17

MATHEMATICAL ANALYSES OF FACTORS AFFECTING CARRYING CAPACITY

When the biological components of the animal-range relationship have been identified, they can be assembled into a sequence of calculations that represent the biological functions involved. The number of components in the calculation of carrying capacity—including both the animal requirements and the characteristics of the range supply—is large, and the use of electronic computing equipment greatly facilitates the analyses. The model that is developed becomes an electronic analog of the system being analyzed, designed in a manner that permits the user to vary biological characteristics within the model, simulating changes that might take place in the natural environment.

17-1 THE CARRYING-CAPACITY MODEL

A basic consideration in the calculation of carrying capacity is that both the requirements of the animal and the range supply must be known before the calculation can be completed. This was illustrated very simply in Figure 16-1 in which the large box represents the range supply and the number of smaller boxes that fit inside this box depends on the sizes of the smaller boxes. Requirements for energy and protein (the small boxes) were calculated and range characteristics (the large box) were discussed.

The assembling of biological information for computer analyses needs to follow a logical pattern that represents biological relationships. A flow sheet showing the relationships between the items of information considered in the current analysis is shown in Figure 17-1. A more detailed verbal description of the model

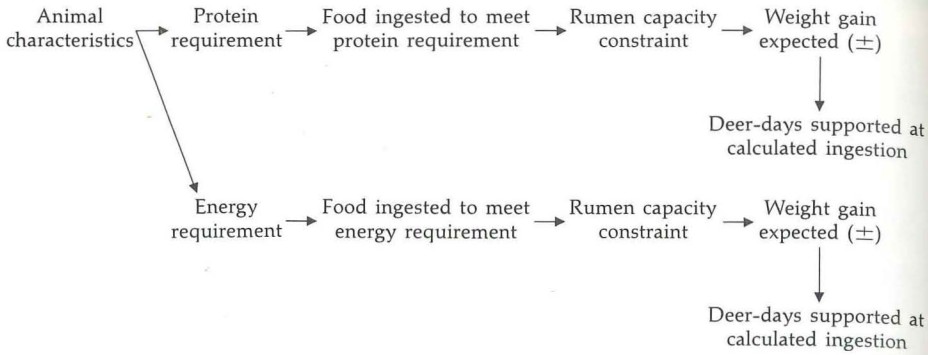


FIGURE 17-1. Animal characteristics are used to calculate the protein and energy requirements and the amount of food necessary to meet those requirements. The expected weight gain is calculated, and the number of deer-days supported by the range is determined on both a protein and an energy base.

is shown in Figure 17-2. The complexity of a flow sheet increases with the size of the model; the most detailed flow sheet used in the present model includes seven sheets of 17″ × 11″ paper. The details in such a flow sheet are continuously undergoing changes.

The schematic displays of the factors considered are followed by the assembling of the mathematical equations for energy and protein requirements and the quantity and quality of the forages on the range into a working mathematical design that represents the interrelationships of these biological factors. The order in which the calculations are made is important because of the characteristics of protein and energy metabolism. The relationship between protein and energy metabolism is essentially a one-way street since protein can be converted to energy but energy cannot be converted to protein. Catabolism of body fat is useful only as a source of energy, whereas protein-containing tissue can be mobilized to supply nitrogen for specific production purposes or as an energy source.

This distinction between protein and energy metabolism is an over-simplification of the simultaneous metabolic processes taking place in body tissue. Energy is necessary for protein metabolism, both in the rumen where the microflora are active and in the body tissue of the ruminant animal. Indeed, Crampton and Harris (1969) suggest that it is the energy needs of the animal that are met first and other nutritive needs are likely to be satisfied also if the diet is balanced.

The distinction between the mobilization of protein-containing tissue for either nitrogen or energy and the mobilization of fat reserves for energy alone is an important one, however. There are times at which the animal can be in a positive energy balance but a negative nitrogen balance. The opposite can also occur. Thus the weight changes (ΔW; ± gain) calculated in the carrying-capacity analyses do not necessarily coincide on both a protein and an energy base.

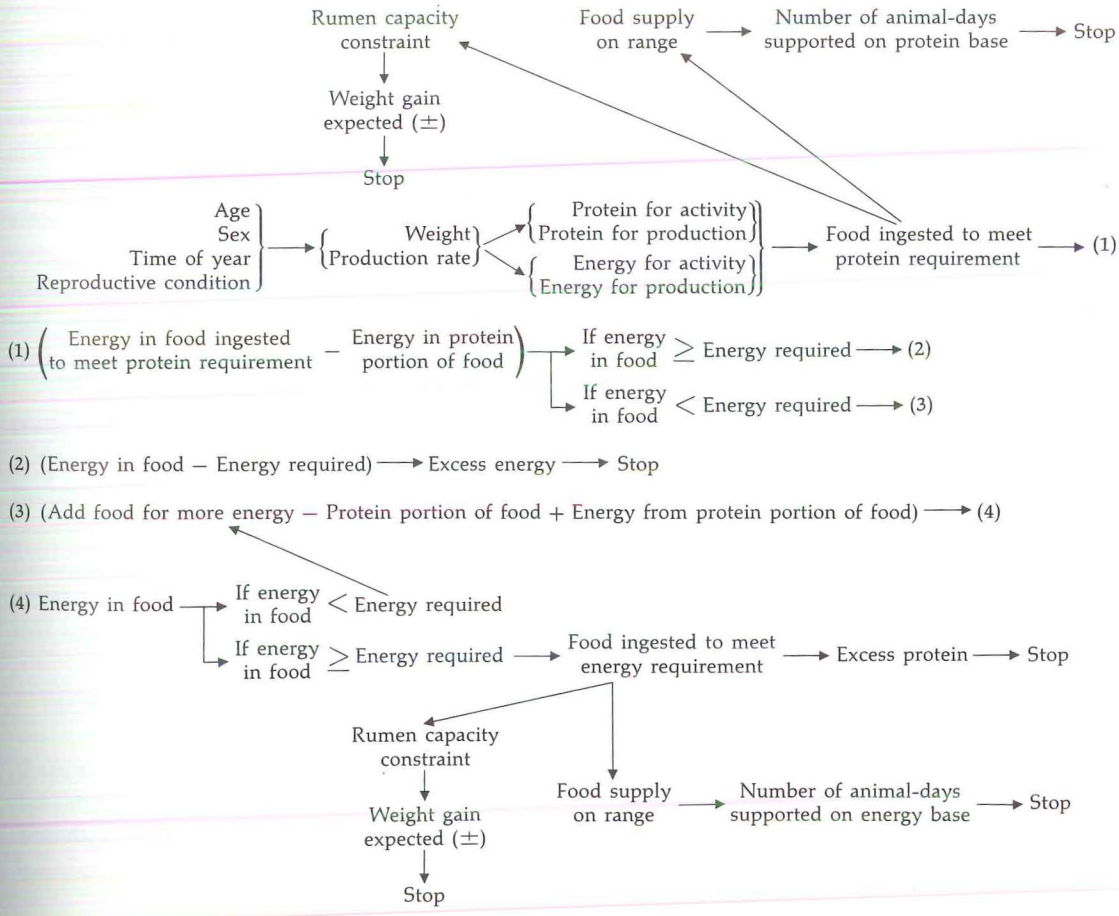
A paradoxical conclusion can be reached in the assembling of such models. Little basic information is known about wild ruminants, but analyses of their characteristics based on biological principles and known facts about domestic animals results in a large body of information of value in the carrying-capacity analyses. Thus although little is known, much can be learned from these analyses.

17-2 THE PROGRAM FORMAT

INPUTS FOR ANIMAL REQUIREMENTS. The items of information used to calculate animal requirements throughout the entire year include the following:

1. Age in years, expressed as the lowest whole number. The number 1 is entered for a $1\frac{1}{2}$-year-old animal.
2. Age in days, above the year entry. The number 183 is entered for a $1\frac{1}{2}$-year-old animal.
3. Body weight in kg.
4. Rumen-fill coefficient.
5. Number of fawns *in utero* or nursing.
6. Protein requirements of nursing fawns in g per kg fawn weight per day.
7. Energy requirements for activity expressed as a multiple of BMR.

