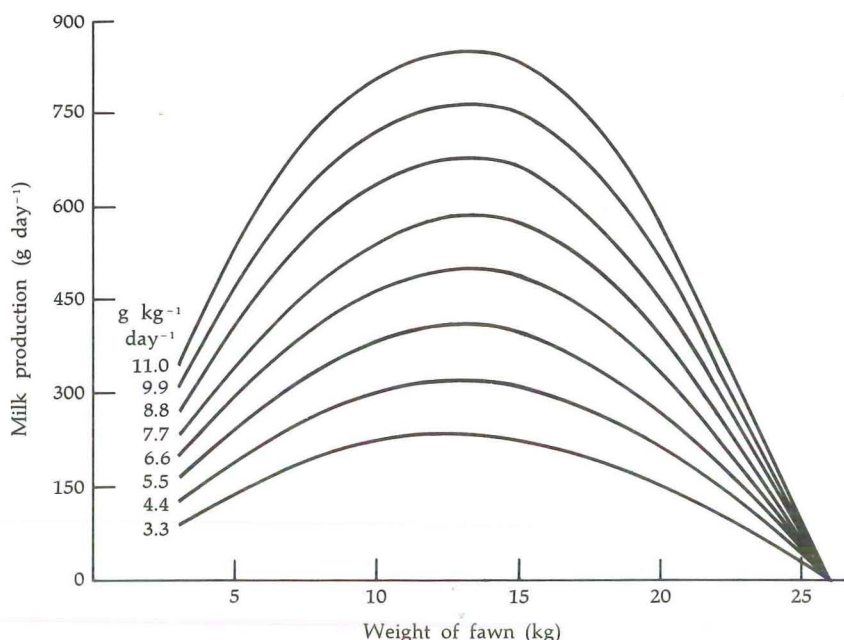.85 = net protein coefficient for milk (Brody 1945)

FIGURE 16-6. Estimations of the daily milk production of a wild doe to meet the protein needs of one fawn.

The results are shown in Figure 16-6 for eight estimates of the protein requirement of fawns. Note that the milk production rises rapidly at first, hits a peak, and then falls gradually to nothing when the young is weaned. A dairy farmer tries to maintain peak production in his cattle for as long as possible; the lactation curve would be flatter on top and elongated to the right.

The protein requirement for supplying milk for twin fawns may not be twice that for one. Twins are often smaller and there may also be a greater dependence on forage when there is competition for the mother's milk. The milk production for two fawns can be estimated to vary between 1.5 and 2 times the amount necessary for one fawn.

The protein requirement for lactation by the doe can be estimated by multiplying the nitrogen in the milk by 6.38 to convert it to a protein equivalent and then by a multiple between 1.25 and 1.50 (Figure 16-7). This multiple [based on data in Crampton and Harris (1969) for dairy cows] represents the cost of "overhead," or the protein costs to the doe over the protein in the milk alone.

SUMMARY OF THE PROTEIN REQUIREMENTS OF THE INDIVIDUAL. The amount of nitrogen metabolized by the body each day can be expressed as follows:

$$
\left\{ \begin{array}{c} \text{Total} \\ \text{nitrogen} \\ \text{used daily} \end{array} \right\} = \left\{ \begin{array}{c} \text{The sum of} \\ \text{endogenous} \\ \text{urinary nitrogen} \end{array} \right\} + \left\{ \begin{array}{c} \text{Metabolic} \\ \text{fecal} \\ \text{nitrogen} \end{array} \right\} + \left\{ \begin{array}{c} \text{Nitrogen} \\ \text{for body} \\ \text{growth} \end{array} \right\}
$$

$$
+ \left\{ \begin{array}{c} \text{Nitrogen} \\ \text{for hair} \\ \text{growth} \end{array} \right\} + \left\{ \begin{array}{c} \text{Nitrogen} \\ \text{for} \\ \text{gestation} \end{array} \right\} + \left\{ \begin{array}{c} \text{Nitrogen} \\ \text{for milk} \\ \text{production} \end{array} \right\}
$$

The equation can be rewritten using symbols:

$$Q_n = Q_{eun} + Q_{mfn} + Q_{ng} + Q_{nh} + Q_{np} + Q_{nl} \qquad (16\text{-}9)$$

where

Q_n = quantity of nitrogen required
Q_{eun} = endogenous urinary nitrogen
Q_{mfn} = metabolic fecal nitrogen
Q_{ng} = nitrogen in gain
Q_{nh} = loss of nitrogen in hair
Q_{np} = nitrogen required for pregnancy
Q_{nl} = nitrogen required for lactation

The amount of nitrogen used in each of the metabolic pathways in equation (16–9) is shown in numerical form in Table 16-7. The nitrogen used can be converted to protein requirements by multiplying the sum of Group A by 6.25, and the nitrogen requirement for milk production in Group B by 6.38.

The relative importance of these different nitrogen requirements is shown in Figure 16-8 for a fawn at different ages after weaning. A constant weight gain of 0.22 kg day^{-1} is used in the calculations. The nitrogen for hair growth is very small compared with the other requirements. Endogenous urinary nitrogen increases with body weight. The constant gain of 0.22 kg day^{-1} results in a constant requirement, of course. This rate of gain changes, but 0.22 kg seems to be a reasonable value for a fawn that is $3\frac{1}{2}$ to 5 months old. The requirement for metabolic fecal nitrogen is the highest of those shown. It is very diet-dependent, however, so its position in relation to the other nitrogen requirements may change.

The relative importance of the nitrogen requirements for different productive
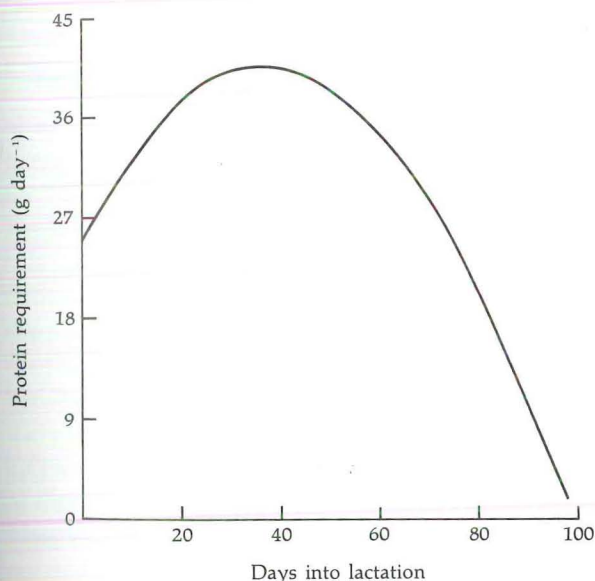
FIGURE 16-7. The protein requirement for lactation by a doe with one fawn.

