19

PREDICTING
POPULATION DYNAMICS

After analyzing animal-environment relationships within the two main concepts presented—the concept of homeothermy and the concept of carrying capacity—it is useful to conclude with a consideration of the relative importance of the different factors and forces that have been a part of the analyses. It is hoped that this summary will result in additional in-depth analyses of animal-environment relationships. The complexity of these relationships is so great that a significant amount of progress can only be made if there are many investigators working toward an understanding of the ecology and management of populations of free-ranging animals in their natural habitats.

19-1 ECOLOGICAL PRODUCTIVITY GRADIENT

Members of a population are dynamic entities whose position on an ecological productivity gradient vacillates. The idea of this gradient was first introduced in Chapter 1, in which animals were considered to be either dead or not dead. If they are dead, their contribution to the ecosystem is through the decomposition of body tissue with the resulting release of energy and nutrients. This is a slow process; it may take many years before the energy and matter contained in an animal's body is once again used in living tissue. Further, the net contribution of a dead animal to a subsequent biological process is always less than the gross energy contained in the body at the time of death because some energy is dissipated into nonuseful channels.

Consideration of the productivity of a living animal rather than factors that cause mortality is much more advantageous in a population analysis because of

the wide variation in potential productivity. Animals that are "not dead" exhibit a productivity potential varying from less than maintenance to maximum weight gains and full reproductive potential. Nonreproductive members of a population are, in some respects, a detriment to the population because they consume resources without contributing additional numbers to the population. Reproductive members contribute new animals. As the population grows, it may become desirable to harvest a percentage of the total population. *The population growth in each generation is far more dependent on conditions that affect the productivity of the living animals than on the number of animals that are removed by harvest or natural causes.*

19-2 THE RELATIVE IMPORTANCE OF DIFFERENT VARIABLES

ANIMAL REQUIREMENTS. The requirements for survival, growth, and reproduction vary throughout the biological year, with a deer's requirement for production being highest at the peak of the lactation period in the summer. At that time, the deer population is dispersed and forage quality is high, resulting in conditions that do not appear to cause an appreciable amount of mortality in the adult population. The effect of the nutritional status of females on the amount of milk produced and hence its effect on the growth and subsequent productivity of fawns is a relationship that needs to be investigated further within a total ecological context.

The importance of the growth rate in relation to reproductive capabilities is shown by data on a large captive deer herd in the Seneca Army Depot near Ithaca, New York. There appears to be a threshold weight that fawns must reach before they conceive (Hesselton, personal communication). The position of these deer on the productivity gradient is an important consideration in population ecology inasmuch as a nonreproducing fawn consumes resources without contributing to the population. This may not be bad, however. When range conditions are poor, fawn growth is reduced. At such a time there is little advantage in having a productive fawn class.

For many years, winter survival has been considered a serious problem in deer management. Each spring dead deer are counted in the northern regions, the cause of death usually classified as winter mortality. The deer may indeed have died in the winter, but the causes of death are not necessarily confined to the winter period alone. The condition of the deer at the beginning of winter is an important factor because it determines the amount of reserves an animal has to carry it through difficult periods when food is either unavailable or of low quality.

The timing of the spring dispersal is another factor that is related to the importance of body reserves at the end of winter. A late spring can cause either reduction in productivity or mortality since the body reserves are normally low at the end of winter. Further, the molt begins in March and the insulating value of the hair is reduced in late March and April. Rain is often a part of the spring weather pattern, and heat loss by evaporation from a wet coat may be quite large. These factors can combine to put an animal in a critical hypothermal condition, resulting in the depletion of body reserves at a rate even faster than normal.

There is an indication that the energy requirements of deer rise in the spring. The requirements for gestation are superimposed on this seasonal shift. Thus the timing of the spring dispersal from a wintering area may make the difference between the realization of full reproductive potential, the resorption of some of the fetuses, the mere survival of the deer, or mortality. Since it is difficult to determine the reproductive level of a free-ranging deer herd, it is likely that the effect of variation in reproductive success on population characteristics is not fully appreciated. Population models that include variations in reproductive rates that can be related to animal requirements in relation to the time of spring dispersal and the changes in the quality of the range should be used to analyze the potential importance of these factors.