FIGURE 17-2. An expanded flow sheet showing the sequence of calculations in the carrying-capacity analyses.



These items are variable inputs into the program. The constants in the equations for calculating protein and energy requirements are written in the computer program; they need not be changed for deer with different characteristics. Some of these constants may vary from animal to animal, but the variation may be small enough to overlook. It may also be that so little is known about the variability of these characteristics of deer of different ages or weights that it is best to use constants first, testing for the importance of these factors in the entire calculation by running a variability analysis or an error analysis.

Another characteristic of inputs such as those listed is that a single number may be used to represent a complex biological process. The energy requirements for activity, for example, may be entered into the analysis as a single value, but the single value may have been determined from a subroutine that is external to the main program. This arrangement is often desirable because the effect of different factors on energy requirements can be treated separately from the main program, yet the main program can be run using a number of possible values that could cover the whole range of energy requirements for activity in the wild. The effect of variation in energy requirements can be analyzed in the main program, with more realistic values determined after further refinement in the subroutine used to determine the energy requirements for activity.

The rumen-fill coefficient has also been treated as an external subroutine that results in a single input into the main program. This is necessary because so little is known about both the appetite of a wild ruminant and the passage rates of different foods. The amount of food in the rumen is a function of the appetite level, the passage rates of diet components, and the physical capacity of the rumen. A lack of this information necessitates the use of a range of somewhat arbitrary values for rumen fill. Resulting outputs expressing the amount of food necessary to meet energy or protein requirements as a fraction or multiple of rumen capacity are useful, however, since the importance of rumen capacity can be displayed on dimensionless graphs and the role of rumen capacity can be evaluated. This is done in later figures in which the importance of rumen capacity for deer of different weights is shown.

The number of fawns *in utero* or nursing is an important input for determining the requirements for pregnancy and lactation. Twin fawns may not necessarily place twice the demand on a doe that a single fawn does, although the outputs displayed in Chapter 18 have been made on that assumption.

INPUTS DESCRIBING THE RANGE SUPPLY. The following characteristics of the range are included in the present model:

1. Quantity in kg of each species of forage available to the deer.
2. Percentage of each species in the ingested diet.
3. Percentage of crude protein on a dry-weight basis.
4. Net protein coefficient (NPC—the fraction of the crude protein that is available for maintenance and production).

5. Gross energy of each forage in kcal kg^{-1}.
6. Net energy coefficient (the fraction of the gross energy that is available for maintenance and production).
7. Percentage of water in the field-condition forage.

These seven characteristics apply to each of the forages in the diets used in the calculations discussed in this chapter. Six forages are included in each of the analyses. Deer eat more than six forages, of course, but analyses of rumen contents seldom show more than six to be present in significant quantities. Thus the use of only six forages in the diet is adequate for analyses of the relative importance of some of the factors that affect carrying capacity.

Each of the characteristics of the range can be varied to test their effect on the total animal-range relationship. The quantity available to deer, for example, can be stratified so that the number of deer-days possible at each one-foot interval can be determined. The effects of snow depth can be analyzed by entering the total quantity available to the deer from 0–6 feet, 1–6 feet, 2–6 feet, and so on. The reduction in the food supply due to snow depths can also be combined with changes in the energy requirements due to the effects of walking through snow.

The percentage of each food in the whole diet can be varied to represent either real diets determined in the field or simulations that can vary from one extreme to another. The effect of passage rate can also be included here. Diet changes due to weather effects, depletion of preferred foods, seasonal shifts in the foods available, and so forth, can be simulated through this input.

The percentage of crude protein varies seasonally. This variation, combined with the variation in net-protein coefficients for different animal requirements, permits an analysis of the effect of food quality. The higher protein content and greater digestibility of spring growth is certainly an improvement in range quality, but its net benefit to the population can be determined only after the animal requirements are considered. Protein requirements for pregnancy and lactation, for example, increase rapidly at the same time that the protein supply on the range increases.

The calculations for both net-protein and net-energy utilization are complicated by the fact that the net coefficients for each are different for maintenance, for production, and at different feeding levels. Thus the net coefficients should not be expressed as single values; however, a lack of information about protein and energy metabolism for different purposes necessitates a simplified approach at this time.

DECISIONS. One of the characteristics of a computer is its ability to make decisions. This consists of the comparison of two numbers—whether n_1 is greater than, equal to, or less than n_2—with the computations proceeding to different subroutines in the program according to the directions following each decision. This capability is used in the carrying-capacity model for determining the reproductive characteristics of the animals.

The decisions on reproductive condition are based on a deer calendar stored in the program. The age of the deer is entered in years and days, with the parturition date set in the present model as June 1. This date can be varied; a more comprehensive program is currently being planned that includes a distribution of parturition dates for a population. With a June 1 beginning date, a fawn is at age 0 + 30 on June 30, and 0 + 100 in September at weaning time. Breeding takes place at 0 + 165 for the fawn, 1 + 165 for a yearling, and so on. The significant dates for deer and moose are given in Chapter 10.

The decision-making capabilities of the computer are utilized by comparing the entered age of the animal with the significant dates in the deer calendar. For example, a deer's age of 0 + 90 is compared with the significant date for weaning—0 + 100. Since the fawn has not yet been weaned, the computer continues to calculate the milk ingested as a part of the total food intake. An age of 1 + 180 is compared with the significant date for breeding (1 + 165), and computations are then made for protein and energy requirements for pregnancy. Parturition occurs after day 365, so for any yearling or adult female over 1 year and between days 1 and 100 a lactation requirement will be calculated, unless it is not pregnant or lactating because of unsuccessful conception or fawn mortality. In that case, the number of fawns entered as an input is zero so the requirements for pregnancy or lactation will also be zero.

Another decision is made in the carrying-capacity program in the calculation of metabolic fecal nitrogen (MFN). All of the nitrogen requirements except MFN are calculated first. This is followed by the calculation of the amount of food necessary to meet these requirements. The requirement for the addition of MFN at that level of food intake is then calculated. A nitrogen requirement for MFN results in a new total nitrogen requirement, and this is followed by a second calculation of food intake. This increased food intake will result in a second calculation of MFN, and the cycle will be repeated again, resulting each time in a new calculation of food intake. When the last food intake calculated is less than one gram greater than the previous one, the cycle stops through the use of a decision-making routine in the program. If the protein component of the food is too low to allow for successful convergent iteration, this subroutine is bypassed and the total nitrogen requirement is calculated on the basis of maximum rumen fill.

17-3 CONSTRAINTS IN THE ANIMAL-RANGE RELATIONSHIP

Factors that affect the extent of a relationship between an animal and its environment are called constraints. They may reduce the rate of a biological process, and if the reduction is sufficient to limit all other processes, then the particular constraint is analogous to a limiting factor. It is important to remember, however, that many constraints are always present, whether or not they are limiting factors at a particular moment in time.

Several constraints are included in carrying-capacity analyses, either as an integral part of the main program or as external subroutines. The rumen-capacity

constraint, analyzed through the use of a rumen-fill coefficient, is an example of a constraint that is an integral part of the main program. When the rumen is filled, the portion of the requirements for energy and protein that have not been met by ingested food must be met by mobilizing body reserves. Thus the amount of food ingested in relation to the rumen-fill constraint is a determinant of the sign (+ or −) for weight gain.

Some constraints are easily handled by external subroutines, or even quick glances at outputs. Summer densities of deer, for example, are never very high, so an abundance of forage at the peak of the growing season may support many more deer than are found on an area because of social constraints operating among deer. Thus psychological characteristics of the animals themselves would limit the density rather than the food supply.

Some factors or interactions that act as constraints are outputs from the computer runs. The relationships between MFN, crude protein, and NPC, for example, are determined through the computer runs, with some outputs indicating that a critical situation exists.

