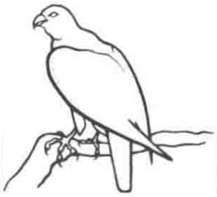
CHAPTER 5



Population Ecology

> ***Living as we do in a world which has been largely denuded of all the large and interesting wild mammals, we are usually denied the chance of seeing very big animals in very big numbers. If we think of zebras at all, we think of them as "the zebra" (in a zoo) and not as twenty thousand zebras moving along in a vast herd over the savannahs of Africa.***
>
> **C. Elton (1927)**

Among the more spectacular members of the rich mammalian fauna that occupies the African continent are two large ungulates, the roan antelope (*Hippotragus equinus*) and the sable antelope (*H. niger*). The roan antelope (Fig. 5-1) inhabits open or lightly wooded land whereas the sable antelope (Fig. 5-2) travels among the acacias of the savanna. In recent decades sable and roan antelopes have been declining in the southern portions of their range.

In the nation of South Africa attempts are being made to preserve and assist in the recovery of these two species by designating large tracts as nature reserves. Because sable and roan antelopes were locally extirpated, animals were live-trapped in the wild, transported, and released on the nature reserves. Growth of their populations in many of the 2,800–13,000-ha reserves has been slow and, in recent years, some herds have declined drastically.

When wildlife biologists David Wilson and Stanley Hirst (1977) were asked to determine why numbers of these two antelopes declined on the South African reserves over the past few decades they were presented with a basic problem in population ecology. Their task was to identify specific causes for the decline of roan and sable antelopes and to make practical recommendations for their preservation and management. Observers had speculated that such factors as habitat deterioration, encroachment by agriculture, illegal or uncontrolled hunting, and (among roan antelope) anthrax were responsible for the decline. But no one really knew.

The methods used by Wilson and Hirst as they began to unravel the mysteries of the disappearing antelopes were not unique to studies of African mammals. Similar methods are employed by biologists working with various animals, whether scarce or abundant, whether they are caribou (*Rangifer tarandus*) in Alaska, cottontail (*Sylvilagus* spp.) in Virginia, or bobwhite (*Colinus virginianus*) in Illinois. These are problems of population management that encompass basic concepts of population ecology. An extensive body of literature exists on theory of population ecology, much of which is still evolving, as ecologists attempt to explain such phenomena as population cycles and general causes for the regulation of numbers of animals. Most of the theoretical population literature is beyond the scope of this book. The purpose of this chapter is to present basic concepts of population ecology and to describe approaches useful to biologists who must solve practical problems involving management of wildlife populations.

Some Definitions

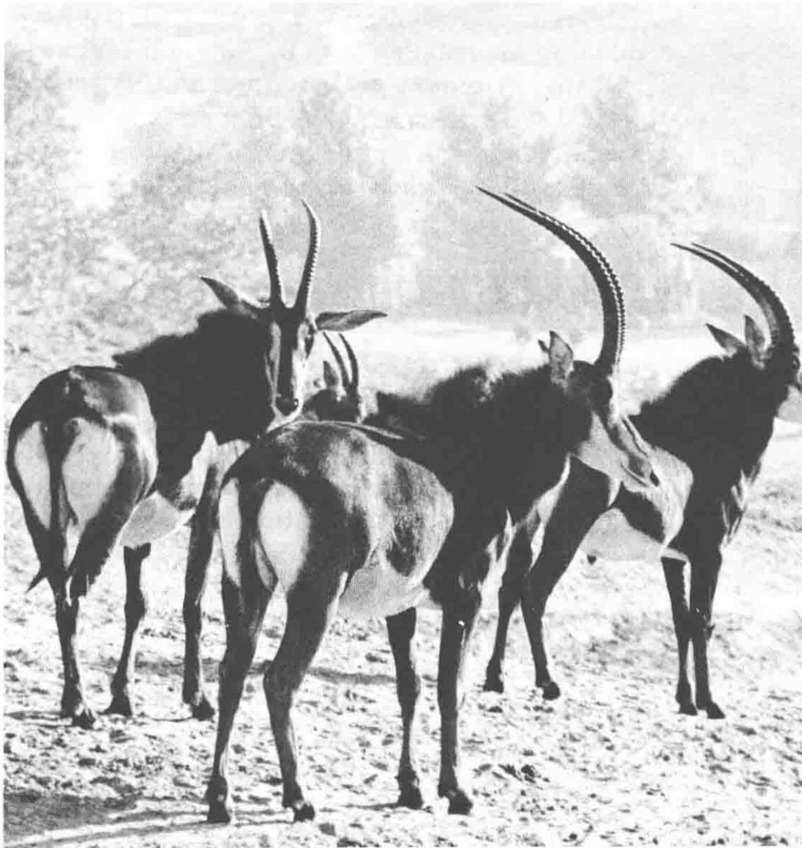
A *population* is defined as a group of organisms usually of the same species occupying a defined area during a specific time. Populations have characteristics not possessed by individual animals. For example, a population has *density,* meaning a certain number of individuals per unit area, such as 20 blue grouse (*Dendragapus obscurus*) per 100 ha, or 144 sugar maples (*Acer saccharum*) per ha. A population has a *birth rate* or *natality,* the number of births per thousand, per hundred, or per individual per year, and a *death rate* or *mortality,* the number of deaths per number of individuals per year. A population has an *age structure*—that is, a distribution of numbers of individuals of various ages. Naturally, the proportion of individuals of breeding age in a population affects the birth rate, strongly influencing its growth. Likewise, the proportion of old animals affects the death rate. Populations also have sex ratios, influencing reproductive potential.