RANGE SUPPLY.   The quantity of forage available on a range is a function of the successional stage of the vegetation and the ingestion rates of the consumers living on that range. The amount of browsing that occurs can affect the total range supply in two different ways. Some plants are stimulated by the removal of part of their current annual growth and forage production is increased by browsing. Too much browsing will cause a decrease in forage production, however, and high populations of wild ruminants can deplete their range supply to the point at which range recovery may take many years.

Canopy characteristics at various stages of plant succession are important determinants of the amount of forage produced within reach of the deer. As the canopy closes, forage production in the understory decreases. A lack of forage due to plant succession, changes in forage quality on a seasonal basis, and the disadvantages of the smaller deer in a population can all combine with severe weather conditions to cause high mortality. It seems apparent that detrimental forces have an additive effect, and if these forces all combine within a single year, both the number and the productivity of deer are noticeably reduced, especially in the younger age classes.

The quality of the forage also influences whether a deer's situation is critical. Low-quality forage is found on some soil types, and deer living on these soils may never reach their full genetic reproductive potential. This situation, coupled with severe winters and short growing seasons, may result in temporary population increases when the successional stage is truly optimum, but later reductions occur more frequently because of the effect of marginal-quality forage on the animal-range relationship. Under these conditions, the relative importance of weather conditions and other stress factors is greater and the rate of mortality is expected to be higher than in situations in which forage quality is generally high.

FACTORS AFFECTING BOTH ANIMAL REQUIREMENTS AND RANGE SUPPLY.   The relative importance of different winter shelter and cover conditions for deer and other ruminants has been discussed by biologists for many years. An analysis of the role of cover in relation to the distribution of energy and matter provides a firm basis for the evaluation of different cover types. Analyses of thermal relationships

of deer indicate that the most important thermal function of cover is in the reduction of wind. The added benefit from the additional infrared radiation from heavy overhead cover is insignificant at low temperatures. In fact, heavy overhead cover may be detrimental because it obstructs solar radiation, which could reduce the thermal gradients in an animal's hair layer. The thermal benefits from lying in the sun have not been analyzed in a quantitiative way yet, however. Further, forage production is less in a stand with a heavy canopy because of the reduction in radiant energy for photosynthesis.

Snow affects an animal's energy requirements as well as the amount of forage available. Its effect on energy expenditure may be less than expected, however. A deer struggling through deep snow, for example, cannot maintain that high rate of energy expenditure for very long, so movement patterns will be confined to trails. Thus snow serves as a mechanical barrier that regulates the distribution of deer and affects their energy expenditure.

Snow affects the amount of forage available by covering some of it and by preventing animals from reaching that which is located away from the trails. Under these conditions, a deer's intake of forage may be less than if it had an unlimited supply. Thus although snow may cause an ultimate reduction in a deer's energy requirement by confining its movement to trails, it also reduces the food supply so that the deer must depend on its fat reserve.

A crust formed on top of the snow can be a benefit to deer and other wild ruminants if it supports them, for it enables them to reach a new food supply. The occurrence of such crust conditions is beyond the control of the manager, however, so it should not be counted on as a way to compensate for other detrimental conditions. Its benefit is merely supplemental.

The effect of canopy density on snow accumulations can be either beneficial or detrimental to an animal. A heavy coniferous canopy intercepts snow, reducing accumulations on the ground. Reduced wind velocities under the canopy result in lightly falling snow that is less of a mechanical barrier. As the snow ages, it develops a large crystal structure, which is less susceptible to crust formation. Although these effects of snow may be considered a benefit to an animal, the snow also tends to trap the animal if it has sought shelter under the heavy cover during the storm. Deer restrict their movement to trails, reducing the area used and, consequently, the food supply available. When this happens, the fat reserve in relation to the size of a deer becomes very important. The amount of fat reserve is dependent on the condition of the summer and fall range. Thus winter mortality is only partially dependent on the density of deer in a winter concentration area.