TABLE 16-7 EQUATIONS USED IN THE CALCULATION OF THE PROTEIN REQUIREMENT

Group		Equation
A. $\dfrac{2 \times 70(W_{kg}^{0.75})}{1000}$	EUN	(16-1)
$+ \; cF_{kg}/6.25$	MFN	(16-2)
$+ \; .025\,\Delta W_{kg}$	NG	(16-3)
$+ \; .02W_{kg}^{0.75}$	NH	(16-4)
$+ \; e^{a + b(t_d/c)}/W_{kg}$	NP	(16-5)

(Σ Group A) 6.25 = protein requirements for all but milk production

B. $\dfrac{(Q_{mg})(N\%)(I_{mp})}{100}$	NMP	(16-7)

(NMP) 6.38 = protein requirements for milk production

Σ(Group A + Group B) = total protein requirement of the animal
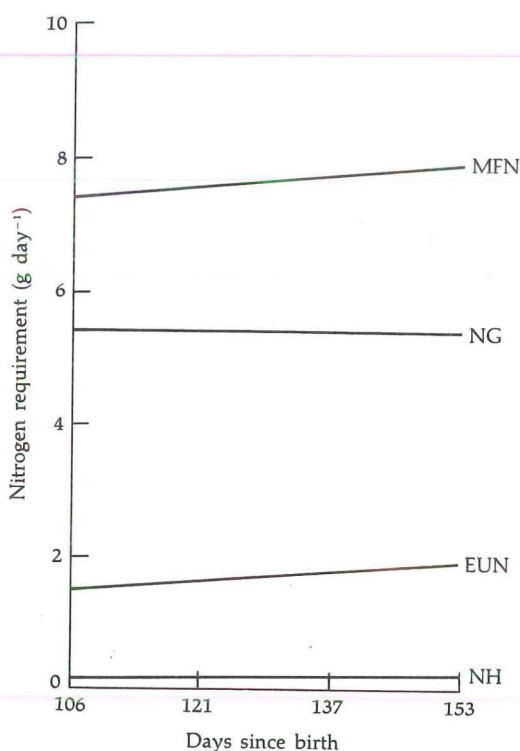
FIGURE 16-8. The nitrogen requirements for a fawn between 106 and 153 days old. The weight gain is 0.22 kg day^{-1}.

FIGURE 16-9. The nitrogen requirements of deer of different weights at three points in the gestation period and two points in the lactation period.

processes of deer of different weights is shown in Figure 16-9. The requirement for pregnancy at 200 days or full term is less than the requirement for lactation just after parturition. The nitrogen requirements at peak lactation are 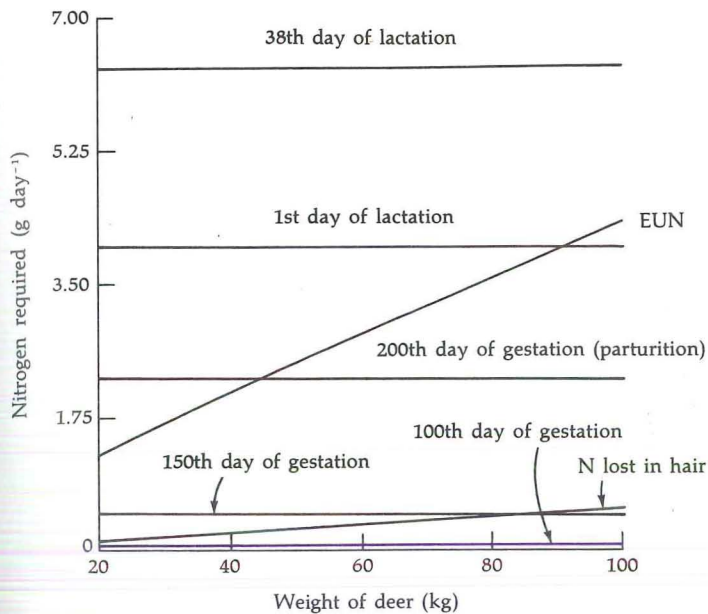greater than for any other process. Deer weighing 60–80 kg on good range will usually have two fawns each year, so the nitrogen requirement for lactation should be increased by a factor of 1.5 to 2.0.

16-3 ENERGY REQUIREMENTS OF THE INDIVIDUAL ANIMAL

ENERGY REQUIREMENTS FOR MAINTENANCE AND ACTIVITY. The transformation of energy is necessary for sustaining life processes. The amount of energy required for basal metabolism is expressed in equation (7-2). The observed similarity between species of widely different weights results in a very useful biological rule since it permits the establishment of a base line for all homeothermic species. Experiments on different wild species have been in fairly close agreement with the predicted rate of basal metabolism (see Chapter 7). Deviations can be attributed to the many uncontrolled variables in the metabolism tests and to differences between individual animals of the same or different species. Most species have daily metabolic cycles, and some have seasonal metabolic cycles also.

The amount of energy expended by free-ranging animals is unknown because at this time there is no feasible method for measuring it in the field. The energy expenditure of the free-ranging animal can be estimated from data for domestic species that have been studied in the laboratory or in pastures. This is useful

because it permits one to test the effect of possible variation in the energy relationships on the total animal-range relationships.

Anything that an animal does "costs" something in terms of energy. The energy requirements for different activities can be calculated, and the sum of these is the total daily energy requirement. The total can be expressed as follows:

$$
\begin{Bmatrix} \text{Total} \\ \text{daily energy} \\ \text{requirement } (Q_{me}) \end{Bmatrix} = \begin{Bmatrix} \text{Basal metabolic} \\ \text{energy} \\ \text{expenditure } (Q_{mb}) \end{Bmatrix} + \begin{Bmatrix} \text{Activity} \\ \text{expenditure} \\ (Q_{ma}) \end{Bmatrix}
$$
$$
+ \begin{Bmatrix} \text{Production} \\ \text{expenditure} \\ (Q_{mp}) \end{Bmatrix} + \begin{Bmatrix} \text{Additional cost} \\ \text{to maintain} \\ \text{homeothermy } (Q_{mh}) \end{Bmatrix}
$$

Factors included in the activity increment include standing, running, walking, foraging, playing, breeding, ruminating, and bedding. Production increments include the energy necessary for the deposition of additional body tissue, such as muscles, bones, fat, and hair, and for the production of fetal tissue during pregnancy and milk during lactation. The additional cost to maintain homeothermy is a part of the total energy requirement only when the sum of the heat production resulting from the first three items ($Q_{mb} + Q_{ma} + Q_{mp}$) is less than the total heat loss of the animal. This was discussed in Chapter 13.