The Logistic Equation

It has been recognized for some time that animals tend to give birth to many more individuals than will survive to breeding age (Malthus 1798; Darwin 1859). If deaths did not offset births the result would be an

Figure 5-1. The roan antelope, widely distributed in Central and Western Africa, has declined in numbers in recent decades, attracting the interest of wildlife ecologists. (Photo courtesy of the San Diego Zoo.)

Figure 5-2. The sable antelope, an inhabitant of the African savannas, with the roan antelope was the subject of an intensive population study by Wilson and Hirst (1977). (Photo courtesy of the San Diego Zoo.)



infinitely growing population. Under certain ideal conditions a population for a time can show a rate of growth that is exponential—that is, growing at an ever-increasing rate. Such conditions may occur when a population is introduced into a new and favorable environment. No shortage of food, cover, or space exists, and no disease, parasites, or predators affect any individuals. The birth rate is maximum, limited only by the reproductive physiology of the species; and the death rate is minimum with deaths occurring only from old age. Such conditions have been created in the laboratory for yeast cultures and mouse populations that were provided with room to grow and plenty of food. The equation for such growth is conventionally expressed as:

$$\frac{\Delta N}{\Delta t} = rN$$

where ΔN = change in number
Δt = change in time
r = the "per head" maximum potential growth rate
N = number of individuals in a population

As an example, suppose we have a population of 50 individuals (N) and each individual has the average capability of contributing one fourth (0.25) of an individual to the population in a given unit of time (r). The change in number per unit time ($\Delta N/\Delta t$) would be expressed as:

$$\begin{aligned} \frac{\Delta N}{\Delta t} &= rN \\ \frac{\Delta N}{\Delta t} &= 0.25(50) = 12.5 \end{aligned} \tag{1}$$

The answer, 12.5, is the number of individuals that is added to the population in the time interval, t. This number then must be added to the original population (N_t) to obtain the number in the new population (N_{t+1}), so that our new population is

$$\begin{aligned} N_{t+1} &= N_t + \frac{\Delta N}{\Delta t} \\ N_{t+1} &= 50 + 12.5 = 62.5 \end{aligned} \tag{2}$$

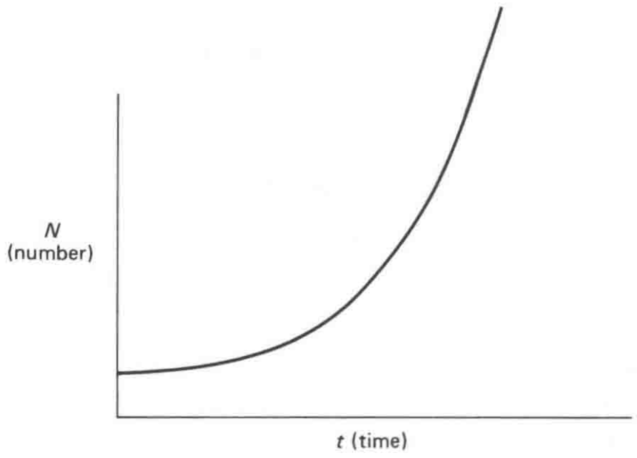
For the next time step we simply repeat the process using the same r value (0.25) but a new N (62.5), to calculate the number added to the population:

$$\begin{aligned} \frac{\Delta N_{t+1}}{\Delta t} &= 0.25(62.5) = 15.5 \\ N_{t+2} &= N_{t+1} + \frac{\Delta N_{t+1}}{\Delta t} \\ N_{t+2} &= 78 \end{aligned} \tag{3}$$

As one can see by continuing this process, the population will grow at an ever-increasing rate (Fig. 5-3). The integrated form of the equation is: $N_t = N_o e^{rt}$, where N_t represents the population at t time intervals, N_o is the original population, r is the per head potential growth rate, e is the base of natural logarithms, and t is the time interval by which r is expressed. Such an equation is most useful for populations of organisms such as bacteria, yeast, some insects, and possibly some small mammals in which breeding and growth is continuous. For most wildlife populations, which have a distinct breeding season, growth takes place in steps, and equations (1) and (2) are more appropriately used.