The basic principle that underlies any consideration of the thermal benefits of cover in relation to an animal's metabolic processes is that these processes use food as a source of energy. Some of the energy used by an animal may come from body fat, but that fat deposit is the result of food eaten and assimilated earlier in its life. Solar radiation, infrared radiation from cover, heat conserved in the insulative layer—none of these can drive the metabolic machinery of the animal; they can only reduce a thermal gradient between it and its environment.

19-3   FACTORS TO CONSIDER IN POPULATION ANALYSES

Population analyses that merely include numbers representing a field situation have limited usefulness for predictive purposes. Extrapolations can be made from such models, but considerable risk is taken in doing so if the factors that cause changes in mortality or natality are not recognized or understood. Life tables are in this category; they are population models built on characteristics of the population at present and/or at different times in the past.

Population models *designed from* biological relationships *rather than from the effects* of these relationships can be used to predict population trends expected under a variety of conditions. Recognition of biological factors that affect populations and the many possible variations in these factors permits the building of a population model that is a multidimensional series of alternatives. The biologist looks upon this kind of a model as a series of analyses, with each analysis representing a different combination of forces that affect natality or mortality. The probability of occurrence of different situations can then be used to predict long-range trends.

The use of electronic computing equipment is absolutely essential for these kinds of analyses. Consideration of the many possible combinations of factors in relation to the different subgroups in a population might lead to the conclusion that the number of combinations is so great that they could never all be included.

19-4   POPULATION ANALYSES FOR $n = 1, 2, \ldots, n$

A frequent approach to the subject of population ecology is based on the establishment of a given population or cohort, measurement of the number of animals that die within that cohort, measurement of the number of animals in the cohort after the next reproductive period, and calculation of the mortality and natality rates from these figures. This is an oversimplification of this kind of analysis, of course, since many considerations can be made in relation to sex ratios, age ratios, different degrees of vulnerability to loss, and so forth. Many of these were mentioned in Chapter 18.

Many useful conclusions have been drawn from population analyses like those just mentioned. These kinds of data have been used to propose various theories of population control, with the recognition of the effect of some factors that seem to be density dependent and some that are density independent. This implies that the operational environment discussed in Chapter 2 needs to be considered in analyzing population growth. Some factors that affect mortality and natality rates are physical, such as weather. Physical factors are usually density independent, but the effect of physical factors may cause animals to crowd together, resulting in interrelationships that are dependent on the density of the population at that time.

This common approach is based on the numerical representation of a single animal as an entity. Its characteristics are often determined from an examination of the dead members of the species at a checking station. The use of hunter-kill data with respect to numbers alone is often used to calculate the population

growth, usually in combination with ground or aerial counts of the remaining population. A problem in using this approach is that it essentially removes the dynamics of an individual in relation to the rest of the members of a population from consideration, treating each animal as if it were equal to others, or, at most, dividing the population into sex and age categories, the two most commonly used population characteristics.

Analyses made with the models of homeothermy and carrying capacity presented in this book indicate clearly that there are distinct differences in thermal and nutritive relationships between animal and environment for deer of different weights. A small deer has been found to be at a disadvantage in just about every situation analyzed so far. The comparisons between small and large deer are nonlinear, indicating that there is a need for analyses of a range of animal sizes to determine the critical weights at which an animal is forced to choose alternatives (e.g., increase ingestion) in order to survive. The number of alternatives available to smaller deer is less than the number available to larger deer (e.g., smaller deer cannot reach as high for forage as larger deer), so smaller deer are usually in a more precarious balance than larger deer.

Recognizing these differences, I propose that students direct their thinking toward the living, productive members of a population, asking questions about these individuals that will permit them to understand the position of each individual on the productivity gradient. Specifically, I suggest that students begin considering the characteristics of a population of *one*, trying to determine its characteristics in time and space, with an understanding of the importance of these characteristics as the individual animal passes from birth through maturity and finally death.