The bedding posture is one of the standard conditions during a basal metabolism test, so the increment due to this activity (I_a), expressed as a multiple of Q_{mb}, is 1.0. Metabolism tests are often continued for several hours, and the experimental animals do stand up during the measurement periods. The amount of energy expended in standing is about 9% of that of basal (Crampton and Harris 1969). The energy cost of standing can then be expressed with an activity increment of 1.1 ($100 \div 9 = 1.1$). Thus a standing animal in thermoneutral conditions and in a postabsorptive state will have an energy expenditure that can be predicted with equation (16-10).

$$
Q_{es} = (70) \ W_{kg}^{0.75}(1.1) \tag{16-10}
$$

where

Q_{es} = energy expenditure of an animal in standing posture in thermoneutral conditions in kcal day^{-1}

W_{kg} = body weight in kg

The energy cost of walking adds to an animal's energy requirement. Clapperton (1961) studied the energy expenditures of sheep walking on a level surface and on gradients in a treadmill. Two levels of nutrition and two speeds were used. His results and the results of measurements on several other species that were summarized by Brody (1945) and by Blaxter (1967) are shown in Table 16-8. The energy cost of lifting the body on a vertical gradient for some of the species included in Table 16-8 is over 10 times greater than that for walking on the level. The energy-cost values for ascent that were determined by Clapperton (1961) show an increase with speed but not with gradient.

TABLE 16-8 ENERGY COST OF WALKING ON A LEVEL SURFACE AND OF ASCENT

Species	Level Walking ($kcal\ kg^{-1}\ km^{-1}$)	Ascent ($kcal\ kg^{-1}\ km^{-1}$)
Sheep	0.59 ± 0.05[A]	6.45 ± 0.47[A]
Cattle	0.452[B]	
Cow	0.48[F]	
Horse	0.385[B]	
Horse	0.40[F]	6.83[F]
Human	0.544[B]	
Human	0.54[C]	6.92[E]
Dog	0.58[D]	

[A] Clapperton 1961.
[B] Brody 1945.
[C] Clapperton citing Smith, Carnegie Inst. Publ. No. 309, 1922.
[D] Clapperton citing Lusk, *The Science of Nutrition*, 1931.
[E] Clapperton citing Lusk.
[F] Baxter 1967.

If basal metabolism and walking are considered together, the energy cost can be expressed mathematically as follows:

$$Q_{ew} = (70)\ W_{kg}^{0.75} + (E_{wl})(W_{kg})(V)(24) + \frac{(E_{wv})(W_{kg})(V)(H)(24)}{100} \qquad (16\text{-}11)$$

where

Q_{ew} = energy expended during walking ($kcal\ day^{-1}$)
W_{kg} = weight in kg
E_{wl} = energy cost of walking on level = $0.59\ kcal\ kg^{-1}\ km^{-1}$
E_{wv} = energy cost of lifting the body weight vertically = $6.45\ kcal\ kg^{-1}\ km^{-1}$
V = rate of speed in $km\ hr^{-1}$
H = vertical height ascended expressed as percentage of km on level

Applying the data for sheep or other species measured under experimental conditions to wild ruminants on free range may result in error. The similarity in the energy cost of different activities for the species listed in Table 16-8 is striking. The amount of energy involved can be compared with the total basal energy requirement of the animal by dividing the part of the equation for walking by the basal energy expenditure as follows:

$$(Q_{ew}/Q_{mb}) =$$
$$\frac{70W_{kg}^{0.75} + (E_{wl})(W_{kg})(V)(24) + [(E_{wv})(W_{kg})(V)(H)(24)]/100}{(70)W_{kg}^{0.75}} \qquad (16\text{-}12)$$

The use of values for E_{wl} and E_{wv} that are midway between the possible extremes, including the variation shown for sheep, results in $E_{wl} = .59 \pm .13$ and

$E_{wv} = 6.45 \pm 0.47$. If a 100-kg animal walks one kilometer a day and ascends 100 meters (or 0.1 km) the amount of energy used in walking compared with the amount required for basal energy processes is 2.7% for walking on the level, 2.9% for vertical ascent, and 5.6% for the two combined (Table 16-9).

These percentages are small, and they are even smaller if other activity and production processes are considered since the total energy expenditure per day is increased. Further, the estimations of distances walked and ascended are probably overestimations of the real situation unless there is a long distance to water, a herd is migrating, or there is some other cause for long-distance traveling. Thus, the error due to estimations from data on domestic species is very small.

No information on the energy cost for ruminants descending a gradient is available. Studies on humans indicate that it is small (ARC 1965), and the authors of the ARC publication consider it sufficient to equate descent with walking on the level.

There is an energy cost for browsing or grazing that can be attributed to the prehension and mastication of the forage material (Young 1966). Young also points out that psychic factors are involved since there is a change in heart rate when food is first given to penned sheep receiving their daily ration at regular times. A wild ruminant would very likely have a lesser response to the onset of feeding because the time of feeding is regulated by the animal itself.

Graham (1964) measured the energy expenditure of a 50-kg sheep while it was grazing in a respiration chamber, with fresh sod brought in to duplicate grazing conditions (Table 16-10). The experiment is quite artificial in many ways, but it does result in a first approximation from which additional calculations can be made. Graham also considered the difference in cost between grazing on good range and on poor range by including the energy cost of walking while foraging

TABLE 16-9   THE ENERGY COST OF WALKING COMPARED WITH BASAL METABOLISM (2214 kcal) OF A 100-kg ANIMAL

Activity	Energy Expenditure (kcal)	%BM	Energy Expenditure (kcal)	%BM	Energy Expenditure (kcal)	%BM
Walking on level	Distance = 1 km		Distance = 2 km		Distance = 3 km	
Upper limit	62	2.8	134	6.1	201	9.1
Midpoint	59	2.7	118	5.3	177	8.0
Lower limit	56	2.5	102	4.6	153	6.9
Vertical ascent	Height = 100 m		Height = 200 m		Height = 300 m	
Upper limit	69	3.1	138	6.2	208	9.4
Midpoint	65	2.9	129	5.8	194	8.8
Lower limit	60	2.7	120	5.4	178	8.0
Walking on gradient						
Upper limit	136	6.1	205	9.3	275	12.4
Midpoint	124	5.6	188	8.5	253	11.4
Lower limit	111	5.0	171	7.7	229	10.3

TABLE 16-10 COMPARISONS OF THE ENERGY COSTS OF VARIOUS ACTIVITIES FOR GRAZING SHEEP

| | | | | Energy Cost (kcal hr^{-1} kg^{-1} of body weight) | |
Comparison	Number of Sheep	Body Weight (kg)	Number of Estimates	Range	Mean with Standard Error
Standing and grazing with standing	4	30–110	23	0.29–0.79	0.54 ± 0.05
Standing and eating with standing or lying	4	40	23	0.24–0.98	0.54 ± 0.05
Standing with lying	1	110	11	0.29–0.42	0.34 ± 0.02
Lying and ruminating with lying	3	30–110	21	0.08–0.52	0.24 ± 0.03

SOURCE: Adapted from Graham 1964.

for food. The additional energy spent while foraging on poor range may not add to the total daily requirements of wild ruminants, however, since an animal that is rapidly filled on good range may spend more time in nonforaging activity, such as investigation or play.