17-4 PROGRAM OUTPUTS

Two categories of program outputs result from the use of the carrying-capacity model under discussion. One is the listing of protein and energy requirements for the particular animal described by the input characteristics. The outputs in this category include the nitrogen requirements for:

1. Endogenous urinary nitrogen
2. Hair growth
3. Pregnancy
4. Milk production
5. Metabolic fecal nitrogen

Energy requirements for (1) basal metabolism and (2) activity are also expressed as kcal day^{-1}.

The second category of outputs includes different relationships between animal and range:

1. Amount of dry-weight forage ingested to meet protein and energy requirements at maintenance (zero gain).
2. Quantity ingested of each forage species to fill the rumen.
3. The rate of gain on both a protein and an energy base at rumen capacity.
4. The number of deer-days that each forage species will support.

The amount of forage ingested is shown both in kilograms and as a multiple of the physical rumen capacity and the rumen fill. The latter output indicates the importance of appetite, rumen size, the passage rate of food, and the quality

of the food in relation to the size of the animal. The changes in body weight can be used to continuously change the input weight of the deer being analyzed, or a series of weights can be analyzed to test the relationships between body weight and the various outputs.

17-5 THE DYNAMIC CHARACTERISTICS OF THE ANIMAL-RANGE RELATIONSHIPS

The complexity of the dynamic relationships between an animal and its environment is so great that the human mind cannot fully comprehend it. Many analyses, covering a range of set conditions, provide insight into the relative importance of different factors. Thus carrying capacity is more a concept than a straightforward, definable, biological relationship. In this respect it is similar to the concept of homeothermy in which the dynamic balance between heat production and heat loss is so complex for a free-ranging animal that thermal energy relationships can be analyzed only to determine the relative importance of different factors.

The use of this biological model for analyzing factors that are important to carrying capacity provides several very interesting insights into their relative importance. Analysis of weight changes in relation to body weight, maintenance-gain comparisons, differences in forage consumption, physiological efficiency, and the calculation of deer-days on different ranges indicate that very definite differences exist among the deer, with weight being a particularly important consideration. The analyses have been made using both field data and arbitrary but representative data for hypothetical situations.

The use of arbitrary data can be an advantage rather than a disadvantage in computer modeling because it permits the analysis of the relative importance of different factors without time-consuming field collections. If a factor is found to be unimportant in the total analysis, then field measurements are unnecessary.

The outputs expressing relationships between factors at different times during the year are handled in the same way. Selected time periods that illustrate certain relationships that appear to be of significance are included in this text. Work is continuing on revised and updated models for the calculation of carrying capacity; the picture will approach completion as more factors are analyzed in the model.[1]

17-6 WEIGHT CHANGES

ABSOLUTE VALUES. Calculations of weight changes of deer on both a protein and an energy base have been made for several diets throughout the year. The predicted weight loss for deer on a winter diet, calculated on an energy base, is shown in Figure 17-3. Note that the actual weight loss predicted for a 20-kg deer is less than the weight loss predicted for a 100-kg deer. The weight loss

[1]Charles T. Robbins, "Biological basis for the determination of carrying capacity" (Ph.D. diss., Cornell University, in preparation).

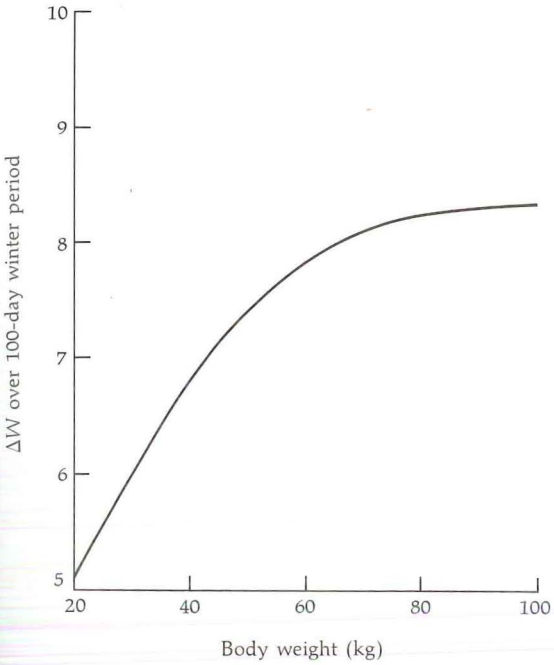


FIGURE 17-3. Predicted weight loss for deer on a winter diet, calculated on an energy base, over a 100-day winter period.

levels off as the animals get larger, however, indicating that deer over 60 kg do not benefit much more from being larger.

PERCENTAGE OF BODY WEIGHT. The expression of the predicted weight loss as a percentage of the initial body weight shows very clearly that smaller deer are at a distinct disadvantage (Figure 17-4). It is predicted that a 20-kg deer, given a winter diet for 100 days, will lose 25% of its initial body weight at the beginning of winter, whereas a 100-kg animal will lose less than 10% of its initial weight. This indicates that the fat reserve of a small deer allows for a much narrower

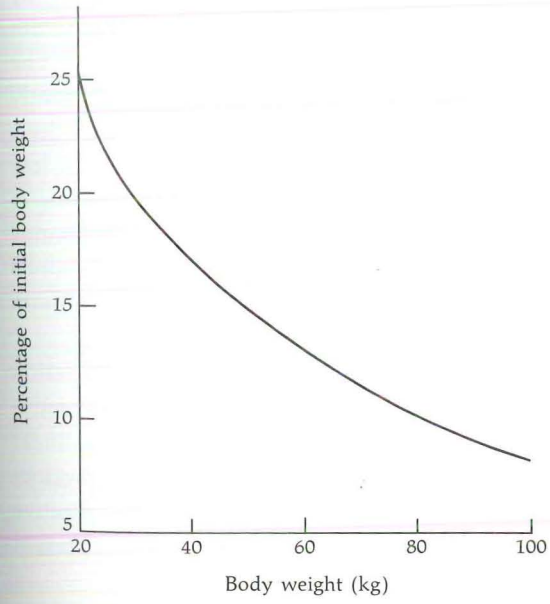


FIGURE 17-4. Predicted weight loss expressed as a percentage of initial body weight over a 100-day winter period, calculated on an energy base.

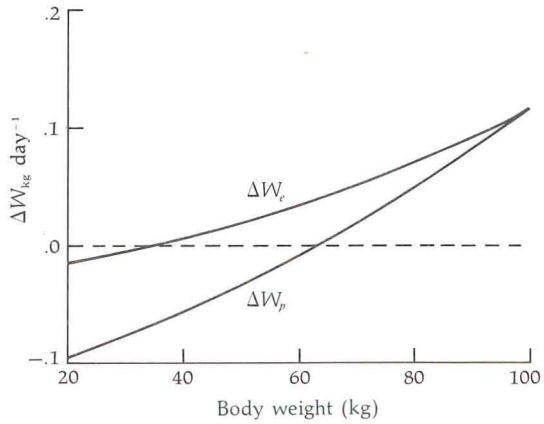


FIGURE 17-5. Predicted weight changes near the end of the lactation period. Calculations on both a protein and an energy base are shown.

margin of safety; therefore small deer are in a more precarious balance during the winter period.

The weight changes shown in Figures 17-3 and 17-4 have been calculated with all other parameters in the program held constant. All deer were on the same winter diet, for example. This may not be the case in the field since small deer are usually the subdominant animals in a population, and the forage available to them may not be as high in quality as the forage ingested by the large, dominant deer. This is frequently observed at feeding stations; the smaller deer eat last and must be content with the leftovers. If the quality of the small deer's diet were reduced in the calculations to simulate the effects of these behavioral factors, the disadvantage shown for the small deer would be accentuated.

LACTATION EFFECTS. Analyses completed to date indicate that lactation is a costly biological process with high weight losses predicted. This is in agreement with data on domestic cattle; weight losses usually occur during peak lactation. The accuracy of these predictions for deer has not yet been analyzed sufficiently because of the lack of information on the summer diets of free-ranging deer. Weight losses have been observed in captive animals, however. A doe on a low plane of nutrition at The Pennsylvania State University weighed 81 pounds at parturition, dropped to a low of 55 pounds 65 days later, and reached 72 pounds by weaning time (36 days later) while on grain. Her fawn reached 33 pounds by weaning (Ondik, personal communication). Verme (1970) stated that minimum weights of female moose were recorded during lactation.