A population of one can be extended to include two organisms that vary in one way only, and the effect of this variation can be studied in relation to productivity, resulting in a prediction of the production of new individuals and of new body tissue of the individuals under consideration. The result then is a model containing several individuals, each generated from the initial one or two under consideration. I call this procedure "building a population model from the inside out." It is a technique that forces consideration of the factors that affect the life of each individual. This has considerable ecological value, for it is each individual that must cope with the factors and forces confronting it each day in the natural world. If the individual is successful, productivity results, including individual gain and the production of a new individual.

MORPHOLOGICAL AND PHYSIOLOGICAL CONSIDERATIONS. A large number of animals is not necessary for the analyses of population trends in relation to different individual characteristics. Suppose that eight animals were considered, with two weighing 40 kg, two weighing 60, two weighing 80, and two weighing 100. The 40-kg animals are representative of fawns and the higher weights are representative of yearlings and adults. The effect of protein quality on animals of different weights can be extended to the effect of protein quality on population dynamics by considering weight changes and productivity of different weight groups. Data presented in Chapter 17 indicate that smaller animals are affected

most by a decline in protein quality. They may be unproductive, and selective mortality could cause the smaller animals to disappear from the population. The effect of this reduction in productivity would be observed for several years.

Another factor that could be analyzed in a population of eight or less is the effect of a late spring on the population. Small deer are in a precarious nutritive balance at that time, with a low safety margin in the form of body protein or energy reserves. Various dates of spring dispersal could be simulated to determine the effect of variation in the time that winter ends and spring begins on the productivity of deer of different sizes. Variations in the reproductive rates of deer of different sizes could then be used to determine the contribution of different weight classes to the population through reproductive processes.

By building a population model from the inside out, the builder is alerted to the effects of a number of possible changes in population structure. An awareness of significant factors allows for a more thorough analysis of population data gathered in the field. The causes for certain changes in field populations can then be understood conceptually, if not numerically, through the use of predictive models.

Analyses of ecological efficiency and natality in relation to body weight suggest that there might be important differences in the stability of populations having different proportions of age or weight classes. It is generally recognized that a younger population has a greater potential for growth because there are more animals approaching their maximum reproductive potential. Conversely, the younger-aged population also exists in a more precarious balance with its food supply. An older-aged population includes more animals that are past their prime, and their productivity will be less. Thus there is a greater potential for variation in numbers of smaller animals because external forces, such as heavy storms, low food quality, late-arriving spring weather, and the like, may have additive or multiplicative effects on the total population number. This general idea has long been recognized in population ecology; smaller animals with high reproductive potentials—insects, for example—exhibit marked population fluctuations over short periods of time. The same principle seems to apply to a single species if different sizes or weights are considered.

BEHAVIORAL CONSIDERATIONS.   The disadvantages of being a small deer, in terms of its requirements and the range supply, are further compounded by the subdominant position of smaller deer in a herd. The social structure of a deer herd is generally dominated by the adult doe. Doe dominance has been observed many times in encounters at feeding sites, and often a larger number of does than other members of a herd are trapped during winter trapping because the dominant doe moves into the trap first to feed. A study in Maine, designed to expose the effects of different cover types on the physical condition of deer (Robinson 1960), showed that the final condition of individual deer seemed related to their position of dominance in the pen.

A THEORETICAL AVERAGE DEER.   The preceding examples of relationships between biological variables and weight have been presented for discrete populations of

one animal each, with each population of one having a different weight characteristic. The different populations have been compared, and it has been shown that the smaller deer are at a distinct disadvantage in each of the relationships shown. The same general pattern emerged in Chapters 13 and 14, inasmuch as the smaller deer were shown to have many disadvantages in the maintenance of homeothermy.