The energy cost of running has been measured in reindeer (*Rangifer tarandus*) by Hammel (1962). The activity increment (I_{ma}) in the metabolic rate equation is 8.0 (from Table 16-15). Crampton and Harris (1969) indicate that sustained work is from three to eight times as costly as standing. If a maximum increment for running of eight times Q_{mb} is used for a first approximation, the energy cost of running can be considered in relation to the total daily expenditure. The amount of time that elk spend running is less than 1% (Struhsaker 1967); it is very likely true that wild ruminants spend very little of their time running unless they are frequently disturbed by man or predators.

The validity of the use of such broad estimates for the energy requirement of a free-ranging animal can be determined with much more confidence after the time element has been realistically included in the calculations. The energy cost of running may have the greatest variability per unit time, but an animal that runs for 30 minutes a day is running only about 2% of the total time. A comparison of the energy expenditure during that time with the basal metabolic requirement of a 100-kg animal can be made with equation (16-13).

$$Q_{er} = \left[\frac{(70)(W_{kg}^{0.75})(I_{ar})(t_h)/24}{(70)(W_{kg}^{0.75})} \right] 100 \qquad (16\text{-}13)$$

where

Q_{er} = % daily energy for running
I_{ar} = activity increment for running
t_h = hours spent in running

At a maximum value of $I_{ar} = 8$, the energy expenditure of a 60-kg animal for running one-half hour a day is about 17% of its daily basal energy expenditure. If other activity and production processes are included in the total daily energy expenditure, the percentage of the total that is attributed to running decreases.

The energy cost of maintaining homeothermy is not a part of the energy requirements of an animal until the heat loss due to prevailing weather conditions exceeds its heat production at that time. The amount of heat energy produced during the exothermic chemical reactions of basic life processes—from muscular activity, the heat of fermentation in the rumen, and the heat of nutrient metabolism in all body tissue—exceeds the heat loss in many situations. Thus the problem often facing a homeothermic animal is the dissipation of heat rather than the conservation of heat. The principles underlying the exchange of heat were discussed in Chapter 13 and the responses an animal can make to changes in the thermal regime in Chapter 14.

Another energy requirement of an animal that needs to be mentioned, but for which no data are available, is the energy cost of a parasite or pathogen load. Any nutrient or body tissue that is absorbed by a parasite represents an energy drain on the host, but the energy cost has not been quantified through research. Further, the metabolic experiments conducted have in most cases been on animals carrying some kind of a parasite load, so the basic energy requirements of the animal include these additional requirements. Parasites and pathogens probably have a greater effect by upsetting the metabolic process of the host than they do as an extra energy demand, but it is well to consider the idea since the first law of the conservation of energy does apply to the host-parasite relationship.

ENERGY REQUIREMENTS FOR PRODUCTION.   Productive processes of wild ruminants include growth of body tissue, growth of the fetus, and the production of milk. The energy cost of these processes has been studied in both domestic animals and wild ruminants under experimental conditions.

The intake of total digestible nutrients (TDN) for different rates of gain in white-tailed fawns was determined by Cowan at The Pennsylvania State University (personal communication), and these values have been converted to caloric intake by multiplying the TDN by 2000 (Figure 16-10). The metabolizable energy can be estimated to be 80% of digestible energy [82% in dairy cattle (Crampton and Harris 1969)]. The net energy available remains after the heat of nutrient metabolism has been considered.

ENERGY REQUIREMENTS FOR GESTATION.   The additional energy requirement due to gestation remains small from conception through the first two-thirds of the gestation period. The last one-third of pregnancy is marked by accelerated growth of the fetus, and the energy requirement increases. The metabolizable energy required for pregnancy in cattle has been computed from data of Jakobsen [see ARC (1965)]. The increase is logarithmic, so a linear regression equation for the log of the energy requirement in relation to gestation time (t_d) can be calculated.
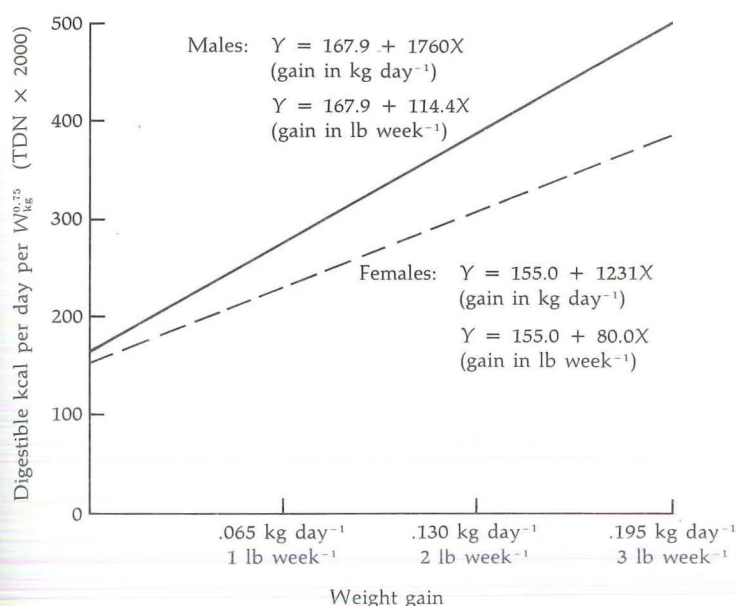
FIGURE 16-10.   Energy in the feed for weight gain in white-tailed deer fawns. (Calculated from data from Cowan, personal communication.)