The predicted weight changes for lactating deer near the end of the lactation period (92 days of lactation) are shown in Figure 17-5. Note that both the energy-base and the protein-base calculations are related to body weight in a nonlinear fashion, with the smaller deer showing the greatest losses. Since the milk production drops off rapidly in the last few days of the lactation period, the positive gains predicted for the large does near the end of the lactation period represent an earlier start in the fall weight-gaining period.

17-7 FORAGE INGESTED

RELATIONSHIP TO BODY WEIGHT. The amount of forage ingested by a small deer to meet its maintenance and production requirements for protein is less than the amount needed by a larger deer (Figure 17-6). The data shown are for a spring diet, or just before parturition. The relative amount of forage necessary to meet the maintenance and production requirements of deer on a spring diet is greater, however, for small deer than for large deer. The quantity of food that must be ingested to meet the needs of a deer, expressed as a percentage of its body weight, is more than 10% for a 20-kg deer and 4% for a 100-kg deer (Figure 17-7). These analyses were completed for pregnant does, each carrying one fawn. The relatively greater efficiency of the larger animal is again clear.

MAINTENANCE-GAIN COMPARISONS. The metabolic efficiency of a large animal is greater than that of a small animal. This suggests that there should be relatively less forage ingested to meet the maintenance needs (0 gain) of a large deer than those of a small one. Predicted ingestion rates show this to be the case (Figure 17-8). However, large deer need to ingest more forage than small deer. The curvature of the line showing field-weight forage ingested in relation to body weight is not very obvious because the greater efficiency of the larger deer is masked by the increase in the absolute quantities of food ingested.

The importance of the higher efficiency of large deer compared with that of small deer is shown clearly in Figure 17-9, in which the amount of forage ingested to meet maintenance and production needs is expressed as a percentage of body weight. For the spring diet used in this calculation, maintenance needs are met if a 20-kg deer ingests an amount of forage equal to 3.6% of its body weight, whereas a 100-kg deer can meet its maintenance needs by ingesting forage equal to 1.4% of its body weight. The nonlinear relationship between the field-weight

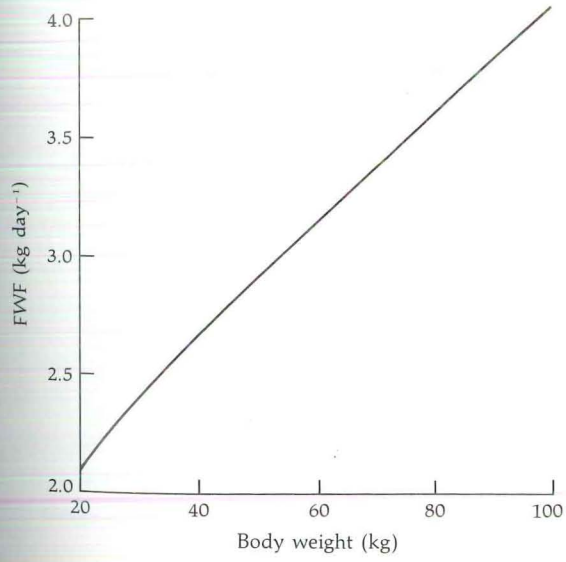


FIGURE 17-6. Field-weight forage ingested (spring diet) to meet the protein requirements of a female deer at the end of pregnancy (one fetus).

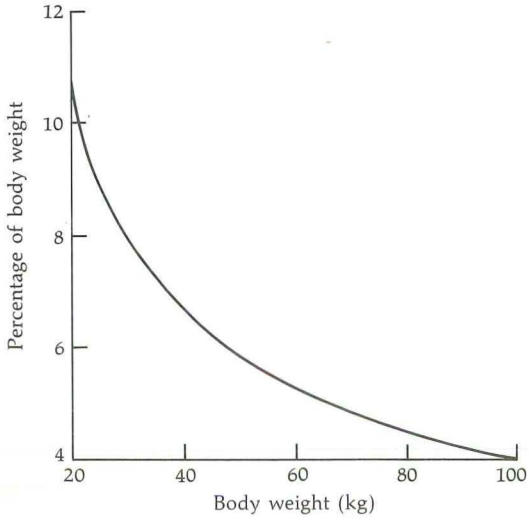


FIGURE 17-7. Field-weight forage ingested (spring diet) in relation to body weight to meet the protein requirements of a female deer at the end of pregnancy (one fetus).

forage ingested, expressed as a percentage of body weight, and body weight is due to the greater metabolic efficiency of the large deer.

The amount ingested to meet the calculated weight gain expressed as a percentage of body weight is constant for all body weights because the rumen capacity was calculated as a constant percentage of body weight. The amount of ingested forage available for production purposes is clearly greater for the large deer, providing a greater likelihood of weight gains for the large animal. This may be very important during the winter when the range quality is reduced and the animal is forced to draw on its body reserves.

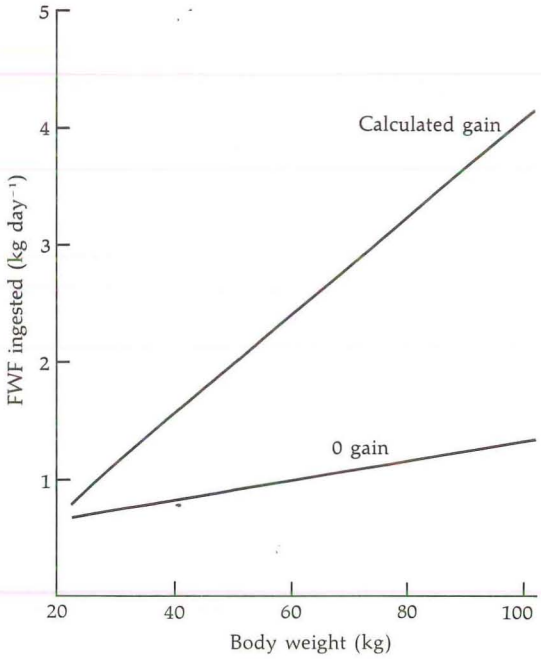


FIGURE 17-8. Field-weight forage ingested to meet maintenance (0 gain) and production needs of a deer on a spring diet.

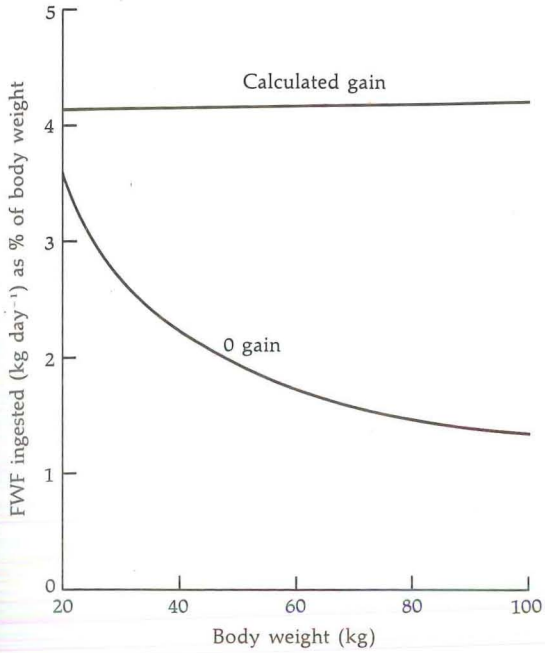


FIGURE 17-9. Field-weight forage ingested, expressed as a percentage of body weight, to meet maintenance and production needs of a deer on a spring diet.