Populations with different weight or metabolic structures can be compared by using a weighted-mean procedure in calculating a theoretical average deer to represent the entire population. This weighted-mean procedure can be used to take into account the number of deer in each weight class, the reproductive condition of the deer, and other factors that affect their requirements for protein, energy, and other essential nutritive elements.

The use of an average deer results in a loss of information and analytical capabilities for a population, however. The averaging of population characteristics tends to mask the dynamic and important relationships that affect the survival of an individual. Ingestion, for example, can be calculated for an average deer, but it has been shown that the relationship between the amount of forage ingested to meet minimum requirements and the size of the rumen is not constant for deer of all weights. The calculation of the rumen size of this theoretical deer would not take into account the disadvantage of being a smaller deer in a population. Thus it might be said that "on the average" theoretical deer will survive, but the smaller deer that constitute a portion of a population may well be at such a disadvantage that they will die.

The importance of considering the individual rather than the average for a population was illustrated further in the relationships between weight loss and initial body weight. An average weight loss could be calculated for all members of a population—0.5 kg day^{-1} was used—but this quantity is far more crucial to a small deer than to a big deer. A small deer cannot tolerate as great a weight loss as a large deer. The importance of weight loss must be analyzed in relation to initial and minimum body weight.

The amount of heat lost from a small deer is greater in proportion to its metabolic rate than the heat-loss–metabolic-rate proportion for a large deer. Convection is relatively greater from a small deer, it has a higher surface area per unit of body weight, and in general is at a disadvantage for survival throughout the winter period. The use of a theoretical mean deer for an analysis of the ability of deer to withstand cold conditions would result in the loss of recognition of basic principles of thermal exchange in relation to the geometry of the animal. Students are cautioned to use average values in any biological analysis *only if there is no loss of significant information when the individual animal is ignored.*

19-5   TIME IN RELATION TO BIOLOGICAL EVENTS

SEASONAL CHANGES IN ANIMALS AND PLANTS.   The concept of time was defined in Chapter 2 as a "measure of the intensity of life." This seems applicable to the wild ruminant; the requirements for protein and energy follow a sequence that tends to distribute the requirements throughout the year. White-tailed deer

gain weight after lactation ceases in late summer or early fall. Conception occurs most often in November, but the requirements for pregnancy do not accelerate until the last one-third to one-fourth of the gestation period. A deer has little more than survival requirements during the winter season. The winter coat is shed from March through May, and the cost of growing the summer coat coincides with maximum requirements for pregnancy. Lactation is a costly biological process, but lactating deer do little more than move about in the summer. They do not gain weight, the summer hair is retained until almost the end of the lactation period, movements are restricted to a home range of less than a mile, and there is foliage to hide in. In late summer and early fall, the summer coat is shed, lactation ceases, and weight gain begins again.

The biomass of a population becomes more stable at each successive trophic level. This is discussed in Jordan, Botkin, and Wolfe (1970) for wolf-moose relationships on Isle Royal. The factors that affect the survival of individuals within a population are age or weight specific. The moose population analyzed by Jordan, Botkin, and Wolfe has a high annual transfer of biomass from the first-year class, with another peak at about 12 years of age. This is to be expected inasmuch as the analyses discussed in earlier chapters reveal that younger, smaller animals are in a more precarious balance than are mature animals. As old age approaches, physiological efficiency again decreases, but its relationship to age is quite variable.

The range supply follows a sequence that coincides with the sequence of animal requirements. The weight-gaining period in the fall is simultaneous with the availability of seeds and fruits, which are usually rich in fats and oils. The falling of leaves is preceded by a redistribution of nutrients from leaf to stem, increasing the food value of current annual growth that will be used as browse later in the winter. The quality of the forage remains fairly constant throughout the period of dormancy, and it may not be high enough to support the daily requirements of deer, especially during periods of severe weather. The quantity of forage available is often limited, especially in areas with deep snows, which cause the deer to remain concentrated. Under these conditions, they are often forced to eat inadequate quantities of low-quality food. If their needs are not met by the range supply, their stored nutrients must be used.