Under what conditions might we expect a wild population to express exponential growth? The happy circumstances of practically unlimited food and no biological enemies of whatever size occur very rarely in nature. But there have been a few instances that have come close to such circumstances and that have been

Figure 5-3. Growth of a population with unlimited food and space, **ΔN/Δt = rN.**



recorded by biologists (Dasmann 1964). These invariably occur when a population is introduced into a new and favorable environment that has been unoccupied previously by its species. Of the several cases reviewed by Dasmann, only one population, that of white-tailed deer (*Odocoileus virginianus*) introduced to the George Reserve in Michigan, expressed exponential growth (O'Roke and Hamerstrom 1948). In 1928, two bucks and four does were introduced into the 480-ha deer-proof fenced enclosure. By 1934 there were 164 deer. Other rapid growth rates occurred among ring-necked pheasants (*Phasianus colchius*) introduced to Protection Island, Washington, and European reindeer (*Rangifer tarandus*) introduced to St. Paul Island off the Alaska coast, but these populations showed less than maximum growth that might be expected under totally favorable circumstances.

Obviously, no population can grow exponentially for very long. The supply of food may not meet the demand of the ever-increasing population, space or cover availability may be limiting, predators may respond to the large numbers of prey, or disease may spread. Either birth rates decline, death rates increase, or both, so that eventually the population must stop growing. The greater the size of the population, the greater its dampening effect on the growth of the population. This effect has been mathematically defined and applied to the growth equation as follows:

$$\frac{\Delta N}{\Delta t} = rN \; \frac{(K - N)}{K}, \qquad (4)$$

where K is defined as the maximum number of individuals the environment can sustain. As the population (N) approaches K, $K - N$ approaches zero so that when a population gets very large relative to the number the environment can sustain, its growth rate becomes nearly zero. That is, its potential growth rate (rN) is multiplied by the factor $(K - N)/K$.

For example, suppose the same population we considered earlier with an r of 0.25 has 990 individuals and the maximum number supportable by the environment is 1000:

$$\frac{\Delta N}{\Delta t} = 0.25(990)\left(\frac{1000-990}{1000}\right)$$

$$= 247.5(0.01)$$
$$= 2.5$$

$$N_{t+1} = N_t + \frac{\Delta N}{\Delta t} = 990 + 2.5 = 992.5$$

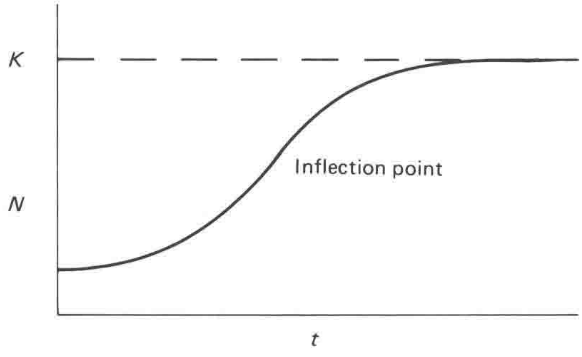
So instead of the population growing by 247 individuals as it would without any limitations, it grows only by 2.5 individuals, owing to limitations placed upon it by the finite environment. Equation (4) is known as the logistic equation. The curve it produces is *sigmoid* (**S**-shaped) and is illustrated in Figure 5-4.

Populations may sometimes exceed the maximum number that can be sustained by their habitat. In such an occurrence the term $(K - N)$ is negative and therefore $\Delta N/\Delta t$ is negative, resulting in a decrease in numbers.

The term K often is referred to as the *carrying capacity*. One must keep in mind that carrying capacity for animals can change from time to time as food production, cover availability, water availability, and other environmental factors vary with the seasons and successive years. Factors such as territorial behavior and response to crowding may interact with these external factors, so that growth of a population may slow down before food, water, or cover shortages are measurable in the habitat.

A factor that causes higher mortality or reduced birth rates as a population becomes more dense is referred to as a *density-dependent* factor. That is, if the probability of an individual being born or surviving is lower as numbers of animals in the population become higher, a density-dependent factor is acting to restrict

Figure 5-4. Growth of population with a maximum number of individuals that can be sustained by the environment, $\Delta N/\Delta t = rN(K-N)/K$.



population growth. Such factors include food supply, predation, disease, and territorial behavior. There are few density-independent factors, and they are mainly related to weather, such as cold, rain, and floods. Usually populations in the central portions of the geographic range of their species are limited by density-dependent agencies. Near the periphery of the range, however, where habitat may be marginal and random weather fluctuations may exceed the tolerance of nearly all animals in the population, density-independent factors may control population numbers (Krebs 1978). Such is the case with bobwhite in the northern parts of their range, where severe winters almost invariably result in a drastic reduction in quail numbers (Leopold 1931). Lack (1951) documented a similar effect on herons wintering in England.