FORAGE CONSUMPTION DURING GESTATION. The increase in the amount of forage necessary at different stages of pregnancy illustrates how the quantity ingested is related to animal requirements (Figure 17-10). There is only a slight increase in the quantity ingested during the first 150 days of pregnancy, but during the last 50 days there is a marked increase. The data in Figure 17-10 are for deer on a constant diet. Normally, there is a shift in a deer's diet during the last part

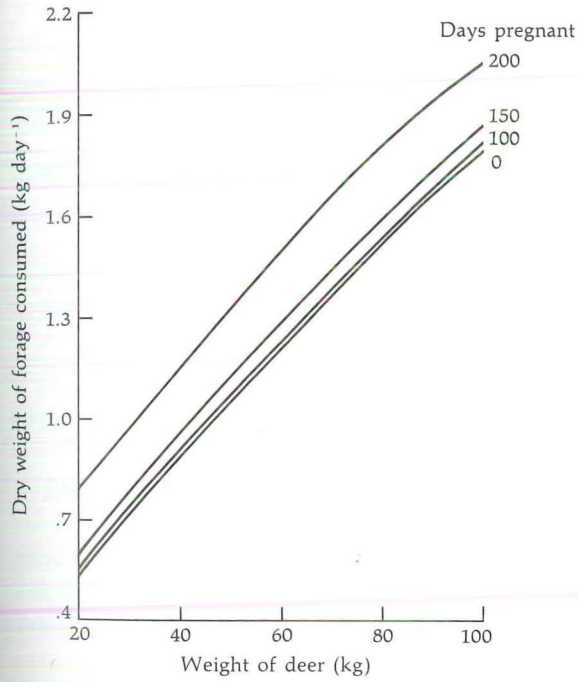


FIGURE 17-10. Predicted dry-weight forage necessary to meet the protein requirements of a pregnant doe on the same diet throughout the gestation period.

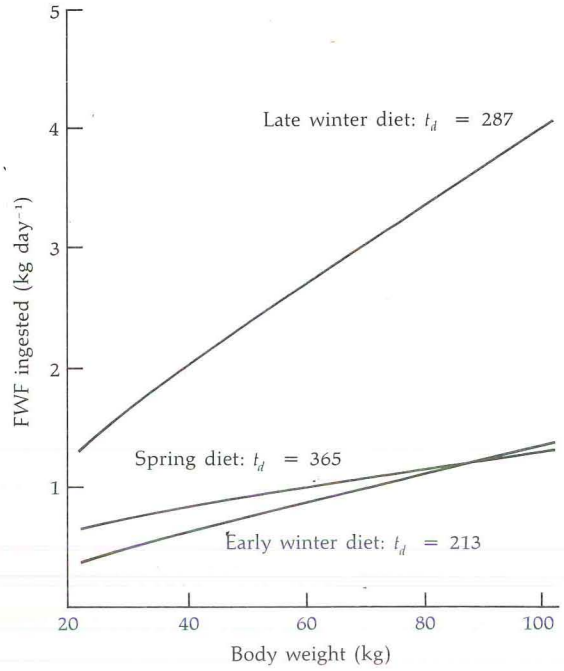


FIGURE 17-11. Predicted field-weight forage necessary to meet protein requirements at three different times in the gestation period: 48 days—early winter diet, time in days (t_d) on the deer-calender = 213; 122 days—late winter diet, t_d = 287; 200 days—spring diet, t_d = 365.

of the gestation period as spring growth begins and deer disperse from the winter concentration areas. The higher quality of forage available in spring results in a reduction in the quantity of forage ingested to meet the protein requirements for gestation (Figure 17-11). This reduction occurs even though the deer has a higher total protein requirement during the last quarter of the gestation period; increased forage quality compensates for the increase in the protein requirement.

FORAGE INGESTED AS A FRACTION OF THE PHYSICAL RUMEN CAPACITY. The absolute quantities of food ingested to meet protein and energy requirements have not been calculated with enough accuracy in the model being discussed to state definitely that these predicted quantities are sufficient. The calculations could be made more precise by considering such factors as the efficiency of protein and energy metabolism for deer of different weights and for different metabolic processes and the recycling of nitrogen. Little is known about these biological functions in deer and other wild ruminants. Research in progress indicates that the recycling of nitrogen can be of definite advantage to white-tailed deer on a low protein diet (Robbins et al., in preparation). Klein and Schonheyder (1970) suggest it may be important in other cervidae.

The amount of forage ingested is important inasmuch as the rumen and reticulum have a finite capacity that can act as a physical constraint. First approximations of the amount of food that should be ingested have been compared with the physical size of the rumen. A base-line expression of 7% of body weight has been used for estimating rumen size. Since the absolute values of both the amount of forage ingested and the rumen size are uncertain, an alternative is to express

the amount of forage ingested as a fraction of the physical rumen capacity on a scale from 0 to 1.0.

A comparison of the fraction of the rumen filled for three calculated diets and one series of field measurements is shown in Figure 17-12. The three calculated rumen fills are based on simulated winter diets, with comparisons of both protein- and energy-base calculations. The field data were collected at the Seneca Army Depot near Ithaca, New York, with measurements made on 52 animals that were field dressed at the check station and the rumens collected for later volumetric measurements.

The two lines are curvilinear, with the smallest animal having a greater fraction of its rumen filled in each case. This is a further indication of the physiological advantage that a larger animal has.

If a constant weight loss of 0.05 kg (50 grams) per day is introduced into the calculations, the fraction of the physical rumen capacity that will be utilized to meet the needs of the deer becomes lower for smaller deer and higher for larger ones (Figure 17-13). This appears at first glance to be an advantage to the small deer, but this is an illusion since a constant weight loss of 0.05 kg for all deer ranging in weight from 20 to 100 kg represents a much faster depletion of body reserves for the small deer. Thus mobilization of the fat reserve that results in similar weight losses for deer of different weights is of greater benefit to a small animal in terms of rumen fill, but the time span over which this benefit can continue will be much less. The small deer will deplete its reserve much earlier in the winter than a large deer.

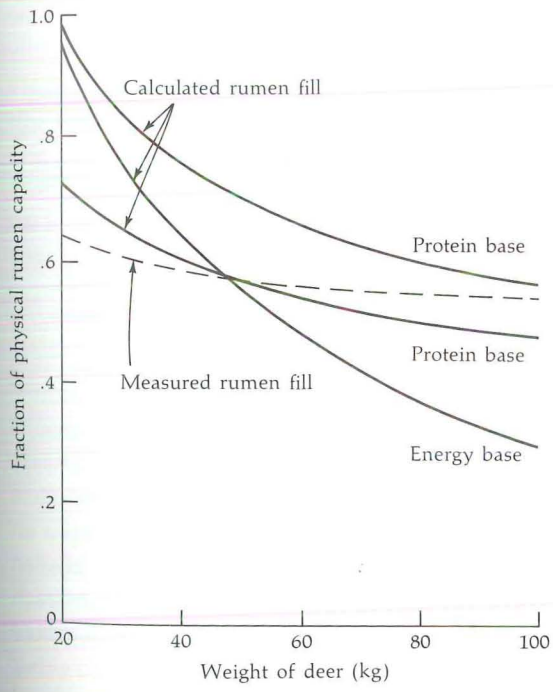


FIGURE 17-12. Rumen fill in relation to body weight for three calculated diets and one series of field measurements at the Seneca Army Depot.

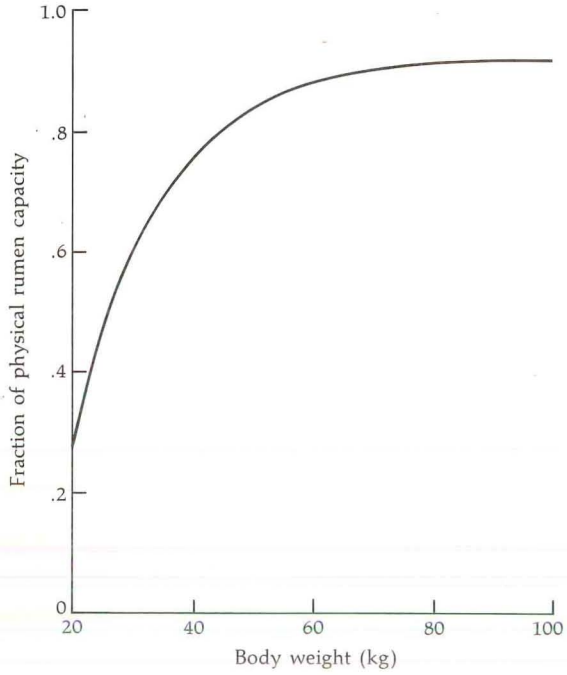


FIGURE 17-13. Fraction of the physical rumen capacity used to meet protein requirements at a daily weight loss of 0.05 kg (50 gms) for deer of all weights.