THE IMPORTANCE OF SEASONAL CHANGES.   The physiological efficiency of animals of different weights within a population depends on the impact of environmental forces on the individual animal. The timing of plant growth and the storage of nutrients by the animal is a function of seasonal shifts in the energy balance of the earth's atmosphere, causing changes in weather patterns. The temporal occurrence of these weather patterns and their subsequent effect on both the animal and the range is most critical when body reserves are low, the animal is molting, plant growth is beginning, or some other change in either animal or plant is about to take place.

The analyses of homeothermy and carrying capacity lend considerable support to the idea that the time at which deer disperse at the onset of spring is especially important. Deer show an increase in metabolic rate in the spring, they molt, pregnancy begins to increase nutritive requirements, and body reserves are at

a low point. If deer cannot leave the winter concentration area because of continued cold temperatures that prevent the snow from melting as well as vegetative growth, they are trapped with accelerating requirements and a deteriorating range. This may cause many deaths. A more subtle effect on population growth may be in the reduction of fawn numbers due to resorption and an increase in the number of stillbirths. Fawn survival, especially during the first month or two, may also be related to the condition of the doe. Alexander (1962) has shown that lambs from well-fed ewes had twice as much fat reserve as those from poorly fed ewes. Those with a higher energy reserve were able to survive longer during starvation since body fat was their largest source of energy. Cold weather also affects the behavior of lambs, with less teat-seeking activity if the lambs are cold (Alexander and Williams 1966). Thus a cold, wet spring may affect both the doe prior to parturition and the fawn in the early stages of suckling.

Continued cold weather in the spring may have a greater effect on the energy requirements for homeothermy than the same kind of weather would have had earlier because of the reduced insulation quality of the summer coat. Further, spring rains may cause an increase in evaporative heat loss. This can become critical inasmuch as the amount of energy dissipated by evaporation is large. Thus a cold spring rain can have a relatively greater effect on energy requirements than severe cold in the winter.

VARIATIONS IN THE TIME OF BREEDING.   Another temporal variation of importance in population dynamics is the distribution of times of conception and parturition. An early fawn is more likely to be exposed to cold weather than a late fawn. Its mother may have a depleted energy and protein reserve because there has been less time between spring dispersal and parturition than there would be for a later birth. The early fawn has more time to grow to a maximum fall weight, however, so it may be in a better position to survive the following winter.

A doe that gives birth to a fawn early in the spring may terminate lactation at an earlier date than one fawning in July. This gives the doe a longer time in which to gain weight, resulting in a larger energy reserve for winter survival. The early-born fawns face the possible disadvantage of cold spring weather. The compensatory benefits of being born earlier compared with the disadvantages of cold weather have not been measured. These conditions can be simulated by computer analysis, but the limiting factor in such simulation is the lack of biological information about not only fawn growth and reproduction, but also the duration of lactation and subsequent growth of the females on the summer and fall range.

A prediction of the importance of the date of breeding, given information on birth weight and growth rate, is shown in the examples below.

EXAMPLE 1

Given: One adult female, bred November 15, gestation period 200 days, one fetus. Fawn birthweight = 3 kg. Fawn growth rate = 200 g day^{-1}, minimum weight for breeding, 38 kg.

Prediction: Productivity pattern of offspring in relation to time of birth.

Year 1: Female fawn born to adult doe on June 3.
Breeding weight reached on November 25.

Year 2: Female fawn born to yearling doe (drop the adult doe from consideration now; we are testing for the effect of birth date on the productivity of the offspring) on June 13.
Breeding weight reached on December 5.

Year 3: Female fawn born to yearling doe (year 2 fawn) on June 23.
Breeding weight reached on December 15.

Year 4: Female fawn born to yearling doe (year 3 fawn) on July 3.
Breeding weight reached on December 25.

Year 5: Female fawn born to yearling doe (year 4 fawn) on July 13.
Breeding weight reached on January 4.

Year 6: Female fawn born to yearling doe (year 5 fawn) on July 23.
Breeding weight reached on January 14.