Equation (16-14) expresses this relationship:

$$Q_{ep} = [e^{(2.8935 + .0174\,t_d)}]/45 \qquad (16\text{-}14)$$

where

Q_{ep} = energy requirement for pregnancy per kg fetus weight at term for cattle
t_d = gestation time in days
45 = calf weight in kg at birth

Note that the energy required is divided by the average calf weight at term. The final expression of this relationship is energy per kilogram of fetus weight at term, and the application of the value obtained to wild ruminants results in a first approximation for use in testing the relative importance of the energy requirement for gestation. This is done for deer with equation (16-15), which includes a conversion factor that makes the gestation time of deer equivalent to that of cattle. Similar curves for other wild ruminants can be calculated with the appropriate conversion factors for gestation time (see Table 16-4). They are shown in Figure 16-11.

$$Q_{ep} = [e^{2.8935 + (.0174\,t_d/0.71429)}]/45 \qquad (16\text{-}15)$$

where

Q_{ep} = energy requirement for pregnancy of deer per kg fetus weight at term
0.71429 = 200/280 = (gestation period of deer)/(gestation period of cattle)
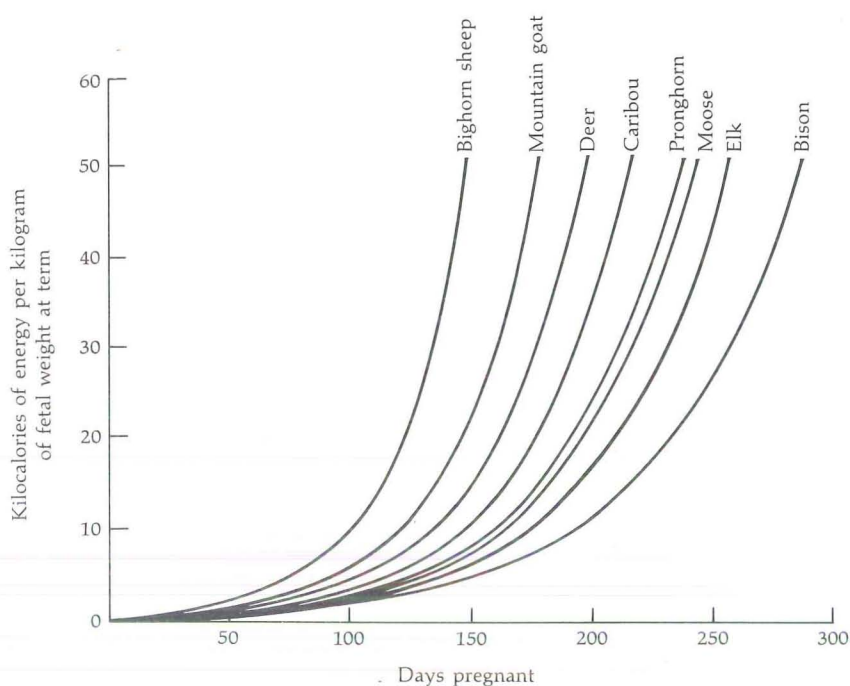
FIGURE 16-11.   Energy required for gestation by wild ruminants.

MILK PRODUCTION.   The energy required for milk production by dairy cattle has been estimated to be over 1.6 times the energy contained in the milk (Crampton and Harris 1969). This is in addition to maintenance. The energy cost of lactation is related to the amount of milk produced, however, so milk production and the energy cost of lactation by wild ruminants can be calculated from known biological relationships, based on the premise that the amount of milk produced is sufficient to meet the requirements of the nursing fawn. The biological relationships involved in estimating milk production were discussed in Section 16-2 and summarized in Figure 16-5.

Nutrient requirements change during growth, and as the rumen develops the percentage of the diet that is composed of forage changes accordingly, along with the percentages of the energy and protein requirements that are met by milk and forage. When the net protein and net energy utilized from milk has been determined, the amount of milk necessary to meet these levels of utilization can be determined.

The first item of information needed is an estimation of the energy requirements of fawns. The energy metabolism of black-tailed deer fawns has been measured by Nordan, Cowan, and Wood (1970), and it is equal to $(2.1)(70)W_{kg}^{0.75}$ (see Table 7-5). This is in line with data on young domestic ruminants, and the range of values for I_{ma} of 2.0 to 3.5 should cover the normal requirements of the growing fawn.

The next step necessary in the calculation of milk production based on energy

needs is the expression of rumen development and its relationship to the digestion and absorption of nutrients from milk and forage. This was discussed in Section 16-2 and illustrated in Table 16-6.

The final step is the calculation of milk production necessary to meet the energy requirements of fawns. The equation is:

$$Q_{mp} = [(I_{ma})(I_{mp})(70)(W_{kg}^{0.75})][(RD)(1/E_{net})]/GE_m \qquad (16\text{-}16)$$

where

Q_{mp} = milk production based on energy requirements
I_{ma} = energy increment for activity of the fawn
I_{mp} = energy increment for production by the fawn
RD = rumen development = $(113.6 - 4.5W_{kg})/100$
E_{net} = net energy coefficient for milk = 0.8
GE_m = energy in milk = 0.7 kcal g^{-1}

Estimates of the milk production necessary to meet a range of energy needs of the growing fawn are shown in Figure 16-12. The shape of the lactation curve is about as expected, with an increase in milk production from parturition up to the age at which the rumen capacity is more than 50% of the total stomach size and a decrease until the young animal is weaned. The absolute amount of energy required by the fawn increases with increasing age, the relative amount decreases with increasing age, and the amount derived from milk increases up to a fawn weight of about 10 kg and then begins to decrease.

The final step is the determination of the energy requirement of the lactating female in order to produce the milk necessary to support the fawns. This consideration is analogous to overhead in a business operation; the total cost of the

FIGURE 16-12. Estimations of the daily milk production of a wild doe to meet the energy needs of one fawn.
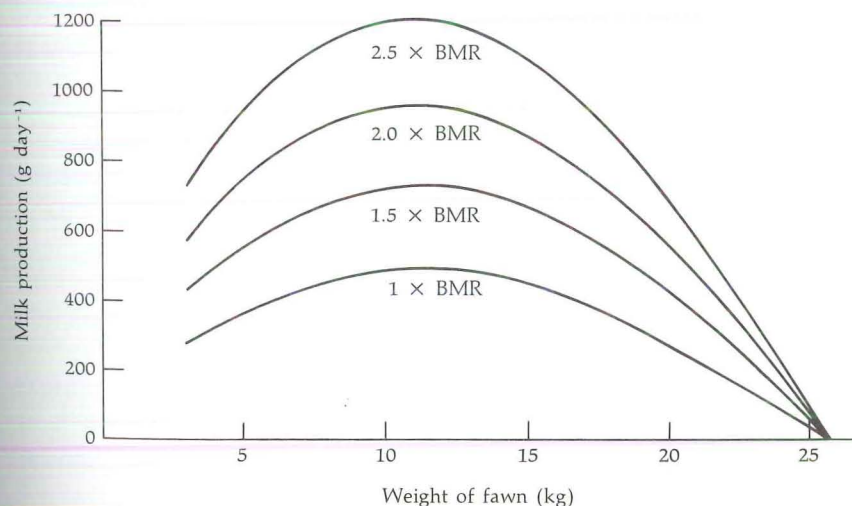
final product includes the cost of materials plus the costs associated with production. Using the increment of 1.6 times the energy contained in the milk produced (Crampton and Harris 1969), the total daily energy requirement can be calculated by adding the requirements for basal metabolism and activity to the energy requirement for milk production.