17-8 PHYSIOLOGICAL EFFICIENCY

METABOLIC FECAL NITROGEN AND NET PROTEIN RELATIONSHIPS. The ingestion of forage results in the production of enzymes for digestion and in the abrasion of the gastrointestinal tract as a result of the physical passage of food material. The amount of nitrogenous material of metabolic origin in the feces is partially dependent on the level of intake. As more food is ingested, more enzymes are produced, and there is more abrasion from the gastrointestinal tract. An analysis of the relationship between the amount of MFN and the NPC indicates a nonlinear relationship between the two (Figure 17-14). As the protein quality goes down, the amount of MFN increases rapidly, with the point of inflection being at an NPC of about 0.40. The animal may be forced to go into a negative nitrogen balance or find an alternative that will have a compensatory effect.

METABOLIC FECAL NITROGEN, FORAGE INGESTED, AND NET PROTEIN COEFFICIENT RELATIONSHIPS. The importance of the forage quality in terms of its *net value* to the animal is shown in Figure 17-15. An NPC of 0.50 compared with one of 0.75 results in a greater MFN requirement and an increase in the quantity of forage necessary to meet this requirement. As the NPC increases, the amount of MFN decreases along with the quantity of forage ingested. Note that the difference between an NPC of 0.75 and one of 1.00 is quite small compared with the difference between an NPC of 0.50 and one of 0.75. It is clear that the net value of forage can reach a low point at which the rumen is not large enough to hold the quantity of ingested material necessary to meet the MFN requirement. The animal will be forced either

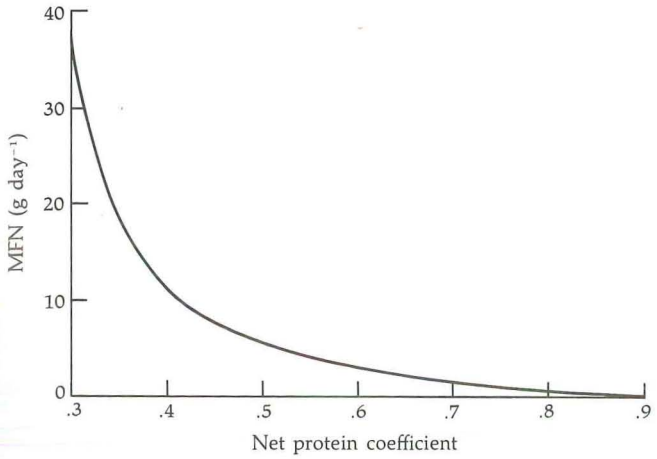
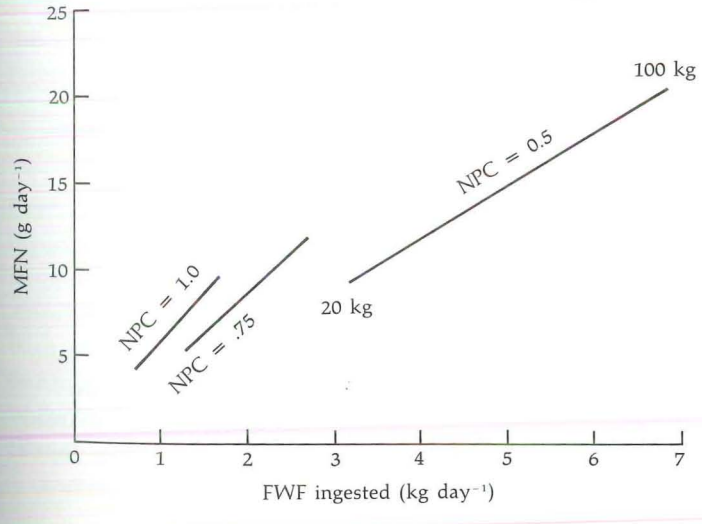


FIGURE 17-14. Metabolic fecal nitrogen in relation to the quality of the food as expressed by net protein coefficients.

to reduce its intake and go into a negative nitrogen balance or to change its diet. When the latter is impossible on depleted winter ranges, weight losses are inevitable. If the body reserves are too low to meet the nitrogen requirements for an extended period of time, death will result.

METABOLIC FECAL NITROGEN, BODY WEIGHT, AND NET PROTEIN COEFFICIENT RELATIONSHIPS. The absolute amount of MFN of a large deer is greater than that of a small deer (Figure 17-16). The effect of differences in the NPC is obvious. There is a slight curvature to the lines expressing this relationship, which indicates that

FIGURE 17-15. Metabolic fecal nitrogen in relation to the amount of field-weight forage ingested at three net protein coefficients. Each line includes deer ranging in weight from 20 to 100 kg.



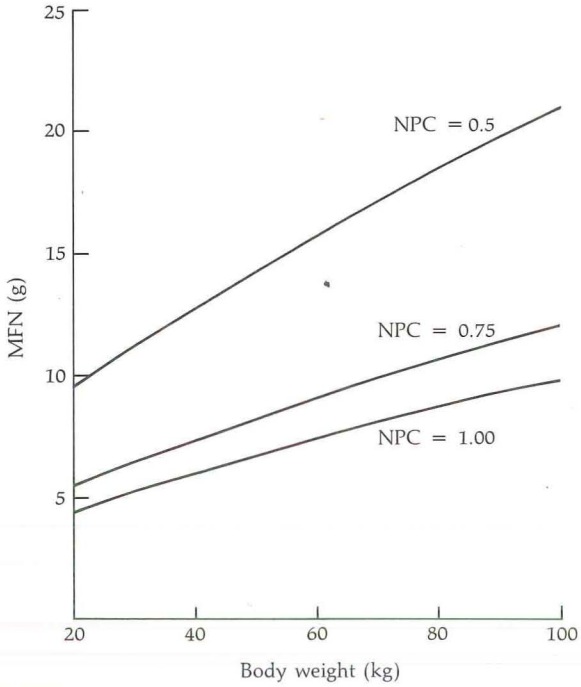


FIGURE 17-16. Metabolic fecal nitrogen in relation to body weight for three net protein coefficients.

large deer have *relatively* lower MFN than small deer. This is shown more clearly in Figure 17-17, in which MFN is expressed as a ratio, MFN (g): body weight (W_{kg}).

BODY WEIGHT, NET PROTEIN COEFFICIENT, AND PHYSICAL RUMEN CAPACITY RELATIONSHIPS. It is interesting to compare body weight, NPC, and the fraction of the physical rumen capacity used to meet protein requirements (Figure 17-18). A small

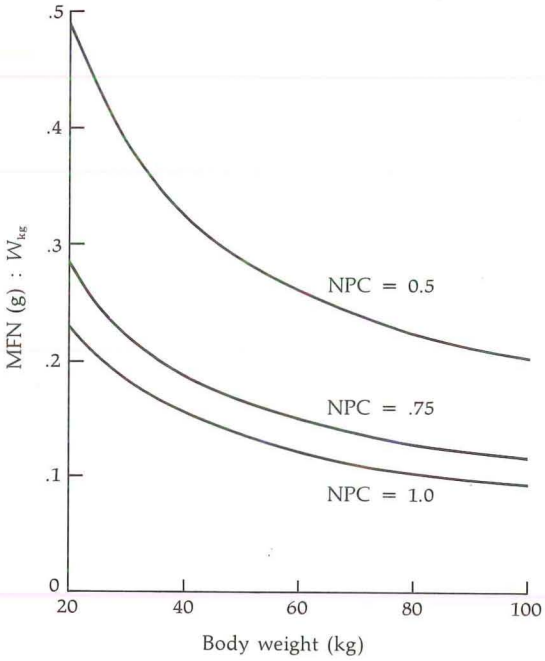


FIGURE 17-17. The ratio of metabolic fecal nitrogen to body weight (W_{kg}) illustrates that the smallest animal has a relatively higher metabolic fecal nitrogen output than the largest one. Data for three net protein coefficients are illustrated.