The pattern described above continues in a linear fashion because the gestation period is a constant length and the growth rate is given as linear (0.2 kg day^{-1}). The fawns born in Year 5 and later may reach the minimum breeding weight after the bucks have lost their reproductive potential, resulting in a lack of conception even if the fawns could conceive.

There are many unnatural conditions in this example. Only female fawns were born each year; a $1:1$ sex ratio might have been used. A female fawn was successfully bred each year as long as it reached a minimum weight; however, a fawn may not necessarily conceive when a threshold weight is reached. The linear growth rate shown may not persist into December and January. The model works, however, subject to the limitation of the set of conditions stated. Let us use the conditions given in this model to test the effect of variation in the minimum breeding weight.

EXAMPLE 2

Given: See Example 1, except for minimum weight for breeding.

Prediction: Productivity pattern of offspring in relation to minimum breeding weights of 30, 32, 34, 36, 38, and 40 kg.

Year 1: Female fawn born to adult doe on June 3.
    Breeding weight of 30 kg reached on October 16.
    Breeding weight of 32 kg reached on October 26.
    Breeding weight of 34 kg reached on November 5.
    Breeding weight of 36 kg reached on November 15.
    Breeding weight of 38 kg reached on November 25.
    Breeding weight of 40 kg reached on December 5.

Year 2: Female fawns born to yearling does of minimum breeding weight of x kg, on
    May 4: Breeding weight of 30 kg reached September 16.
    May 14: Breeding weight of 32 kg reached October 6.

May 24: Breeding weight of 34 kg reached October 26.
June 3: Breeding weight of 36 kg reached November 15.
June 13: Breeding weight of 38 kg reached December 5.
June 23: Breeding weight of 40 kg reached December 25.

The productivity pattern, given different breeding weights, shows that the threshold weight for breeding without the delay and subsequent parturition is 36 kg, resulting in breeding on November 15 each year. If deer were to breed at weights less than 36 kg, the conception date would arrive earlier each year, with a 30-kg minimum breeding weight reached on September 16 of year 2, which may be before the bucks are able to service them. Thus there is no particular advantage to a lighter minimum breeding weight if the reproductive capability of the males is controlled by a constant seasonal factor such as day length.

The conditions given in this example are unnatural, too, of course, so the results are applicable only if confined to the stated model. The results indicate that variation in the minimum breeding weight can affect subsequent productivity, and this raises further questions. For example, the observed minimum breeding weight of fawns in one area in western New York is 65 pounds, or about 30 kg. The results from this example indicate that 30 kg is well below the predicted threshold of 36 kg. This raises additional questions, such as the relative importance of weight in relation to age. Maybe a large fawn, born early in May and well nourished, will not come into breeding condition until November because of other influences. In other words, its weight is sufficient, but the hormone balance necessary for reproduction may not be reached. Indeed, the dates of conception by fawns were shown to be confined to December in one of the displays of population dimensions in Chapter 18. Thus there should be further consideration of the factors regulating the reproductive biology of white-tailed fawns, including nutritional factors.

The birth date of a fawn also has an effect on the doe since a late-born fawn will most likely not be weaned as early as an early-born fawn. Since the lowest weights of the annual cycle are often reported for lactating females, an early fawn, weaned for a longer period of time prior to the onset of winter, releases the doe, enabling her to gain weight in the fall. A simple example of weight gains necessary to reach a given late fall weight follows.

EXAMPLE 3

Given: Birth dates of Year 2 in Example 2. Lactation period = 100 days. Weight of doe at end of lactation = 50 kg. Prewinter (December 1) weight desired = 70 kg.

Prediction: Weight gains needed to reach 70 kg by December 1.