SUMMARY OF THE ENERGY REQUIREMENTS OF THE INDIVIDUAL. The energy requirement of an individual animal is dependent on its basal metabolic characteristics, its activity, and the amount of production occurring. The total daily energy requirement is composed of the energy requirements for each of these biological processes. The energy cost equation is:

$$\left\{ \begin{array}{c} \text{Total daily} \\ \text{energy required} \end{array} \right\} = \left\{ \begin{array}{c} \text{The sum of the energy} \\ \text{required for bedding} \end{array} \right\} + \left\{ \text{Ruminating} \right\}$$

$$+ \{\text{Standing}\} + \{\text{Feeding}\} + \{\text{Walking}\} + \{\text{Running}\}$$

$$+ \{\text{Breeding}\} + \{\text{Social activity}\} + \{\text{Production energy}\}$$

The energy cost of each of these activities is summarized in Table 16-11, with a comparison of the rate of energy expenditure for each activity compared with

TABLE 16-11 ENERGY EXPENDITURE PER HOUR BY A 100-kg ANIMAL IN DIFFERENT ACTIVITIES

Activity	Rate per Hour	Cost above Basal Metabolism ($kcal\ hr^{-1}$)	Basal Metabolism + Activity Cost as Multiple of Basal Metabolism
Basal metabolism	$[(70)(W_{kg}^{0.75})]/24$	0 (BM = 92)	1.0
Standing[1]	$[(70)(W_{kg}^{0.75})(1.1)]/24$	9	1.1
Running[2]	$[(70)(W_{kg}^{0.75})(8)]/24$	646	8.0
Walking 1 km on level[3]	$(0.59)(W_{kg})(D_{km})$	59	1.64*
Vertical ascent of 0.1 km[3]	$(6.45)(W_{kg})(H_{km})$	65	1.71*
Walking 1 km, 10% gradient	(Sum of rates for walking and vertical ascent)	124	2.35*
Foraging[4]	$(0.54)(W_{kg})$	54	1.59*
Playing	$[(70)(W_{kg}^{0.75})(3)]/24$	185	3.0
Ruminating[4]	$(0.24)(W_{kg})$	24	1.26*

[1] Crampton and Harris 1969.
[2] Estimated from Hammel 1962 and Crampton and Harris 1969.
[3] Clapperton 1961.
[4] Graham 1964.
* These values are dependent on body weight and cannot be applied directly to all weights. New multiples must be determined since the values will decrease at higher weights because of the combined effect of the basal metabolic component and the activity cost.
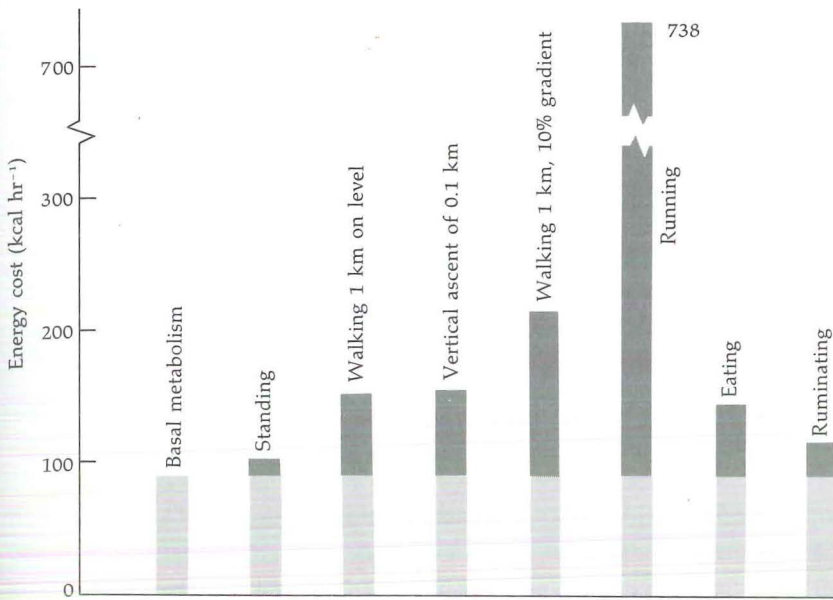
FIGURE 16-13. Energy cost of different activities to a 100-kg animal.

the basal metabolic rate of $Q_{mb} = 70 \ W_{kg}^{0.75}$ for a 100-kg animal (Figure 16-13).

When the daily proportion of time spent in each of these activities is considered, the total daily requirement can be calculated. The results for five activity regimes of a 60-kg animal are shown in Table 16-12. Note that the daily energy expenditure, expressed as a multiple of the basal rate, varies from 1.23 to 1.98 for the five different activity regimes. This result provides an insight into the amount of normal variation expected for free-ranging animals. The maximum value (1.98) is found for an extremely active animal—far in excess of the expected amount of activity of a deer in its natural habitat.

The activity patterns of a 39-kg female white-tailed deer monitored by telemetry in the summer (Jeter and Marchinton 1964) have been used in the calculation of energy expenditure calculated (Table 16-13). Three 24-hour observation periods were used in the calculations, including the two extremes and an intermediate activity pattern. The multiples of BMR range from 1.24 to 1.45, indicating that different observed activity regimes for 24-hour periods do not cause very great differences in the total energy expenditure.

Montgomery (1963) observed nocturnal behavior of white-tailed deer in central Pennsylvania, and estimates of the percentage of time spent in different activities have been made for the calculation of seasonal differences in the energy expenditure for nighttime activity (Table 16-14). There is a general trend from higher activity levels in the summer to lower in winter. Values for the actual energy expenditure compared with the basal metabolic rate $Q_{mb} = (70)(W_{kg}^{0.75})$ range from 1.59 to 1.70. The seasonal differences in energy expenditure parallel seasonal differences in basal and fasting metabolic rates reported by Silver (see Tables 7-2 and 7-3).