The logistic equation is based purely on operation of density-dependent factors. If a fatal flood or snowstorm strikes at some point, the irregularity in population growth will not be explained by the logistic equation.

The logistic equation, for the wildlife biologist, is useful in illustrating general principles of population growth and the theoretical effect of carrying capacity on reducing or stopping population expansion. The early portion of the sigmoid curve can serve as a theoretical model with which the manager can compare the growth rate of the population being managed. A value for r can sometimes be obtained from knowledge of natality and mortality of the species under ideal captive conditions or from potential birth rates and longevity information in the field. If population growth is close to the growth rate predicted by the early phases of the logistic equation, there is little the manager can do to increase growth of the populations.

There is a further practical application of the logistic equation. If a student runs through the equation, setting N at various levels, it will be discovered that the largest value of $\Delta N/\Delta t$ is obtained when N is half of the carrying capacity. At half the carrying capacity an inflection point occurs in the growth curve (Fig. 5-4), the point at which population growth changes from an increasing to a decreasing rate. In managing for maximum yield of a population, it is therefore desirable to attempt to keep the population at about half of the carrying capacity. For example, using the previous hypothetical population with K of 1000 and r of 0.25, and $N = \frac{1}{2}K$:

$$\frac{\Delta N}{\Delta t} = 0.25(500)(\frac{1000-500}{1000}) = 62.5$$

The maximum number of individuals that can be produced in a unit of time is about 62. At any other N the number produced is fewer.

The factor, $(K - N)/K$, in the logistic equation, has no biological meaning or influence by itself. It must, in a real population of animals, represent some modification of birth rates or death rates. Therefore, the field biologist usually seeks an explanation for increasing or decreasing numbers of animals by examining the ratio of birth rates to death rates and the reasons for irregularities in either or both.

Most animals dealt with by wildlife managers reproduce seasonally, producing an annual spurt of offspring. Only if we stand back and view such a population over 50 or 100 years would these spurts become less visible. In such a long period of time comparisons with the logistic equation could be made by wildlife biologists; but management results frequently are required in a much shorter time and the wildlife manager must use other methods to assess the health of a population and evaluate its growth.

Field Studies

Returning to the African antelopes, Wilson and Hirst (1977) noted that population limitation could be effected through poor reproductive performance brought about by physiological factors, or by increased mortality among juveniles or adults. They set about to identify the main factors that were impeding the growth of the antelope populations on Transvaal Nature Reserves first by reviewing available literature on their food and cover. These animals were both found to be specific in their feeding and habitat requirements. Because the soil on several of the nature reserves was poor, they decided to concentrate on feeding habits, food, and nutrient availability, habitat selection and availability, and seasonal body condition, especially of breeding females.

With these factors in mind, they moved into the field, particularly the Percy Fyfe Nature Reserve, a primary study area that contained both sable and roan antelopes, and three other reserves in Transvaal. A reserve in Rhodesia (now Zimbabwe), where these two species thrived, served as a basis for comparison. Every day for seven months, with binoculars and a tough vehicle, they made detailed observations of two herds of antelope, one of each species, and, for three years beyond that, antelope on two reserves were watched intensively. When a calf would disappear a team of 16–20 searchers would comb the area to find it, dead or alive. Blood samples were taken from captured living animals; and, with recently dead animals, digestive tract contents were collected, and smears and sections were taken from the spleen, liver, kidney, lung, heart, adrenals, lymph glands, and brain. Such organs and tissues were examined for lesions and for parasites. Healthy live animals were immobilized with a tranquilizer gun and examined and fitted with colored collars for individual identification. Species and densities of vegetation were recorded and soil fertility assessed in their search for specific factors that caused the antelope populations to decline.

Among sable antelope studied intensively on two reserves, pregnancy rates were 100 percent when a bull was present during the May–July mating season. In a herd in which females were divided and a bull was not in full-time attendance, only 50 to 70 percent of the potentially breeding females were pregnant. Even where pregnancy rates were high, however, antelope less than two years old suffered high mortality.

Wilson and Hirst found that these young animals carried heavy infections of four different protozoan parasites. Although these parasites appeared to be important in causing death of the young antelopes, further study revealed that parasites were fatal only if the young antelopes were in poor nutritional condition. The researchers then compared body condition, as indicated by body weight, blood plasma proteins, packed cell volume of blood, and albumen content of the blood, between antelopes from the Transvaal, where populations were doing poorly, and Rhodesia (Zimbabwe), where populations were thriving. The Transvaal animals were in very poor condition.