May 4 birth of fawn: 0.18 kg day^{-1} = 0.40 lb day^{-1}
May 14 birth of fawn: 0.20 kg day^{-1} = 0.44 lb day^{-1}
May 24 birth of fawn: 0.22 kg day^{-1} = 0.48 lb day^{-1}

June 3 birth of fawn: 0.25 kg day^{-1} = 0.55 lb day^{-1}
June 13 birth of fawn: 0.27 kg day^{-1} = 0.59 lb day^{-1}
June 23 birth of fawn: 0.29 kg day^{-1} = 0.64 lb day^{-1}

Now suppose that 0.25 kg day^{-1} (0.55 lb day^{-1}) was the maximum weight increase possible. The doe bearing a fawn on June 13 would reach a prewinter weight of 68 kg. A subsequent 30% loss in weight that winter would put the doe and her fawn 3.4 and 4.5 kg below the previous summer's minimum, respectively. This may result in a loss of reproduction, although the doe might survive.

These examples illustrate an approach to an analysis of productivity that starts with a single animal in a simple model and progresses to an array of values that might be present in a population of many animals. The next step in building this type of population model is to determine the distribution of these values in a population. There are data in the literature for many of these. Conception dates were given in Chapter 18 for deer in northern and southern New York and for deer in adult and fawn age classes. The distribution of deer in these classes can be related to the distribution of birth dates of the fawn, the distribution of weaning, and the distribution of weight gains necessary to reach a given prewinter weight by a given date. In other words, the examples given can be applied to real populations. Combinations of conditions that result in predicted distributions that are similar to observed distributions stimulate thought concerning the feasibility of these conditions in the wild. If the combinations are unrealistic, the model must be modified to correct for the disparities between the theoretical and the real. If the combinations are realistic, the next step is to make the analysis less descriptive and more analytical. Logical questions follow, centered on such things as the constraints affecting the biological potential for weight gains, the factors regulating the phenology of breeding, and other factors that regulate productivity.

If all were known about the factors that affect productivity, predictions could be made about numbers, mortality rates, natality rates, trophic levels, and all of the other characteristics that are considered in looking at a population as a whole. In other words, the analytical ecologist who starts with a population of one should eventually meet the population ecologist who works with large numbers of animals. At that time, the analytical ecologist will have explanations for the many changes observed by the population ecologist, and the population ecologist will be in a position to present comprehensive equations that represent the effects of these biological functions over appropriate time periods.

This approach relies heavily on a knowledge of the biological factors affecting productivity. Biological systems are always complex, so many alternatives to given conditions or constraints can be expected, and the perfect biological model will probably never be built. The process described is of value, however, since it forces consideration of the processes involved in organism-environment relationships. If these processes are not understood, then the management of natural resources can continue only on the basis of opinion. Chapter 20 includes a discussion of the need for establishing a firm biological base for the decision-making process.

LITERATURE CITED IN CHAPTER 19

Alexander, G. 1962. Energy metabolism in the starved new-born lamb. *Australian J. Agr. Res.* **13**(1): 144–164.

Alexander, G., and D. Williams. 1966. Teat-seeking activity in new-born lambs; the effects of cold. *J. Agr. Sci.* **67:** 181–189.

Jordan, P. A., D. B. Botkin, and M. L. Wolfe. 1971. Biomass dynamics in a moose population. *Ecology* **52**(1): 147–152.

Robinson, W. L. 1960. Test of shelter requirements of penned white-tailed deer. *J. Wildlife Management* **24**(4): 364–371.

IDEAS FOR CONSIDERATION

Develop very simple models of very small populations of any species, adding factors only if the effect of each factor can be predicted. Remember that the main purpose of this exercise is the demonstration of mechanisms, and not the display of real numbers for large populations.

SELECTED REFERENCES

Burger, G. V., and J. P. Linduska. 1967. Habitat management related to bobwhite populations at Remington Farms. *J. Wildlife Management* **31**(1): 1–12.

Gross, J. E. 1969. Optimum yield in deer and elk populations. *Trans. North Am. Wildlife Nat. Resources Conf.* **34:** 372–387.

Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *J. Wildlife Management* **32**(2): 350–367.

Silliman, R. P. 1969. Population models and test populations as research tools. *BioScience* **19**(6): 524–528.