TABLE 16-12 ENERGY EXPENDITURE (Q_e = kcal day^{-1}) OF A 60-kg DEER IN FIVE DIFFERENT

Activity	Hours	Q_e	%Q_e	Hours	Q_e	%Q_e
Standing	0.50	35	1.8	0.75	52	2.4
Running	0.00	0	0.0	0.25	126	5.9
Walking	1.00	172	9.2	2.00	306	14.3
Foraging	4.00	387	20.8	6.00	581	27.1
Playing	0.50	94	5.0	0.75	142	6.6
Bedding and ruminating	18.00	1175	63.1	14.25	939	43.8
Totals	24.00	1863	99.9	24.00	2146	100.1
Multiple of BMR		1.23			1.42	

Seasonal differences in the energy expenditure of elk in different reproduction conditions, calculated from behavior data reported by Struhsaker (1967), are shown in Table 16-15. The amount of time spent in different activities clearly reflects the reproductive status of the individual within the herd. A spike bull in velvet is more sedentary than one with no velvet; they bed 50% and 21% of the time, respectively. The two-and-one-half-year-old bull spends 21% of the time bedded, and the three-and-one-half-year old solitary bull beds 39% of the time, but 46% of the time is spent standing, with little running or walking. In general, an aggressive but subdominant bull is considerably more active than older bulls, and the energy expenditure is clearly related to the reproductive activity regime.

TABLE 16-13 ENERGY EXPENDITURE OF A 38.6-kg FEMALE WHITE-TAILED DEER DURING THREE 24-HOUR MEASUREMENT PERIODS

Gross Activity Pattern	June 29–30			July 8–9			July 18–19		
Moving	38%			60%			83%		
Still	62%			40%			17%		
Activity	% Time	Q_e	%Q_e	% Time	Q_e	%Q_e	% Time	Q_e	%Q_e
Basal Metabolism	100	1084	—	100	1084	—	100	1084	—
Bedding	31	336	25	20	217	14	9	98	6
Standing	31	370	28	20	239	16	9	108	6
Feeding	29	143	11	45	225	15	62	311	20
Ruminating	4	9	<1	6	13	1	9	19	1
Walking	38	487	36	60	829	54	83	1046	67
Totals	*	1345		*	1523		*	1582	
Multiple of BMR		1.24			1.40			1.46	

SOURCE: Based on behavior data reported by Jeter and Marchinton, 1964, using telemetry, and analyzed by Stevens 1970.
* Some activities are concurrent; total exceeds 100.

ACTIVITY REGIMES

Hours	Q_e	$\%Q_e$	Hours	Q_e	$\%Q_e$	Hours	Q_e	$\%Q_e$
1.00	69	2.8	1.25	86	3.2	1.50	104	3.5
0.50	252	10.4	0.75	377	13.9	1.00	503	16.8
3.00	440	18.1	4.00	573	21.2	5.00	707	23.6
8.00	774	31.9	10.00	968	35.7	12.00	1161	38.8
1.00	189	7.8	1.25	236	8.7	1.50	283	9.5
10.50	703	29.0	6.75	468	17.3	3.00	232	7.8
24.00	2427	100.0	24.00	2708	100.0	24.00	2990	100.0
	1.61			1.79			1.98	

The difference in the multiple of BMR for a spike bull in velvet and after the velvet has been shed is considerable—1.44 to 1.82. Older bulls expend 1.74 times the basal rate, with more time spent in standing and breeding and less in feeding and moving about. The percentage of time spent in breeding activity and the relative cost of breeding for elk of different ages and reproductive status are shown in Figure 16-14. The energy cost of activity during the breeding season is related to the social position of the bull in the herd!

TABLE 16-14 ENERGY EXPENDITURE FOR NOCTURNAL ACTIVITY OF A 75-kg WHITE-TAILED DEER DURING DIFFERENT SEASONS

Gross Activity Pattern	Summer			Fall			Winter		
Bedded	16%			18%			25%		
Other activity	84%			82%			75%		
Activity	% Time	Q_e	$\% Q_e$	% Time	Q_e	$\% Q_e$	% Time	Q_e	$\% Q_e$
Basal metabolism	100	1784	—	100	1784	—	100	1784	—
Bedding	16	280	9	18	318	11	25	442	16
Standing	16	308	10	18	349	12	25	487	17
Feeding	69	667	22	64	626	21	50	490	17
Ruminating	16	68	2	18	77	3	25	107	4
Walking	69			64			50		
On level		(1529)			(1437)			(1124)	
Vertical ascent		(179)			(179)			(179)	
Total for walking		1708	56		1616	54		1303	46
Totals	*	3031		*	2986		*	2829	
Multiple of BMR		1.70			1.67			1.59	

SOURCE: Activity pattern based on data in Montgomery 1963; analyzed by Stevens 1970.
* Some activities are concurrent; total exceeds 100%.

**TABLE 16-15**   THE ENERGY EXPENDITURE OF ELK DURING THE RUT

Activity	160-kg Cow			145-kg Spike in Velvet			170-kg Spike (no velvet)		
	% Time	Q_e	% Q_e	% Time	Q_e	% Q_e	% Time	Q_e	% Q_e
Basal metabolism	100	3149	—	100	2925	—	100	3296	—
Bedding†	34	1083	21	50	1460	35	21	683	11
Standing†	41	1428	28	28	887	21	42	1529	26
Eating†	46	947	19	38	714	17	63	1379	23
Ruminating	26	241	5	29	244	6	16	155	3
Walking†	24	1310	26	21	790	19	35	2035	34
Running†	0	0	0	<1	13	<1	0	0	0
Breeding†	1	53	1	1	92	2	2	210	4
Totals	*	5062		*	4200		*	5991	
Multiple of BMR		1.61			1.44			1.82	

† Percentages for different activities calculated by Stevens 1970, from data in Struhsaker 1967.
* Some activities are concurrent; total exceeds 100%.