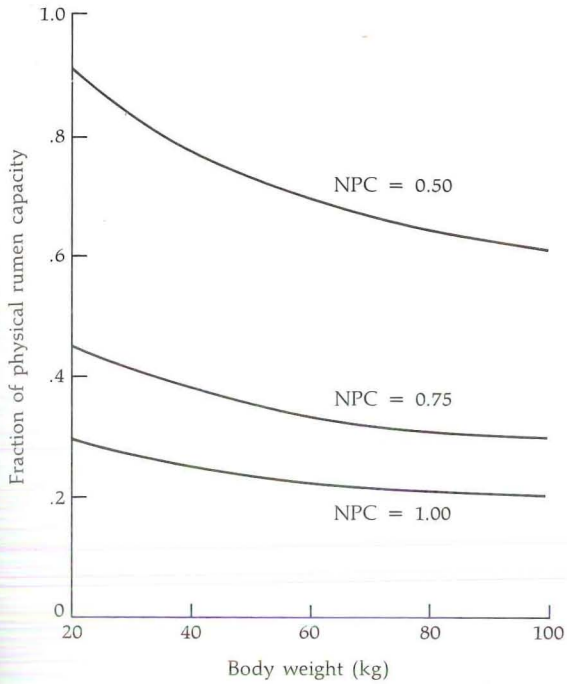


FIGURE 17-18. Fraction of the physical rumen capacity used to meet protein requirements for different net protein coefficients.

deer uses a greater fraction of its rumen capacity to meet protein requirements than does a large deer. The difference between deer of different weights is greatest at low NPCs. Body weight makes little difference for an NPC of 1.00, but such an NPC is biologically unrealistic because no animal is 100% efficient in the utilization of the protein in forage. An NPC of 0.75 results in some differences between the 20- and 100-kg deer, but the disadvantage for the smaller deer is still quite small. As the NPC is reduced to 0.50, the smaller deer are at a distinct disadvantage, with less space in the rumen for forage that can be utilized to meet production needs. Note also the relative spacings of the three NPC curves in Figure 17-18; the effect of reduction of the NPC from 0.75 to 0.50 is much greater than the effect of reduction from 1.00 to 0.75. This again illustrates the diminishing returns for the animal in relation to net protein values.

17-9 THE EXPRESSION OF CARRYING CAPACITY IN DEER-DAYS

Carrying capacity can be expressed in deer-days by dividing the amount of forage ingested per deer each day into the quantity available on the range. These calculations can be made on a protein base, by using the protein requirements of an animal to determine the amount of food that needs to be ingested, or on an energy base, by using its energy requirements to determine the ingestion. The quantity of forage available on the range is expressed in the model in terms of each species of forage, so that the number of deer-days that each forage will support—given the percentage of the diet composed of that forage—can be calculated.

If deer ate forages in strict proportion to their abundance on the range, all

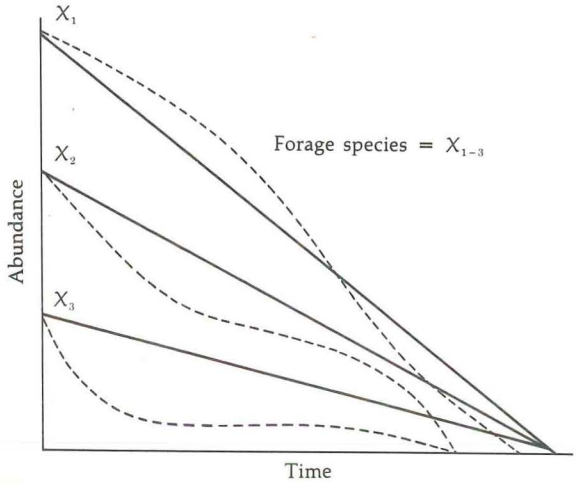


FIGURE 17-19. Changes in the abundance of forage species over time: solid lines indicate proportional utilization of each species; dotted lines indicate disproportionate utilization.

forages would be used up at the same time. This does not happen, however; some forages are depleted more quickly than others (Figure 17-19). Short-term (daily, if necessary!) shifts in diet can be analyzed with the model. Little is known about the amount of each forage consumed in relation to forage abundance in the field, however, so such precision is hardly necessary at this point in the analysis.

Forage abundance has been measured in three different stands in the vicinity of Ithaca, New York. Measurements were made at one-foot intervals from zero to six feet high. These data may be used to test the effect of differences in vertical stratification in relation to snow depths, as well as determining the total number of deer-days supported by each stand based on the requirements of the deer. In the calculations, the percentage of each forage in the diet has been taken as the percentage of each forage on the range; any preference for certain forages would lower the available number of deer-days. The actual numbers expressed in Figures 17-20–17-23 are somewhat arbitrary, but the relationships between the relative importance of such things as body weight, snow depth, and successional stages is clear.

EFFECTS OF BODY SIZE. The amount of food ingested to meet the requirements of a small animal is less than the amount ingested to meet the requirements of a large animal. The metabolic efficiency of a large animal is greater, however, so less food per unit of body weight is necessary to meet the requirements of a large animal. This is expressed in the exponent 0.75 in equation (7-2) for basal metabolism.

A comparison of weights from 20 to 100 kg indicates that the number of deer supported declines in a curvilinear fashion with increasing weight (Figure 17-20). The greater efficiency per unit weight of larger deer and its effect on the number of deer-days supported is striking if a range of possible deer weights are analyzed. More small deer can be supported, but the curvature of the line clearly indicates that the larger deer are relatively more efficient in utilizing the food supply. The

relationship between deer-days and deer weight shown in Figure 17-20 would be the same for any diet, unless there are compensatory differences in nutrient utilization by deer of different weights.

The curvature in the line showing the relationships between body weight and deer-days on an energy base is due entirely to the effect of the 0.75 exponent in the metabolic rate equation. It is interesting to see the importance of the relative efficiency of deer of different weights; the effect of the 0.75 exponent is much more dramatic in an ecological context such as the expression of carrying capacity than it is in the expression of heat production as shown in Chapter 7.

The energy requirements or "ecological metabolic rates" of free-ranging animals are higher than basal metabolic rates, of course. The energy requirements of deer of different weights vary because of behavior differences, differences in reproductive condition, and many other factors. Some of these variations are compensatory. Small fawns, for example, are at a disadvantage in snow because their legs are shorter than those of large deer. Small fawns, however, are less likely to be pregnant so their energy requirements do not include the metabolic cost of pregnancy. Smaller, subdominant animals may have a lower energy requirement because they do not have to maintain a high social position in the herd. The energy requirement may be lower because they need not be as alert as older deer; they can rely on older deer to signal approaching danger. These are interesting considerations, but it is doubtful if these factors compensate enough to equalize the effect of weight on the metabolic efficiency of small and large deer.

Some variations are additive in their effect on energy requirements inasmuch as smaller deer cannot reach the forage that larger deer can. As subdominant

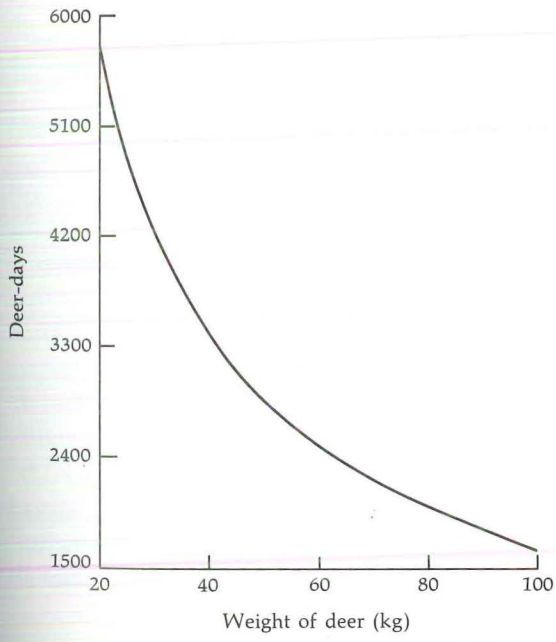


FIGURE 17-20. The number of deer-days supported in relation to deer weight in a mixed upland hardwood stand in winter.

members of a population, they are "last in line" for whatever food is available. The quality of this food is likely to be lower than that of food selected first by larger deer.