This led Wilson and Hirst to examine the Transvaal range, analyzing nutrient availability in soil, water, and vegetation collected from preferred feeding areas, and animal tissues (liver, blood, and milk). Deficiencies in phosphorus, selenium, and protein were found in food plants during the critical dry season. On one reserve Wilson and Hirst found, by examining digestive tract contents and observing feeding behavior of large herbivores, that competition from zebra (*Equus* spp.), water buck (*Kobus ellipsiprymnus*), and impala (*Aepyceros melampus*) limited the amount of food available to sable antelopes.

Roan antelope bred throughout the year, with a gestation period of about 275 days and estrus occurring 2–3 weeks after parturition (giving birth). Thus, female roan antelopes could give birth to a calf every 10–10.5 months. Sable antelope, on the other hand, had a shorter gestation (240–248 days) but bred only once a year. Bulls were capable of producing viable sperm at 16–18 months. In smaller reserves, the dominant herd bull of roan antelope sometimes killed young maturing bulls, thus disrupting breeding and reducing the population. Breeding success of sable antelope was satisfactory.

Wilson and Hirst found that, although numbers of sable antelope on the relatively small Transvaal reserves were not high (less than 100 animals), the densities there (up to 9/km^2) were as high as, or higher than those of good populations in Rhodesia (Zimbabwe). Given the competition for food and the lower quality of range, the biologists concluded that decline in antelope numbers in the Transvaal would be expected.

They recommended that two Transvaal reserves be abandoned for conservation of sable antelope on the basis of nutritional and space inadequacy. In other reserves they recommended use of salt licks to provide lacking minerals, fertilizing and burning the range to enhance protein availability in forage, and maintaining lower densities of antelope to reduce strain on the limited food resources.

Births and Deaths

The antelope study of Wilson and Hirst (1977) illustrates the elements of an excellent study of a population with management objectives. Such study involves investigation of adequacy of habitat, specifically nutrition in this case, and its effects upon birth and death rates. A population grows according to the simple equation:

$$r = b - d$$

where r = actual growth rate of the population

b = birth rate
d = death rate

In some populations animals moving in or dispersing from a population may also play a role in its growth rate. The equation then becomes:

$$r = (b - d) + (i - e)$$

where i = immigration
e = emigration

A rate represents a change per unit time. Growth rate is the number of individuals added per individual in the population per week, per month, or per year. For example, suppose in a population of 1000 cottontails there are in a year 3000 rabbits born. This represents a per head birth rate of 3.0. During the same period, to have a stationary population, we must have a per head death rate of 3.0, which means that for every individual present in the spring population three must die over the course of the year. This would offset the per head birth rate of 3.0. The population growth would then be zero ($r = 3.0 - 3.0 = 0$).

Birth rates and death rates differ with age structure and sex ratios of populations. If there are relatively many females of prime reproductive age, naturally a population will reproduce faster than one with few females at such an age. Therefore, the wildlife biologist, to understand population growth, should consider the following seven characteristics pertaining to birth rates:

1. Age of sexual maturity of both males and females.
2. Length of the gestation period.
3. Sex ratios.
4. Whether species is monogamous or polygamous.
5. The number of females that breed at each age.
6. Number of young per female of various ages.
7. Influence of nutritional condition on reproduction.

The information required must be obtained by careful sampling of animals in the field, examination of their reproductive tracts, and controlled studies of animals in captivity.

Regarding mortality, the wildlife manager should have information on causes of mortality and the age groups most affected. Specific information on mortality is more difficult to obtain than on natality and therefore remains vexing for wildlife managers. Animals that die or are killed in the field usually do so out of sight and often are consumed by predators, scavengers, or decomposing organisms before biologists can locate them. Development of miniature radio transmitters in the past two decades has permitted researchers to monitor some animals in a population and frequently to locate a radio-marked animal shortly after its death. Such a method has given us some data on causes of mortality (Schladweiler and Tester 1972; Mech 1977a). Often the immediate cause of death of an animal may be only a symptom of some other factor that makes the animal more vulnerable to mortality. Errington (1967) observed that although many muskrats (*Ondatra zibethicus*) in crowded populations were killed by minks (*Mustela vision*) they were already suffering from malnutrition caused by competition for food. They were, as he put it, "walking corpses" destined to die soon anyhow. In the African antelope study of Wilson and Hirst (1977), infection by protozoan parasites was the immediate cause of death, but animals in good range and in good nutritional condition were able to survive the protozoan infections. Among bighorn lambs (*Ovis canadenis*) in the Rocky Mountains, many die of lungworm infection, but only if the summer weather is cool and damp (Woodard 1974).