The energy expenditure of pronghorn of different weights has been calculated using activity data based on observations by Prenzlow, Gilbert, and Glover (1968). Resting activity consumed 46% of the animal's time, with feeding and other activities 54%. Differences between the energy cost of activity for pronghorn of 30, 45, and 60 kg are slight, with the multiples of BMR equal to 1.40, 1.42, and 1.45, respectively (Table 16-16). The middle activity regime shown in Table 16-12

FIGURE 16-14.   The percentage of time spent in breeding activity and the percentage of the total daily energy expenditure for breeding activity by elk of different ages and reproductive status.
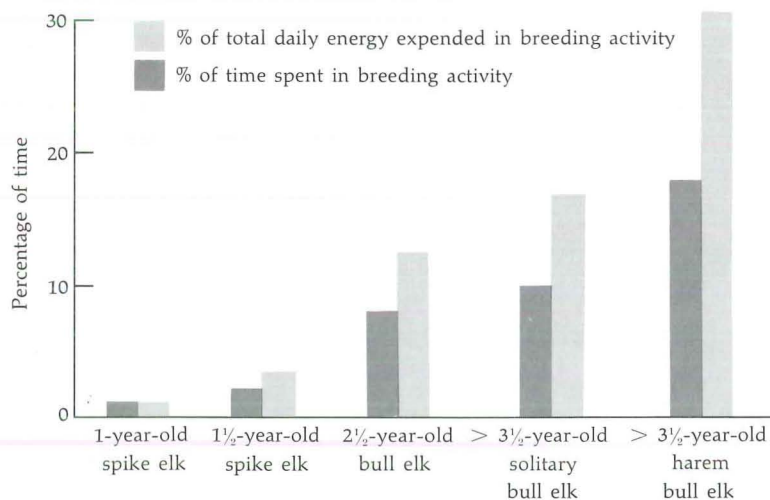
215-kg 2½-year-old Bull			327-kg < 3½-year-old Solitary Bull			327-kg < 3½-year-old Harem Bull		
% Time	Q_e	% Q_e	% Time	Q_e	% Q_e	% Time	Q_e	% Q_e
100	3930	—	100	5383	—	100	5383	—
21	835	11	39	2121	23	19	1029	11
44	1886	26	29	1736	18	46	2694	29
48	1329	18	27	1146	12	17	615	7
21	254	3	28	520	6	28	446	5
27	1893	26	21	2173	23	18	1681	18
<1	205	3	<1	150	2	<1	41	<1
8	927	13	10	1566	17	18	2836	30
*	7329		*	9412		*	9342	
	1.86			1.75			1.74	

TABLE 16-16 THE EFFECT OF WEIGHT ON THE DAILY ENERGY EXPENDITURE OF PRONGHORN

	Weight of Animal (kg)								
Gross Activity Pattern	30			45			60		
Resting	54			54			54		
Nonresting activity	46			46			46		
Activity	% Time	Q_e	% Q_e	% Time	Q_e	% Q_e	% Time	Q_e	% Q_e
Basal metabolism	100	897	—	100	1216	—	100	1509	—
Bedding	23	206	16	23	280	16	23	347	16
Standing	23	227	18	23	308	18	23	382	17
Eating	54	210	17	54	315	18	54	420	19
Ruminating	23	40	3	23	60	3	23	79	4
Walking	53	499	40	53	668	38	53	846	39
Running	1	72	6	1	97	6	1	121	6
Totals	*	1254		*	1728		*	2195	
Multiple of BMR		1.40			1.42			1.45	

SOURCE: Activity times based on data in Prenzlow, Gilbert, and Glover 1968; analyzed by Stevens 1970.
*Some activities are concurrent; total exceeds 100.

has been used to calculate the energy requirements of deer weighing 30, 60, and 90 kg with similar results. This illustrates that the weight effect is not an overriding consideration in the calculation of the energy requirements if activity levels are held constant.

The energy requirements of 60-kg deer at different levels of production are shown in Figure 16-15. The energy expenditure for activity is 1.42 times basal, increasing to 1.53 at the end of gestation with one fawn, 1.64 with two fawns, and then rising to 1.86 and 2.30 at the peak of lactation with one and two fawns, respectively. A gain of 0.15 kg day^{-1} results in an energy expenditure of 1.82.

The energy requirements of free-ranging animals have been estimated in the preceding calculations by using data from different sources in the literature. An interesting fact that emerges is that energy expenditure of a 60-kg deer, expressed as a multiple of basal metabolism, does not exceed 2, except at the peak of lactation when it is 2.3. This indicates that lactation is a costly process and that variations in weight, activity, and pregnancy all have a lesser effect. This does not mean that the latter are not important cost items in the energy budget; their importance must be evaluated in relation to the energy available on the range and the efficiency of the animal in using it.

Biologists have recognized differences in the energy and protein requirements of animals for years, but little effort has been made to analyze the importance

FIGURE 16-15.   Energy cost of activity and production by a 60-kg deer.
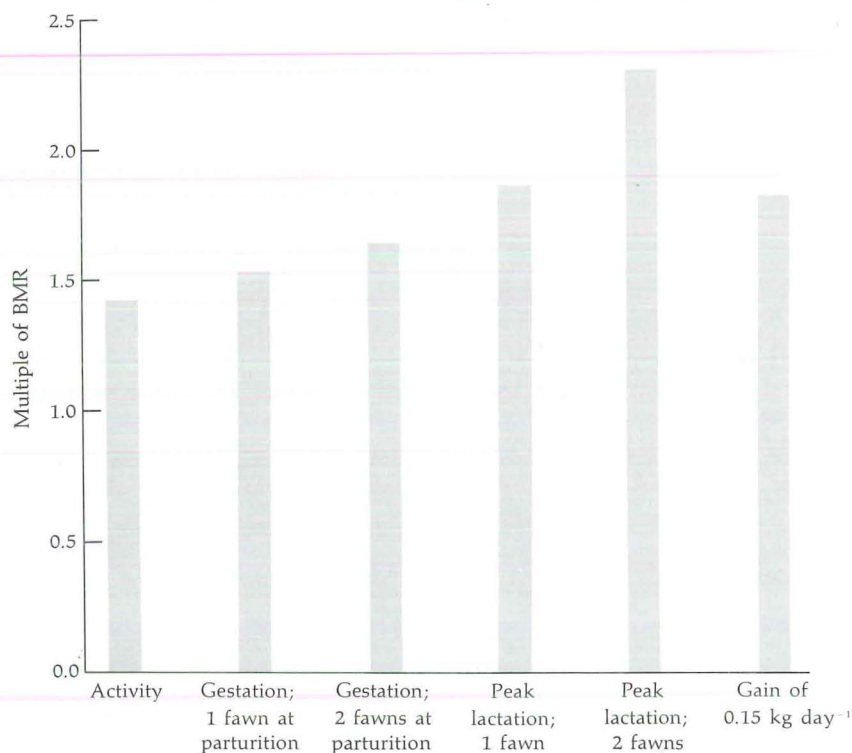
of these requirements for free-ranging animals. The calculations in this chapter illustrate what can be done to make first approximations. The results indicate that animals of different weights and at different activity levels may not vary widely in some energy requirements. Since range characteristics change also, it is necessary to relate animal requirements with range conditions throughout the annual cycle in order to determine the times at which more critical balances between the two exist. The importance of these biological characteristics, both inputs and outputs, is analyzed in Chapter 17.

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