EFFECTS OF SNOW DEPTH. Calculation of the number of deer-days that each of three forest types near Cornell University will support shows the effect of differences in the vertical distribution of food in these stands. The reduction in deer-days in McGowan's Woods amounts to about 50% after the first foot (0–1) of forage is removed from the calculation. The removal of another foot of forage, from 1 to 2 feet, results in another reduction of approximately 50% (Figure 17-21). These reductions could be a result of the effect of snow, which would make this forage unavailable.

Measurements of the quantity of forage available to deer in an invasion zone between a stand of mixed hardwoods and conifers and an abandoned field in Connecticut Hill Game Management area south of Ithaca show that the effect of a foot of snow is much less important in that habitat (Figure 17-22). The reduction in deer-days is less than 10% when the first foot of forage becomes unavailable in that stand, with a further reduction of less than 20% when the second foot of forage is covered with snow. Most of the forage in this invasion zone is between 2 and 6 feet.

The effect of one foot of snow is quite different in a second-growth hardwood stand in the Connecticut Hill Area (Figure 17-23). The number of 30-kg deer-days is reduced from 300 to 8 when 1 foot of snow is on the ground. This is a result

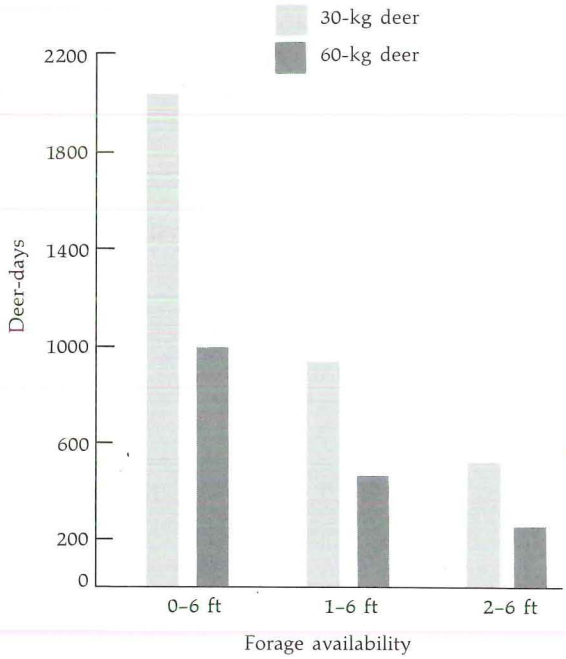


FIGURE 17-21. The number of deer-days per square mile in a second-growth hardwood stand with a comparison of snow depths of 0, 1, and 2 ft (calculated on a protein base).

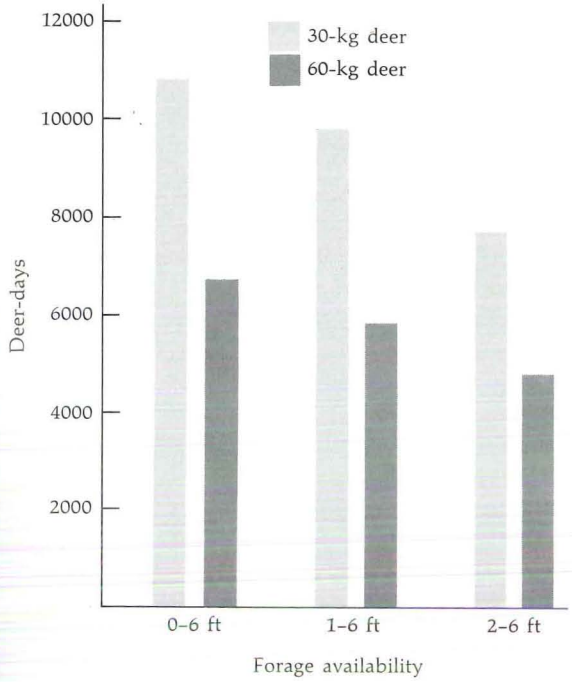


FIGURE 17-22. The number of deer-days per square mile in the invasion zone of an abandoned field with a comparison of snow depths of 0, 1, and 2 ft.

of a very uneven vertical distribution of forage. About 97% of the forage is seedlings located in the first vertical foot of the stand.

An interesting analysis of the effect of error in estimating net-energy coefficients in relation to the effect of a foot of snow on carrying capacity can be made. If the net-energy coefficient for each forage is varied $\pm$ 10%, the number of deer-days supported by the stand shown in Figure 17-23 varies from 270 to 330 for a 30-kg deer foraging at heights between 0 and 6 feet. This is a small variation compared with the effect of a foot of snow that reduced the carrying capacity from 300 to 8! In this particular case the effect of a foot of snow is far greater than the effect of experimental error due to estimation of the net-energy coefficient. This clearly indicates that the importance of errors or variation in one parameter cannot be determined until the importance of that parameter has been analyzed in relation to other factors.

The effect of 1 or 2 feet of snow on the total animal-environment relationship extends beyond a simple reduction in the food supply. Snow depths of 16 to 24 inches cause deer, especially smaller deer, to expend additional energy for walking. The reduction in the food supply plus the added energy requirements act together to reduce the carrying capacity. Further, snow may be a mechanical barrier causing deer to remain on well-traveled paths. The restricted movement further reduces the quantity of forage available to the deer, and they are forced to depend more and more on their body reserves.

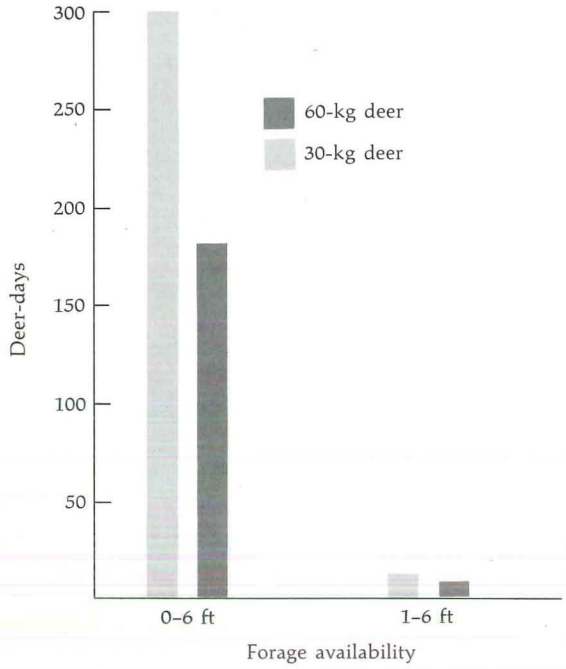


FIGURE 17-23. The number of deer-days per square mile in a second-growth hardwood stand in the Connecticut Hill Game Management Area south of Ithaca, New York. The effect of snow depths of 0 and 1 ft are shown.

FORAGE PRODUCTION AT DIFFERENT STAGES IN SUCCESSION. The number of deer-days expressed in Figures 17-21, 17-22, and 17-23 indicates the importance of successional stages in providing forage for deer. The invasion zone supports many more deer per square mile than either of the other stands. The second-growth hardwood stand on Connecticut Hill, which includes many seedlings but little else in the understory, supports an insignificant number of deer.

17-10 SUMMARY

Analyses of the interactions between a deer and its range clearly indicate that there are many relative and compensatory factors to consider. Because of such considerations, the idea of carrying capacity is best approached as a concept rather than a simple, definable entity. It may be that significant factors will be isolated, which can be used to quantify carrying capacity in a very practical manner. The identification of one or more significant factors is best made after a thorough analysis of animal-range interactions rather than by selecting a particular relationship and hoping that it proves to be suitable for practical use.

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