Life Tables and Survivorship Curves

Comparisons of mortality between populations can be made by use of *life tables* and *survivorship curves.* A life table is a systematic means of describing mortality as it affects various age groups in a population. Deevey (1947) published a classic review of life tables for natural populations of animals. Murie (1944) described mortality of Dall sheep (*Ovis dalli*) in Mount McKinley National Park, Alaska. Over a period of several years he collected skulls of sheep found in the park. The horns of sheep grow in annual bursts, leaving a ring between each annual increment so that the age of a Dall sheep can be estimated by counting annual growth segments. From 608 sheep Murie constructed the life table shown in Table 5-1.

The columns of a life table are as follows:

TABLE 5-1. Life Table for the Dall Mountain Sheep (Ovis dalli) Based on the Known Age at Death of 608 Sheep Dying Before 1937 (Both Sexes Combined).[a]

x	x'	d_x	l_x	$1000\ q_x$	e_x
Age (Years)	Age as Percent Deviation from Mean Length of Life	Number Dying in Age Interval Out of 1000 Born	Number Surviving at Beginning of Age Interval Out of 1000 Born	Mortality Rate Per Thousand Alive at Beginning of Age Interval	Expectation of Life, or Mean Life-Time Remaining To Those Attaining Age Interval (Years)
0–0.5	−100.0	54	1000	54.0	7.1
0.5–1	−93.0	145	946	153.0	—
1–2	−85.9	12	801	15.0	7.7
2–3	−71.8	13	789	16.5	6.8
3–4	−57.7	12	776	15.5	5.9
4–5	−43.5	30	764	39.3	5.0
5–6	−29.5	46	734	62.6	4.2
6–7	−15.4	48	688	69.9	3.4
7–8	−1.1	69	640	108.0	2.6
8–9	+13.0	132	571	231.0	1.9
9–10	+27.0	187	439	426.0	1.3
10–11	+41.0	156	252	619.0	0.9
11–12	+55.0	90	96	937.0	0.6
12–13	+69.0	3	6	500.0	1.2
13–14	+84.0	3	3	1000.0	0.7

Source: Deevey (1947); original data from Murie (1944).

[a] A small number of skulls without horns, but judged by their osteology to belong to sheep nine years old or older, have been apportioned *pro rata* among the older age classes.

x = An appropriate time interval.
l_x = The number of animals living at the beginning of interval x. It is traditional to convert whatever sample size one has to 1000 at the beginning of the l_x column, representing 1000 animals born or hatched.
d_x = The number of animals dying during interval x.
$1000\ q_x$ = The proportion of animals that die per interval x. It is computed as follows: $1000\ q_x = (d_x \div l_x) \times 1000$.
e_x = The life expectancy expressed as the number of additional intervals an individual animal can expect to live at the beginning of interval x.

The calculation of e_x involves a few extra calculations, as follows:

$$e_x = \frac{T_x}{l_x},$$

and

$$L_x = \frac{l_x + l_{x+1}}{2},$$

or the average number of animals at the midpoint of an interval x.

T_x is the sum of the L_xs from the bottom of the table up through the desired x interval.

Biologists often are asked questions such as, “How long does a robin live?” or “How long does a mule deer live?” The answer to such questions depends upon what age the animal has achieved. The American robin (*Turdus migratorius*) can live to be seven years old, but the probability of a newly hatched robin doing so is much less than 1 percent (Farner 1945). Early mortality, in fact, is so high among songbirds that most life tables for them do not begin until late in the summer or early fall of a bird's first year. Once a robin has lived to November 1, on the average it will live another 1.37 years. Over half of them will die in the next year (Farner 1945).

Examining Murie's life table for Dall sheep (Table 5-1) shows that life expectancy is 7.1 years for a newborn lamb. There was a flaw in Murie's data, however, in that the skulls of very young lambs that died possibly were consumed totally by scavengers or predators. Thus, young animals would be underrepresented in his life table and life expectancy at birth would be overestimated. Once a sheep reached the age of six years one may see that it can expect to live, on the average, another 3.4 years, to reach the age of 9.4 years.

A survivorship curve is constructed by plotting the l_x column of a life table against time. A classic use of survivorship curves in wildlife management was described by Taber and Dasmann (1957) for black-tailed deer (*Odocoileus hemionus columbianus*) in two habitats in California. By use of survivorship curves (Figs. 5-5 and 5-6) the researchers were able to compare survival rates of both sexes of five populations of ungulates. All survivorship curves were found to decline steeply in the first year, indicating high death rates of young animals. After that, considerable variation among populations occurred. (The logarithmic scale is used on the abscissa to expand the lower parts of the curve. On a logarithmic scale the removal of a constant proportion of animals would result in a straight declining line, such as occurs in female red deer (*Cervus elaphus*) from age three through fourteen in Fig. 5-5.)

Survival of male black-tailed deer was lower than for females because of selective hunting of males. Taber and Dasmann noted from their survivorship curves that survival of black-tailed deer was much less for both sexes in shrubland than in chaparral. By examining other population features they found that fawn production in the shrubland deer was higher than in the chaparral deer (0.76 fawns per adult doe in shrubland to 0.53 per doe in chaparral in December). This higher production in the shrubland resulted in more intense competition for food, poorer nutrition, and higher mortality. Chaparral is a mixture of woody shrubs, while "shrubland" consists of scattered shrubs and herbs. In the shrubland, deer food was more abundant, and this permitted deer to maintain higher densities (25 per km²) than in chaparral (11 per km²). Survival rates in the shrubland, however, were lower than in chaparral, presumably because the shrubland was fully stocked and the higher birth rates resulted in consequent higher losses through starvation. Once the carrying capacity of the shrublands had been attained, a proportion of deer that were not removed by hunting starved, so that the growth rate in both shrublands and chaparral was essentially zero.

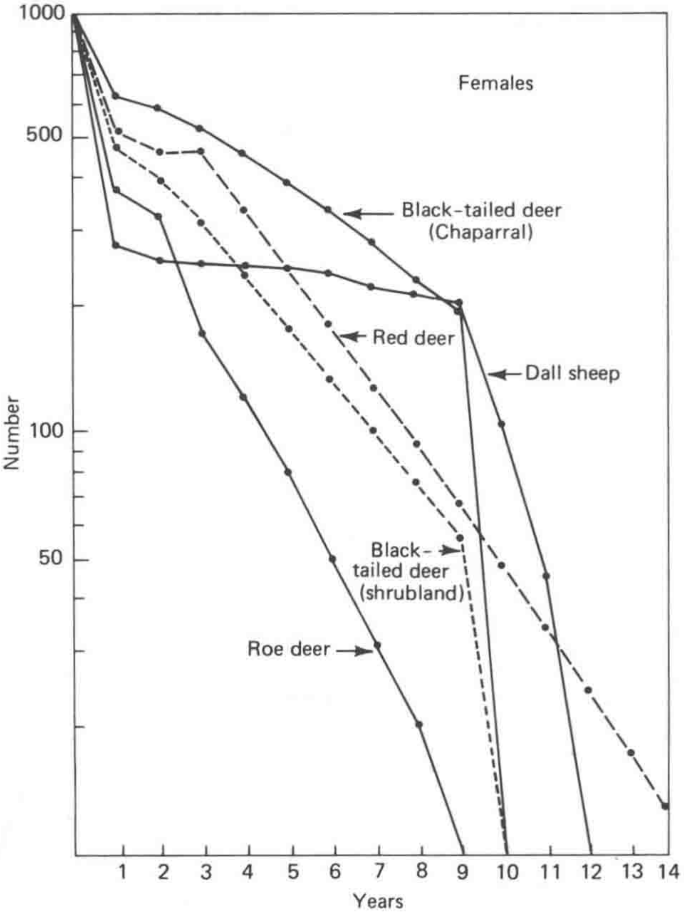


Figure 5-5. Survivorship curves for females of five ungulate populations. (From Taber and Dasmann 1957.)

Taber and Dasmann also pointed out that dynamics of different populations of the same species may vary widely from place to place. It is therefore difficult to say that birth and death rates of a particular population are "typical" of a species; differences among pop-

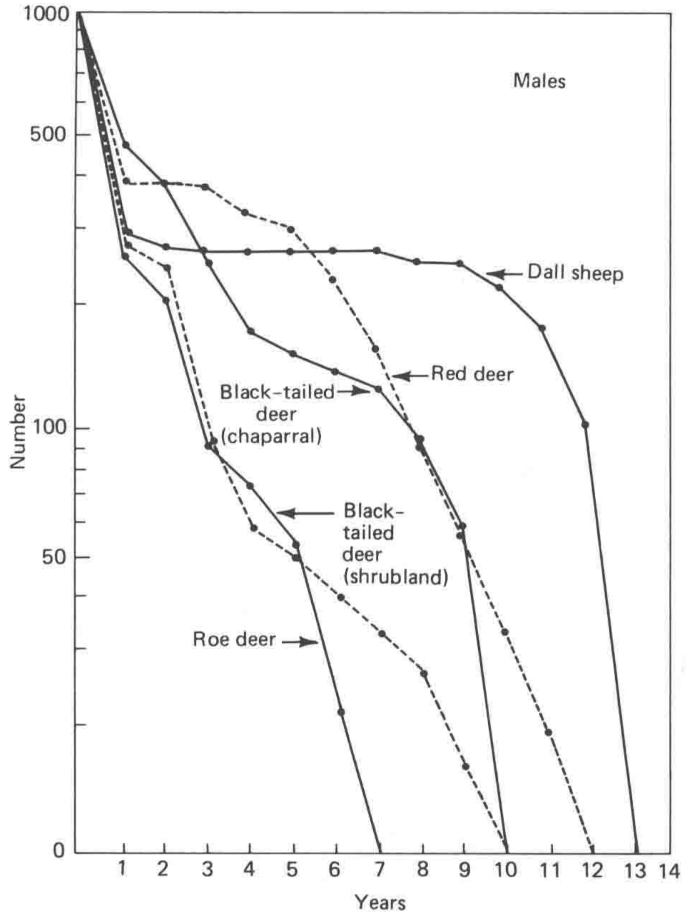


Figure 5-6. Survivorship curves for males of five ungulate populations. (From Taber and Dasmann 1957.)

ulations of the same species reflect different environmental conditions.

There also is evidence that the genetic makeup of a population may change with the passage of time or in response to some environmental factor. (Such change is the basis for the theory of evolution.) Some changes can take place quite rapidly. For example, European rabbits (*Oryctolagus cuniculus*) in Australia were in the 1950s intentionally infected with myxomatosis, a viral disease, to control their numbers. The rabbits declined rapidly. There are still rabbits in Australia—not as many, but they are genetically more resistant to the virus than the rabbits in Australia in the 1940s (Pimentel 1961). Other less noticeable and unmeasured genetic changes possible occur in many populations, changes which influence their birth rates and death rates (Krebs 1978), and which may be responsible for population irruptions and crashes for which no external cause may be apparent.

Organization of a Population-Management Problem

A wildlife manager charged with solving a problem of population ecology may be faced with a somewhat bewildering array of possible causes of an "unsatisfactory" performance by the animals he or she wishes to manage. The following outline is intended to suggest a means of organizing efforts. The objective, of course, is to identify those factors that are most responsible for preventing the further growth of the population, by impeding births, increasing deaths, or both.

A. Extrinsic Factors
  1. Density-independent (primarily weather conditions)
    a. Cause of direct mortality?
    b. Center or periphery of species range?
    c. Does weather have a substantial influence on food quality or quantity—which are density-dependent factors?
  2. Density dependent
    a. Food
      1) Quality. Are necessary nutrients present?
      2) Quantity. Is enough food available?
    b. Cover
      1) Shelter from elements. Is quality and quantity sufficient?
      2) Escape or hiding cover—for predators or from predators. Is quality and quantity sufficient?
    c. Refugia available. Are there patches of habitat in the range of the population in which animals have a high likelihood of escaping various mortality factors, such as predators, hunters, parasites, and disease?
    d. Competitors. Is there competition for resources by other species?
    e. Diseases and parasites. Are these factors influencing birth and death rates?
    f. Predators. Are predators controlling the population?

   - **g.** Buffer species. Are other prey species present which absorb some of the impact of predation, particularly when the species being considered is at low densities?
   - **h.** Hunting harvest. Is harvest toll replaced by the next season's production of huntable animals?
   - **i.** Interactions among various factors. What interactions occur? Food supply–disease? Food supply–predation? Food supply–competition? Cover–predation? Buffer species–predation?

B. Intrinsic Factors
   1. Genetically stable factors
      - **a.** Litter or brood sizes. What is the inherent potential of the species to reproduce?
      - **b.** Longevity. How long can individuals live?
      - **c.** Habitat selection for breeding, feeding, resting. Is it available according to inherent needs of the species?
      - **d.** Self-limiting factors. Does the species possess self-limiting behavior such as territorial spacing, or restricted breeding among selected members of a group?
      - **e.** Dispersal. Is there an opportunity for immigration and emigration?
      - **f.** Interactions. How do inherent features interact, such as territorial behavior–food supply, dispersal–food supply, birth rates–food supply?
   2. Genetically variable factors
      - **a.** Birth rates. Within the physiological limits of the species does the population show varying birth rates?
      - **b.** Survival rates. Does a population differ genetically from time to time in the ability of individuals to withstand stress, or has there been a response to a strong selective factor such as disease or biocides?

As can be seen, answering questions about a population may be a complex task. The most fruitful and simplest approach is usually to examine the more obvious factors first, such as weather, food, cover, and the behavioral nature of the animals. Should such an approach fail to provide satisfactory answers, the more subtle interactions must be examined. Usually the talents of a team of researchers, with various forms of expertise, must be called upon. Once the most important factors (key factors) limiting a population are identified, the manager may attempt to modify those factors. Sometimes nothing can be done, such as when the weather or climate of a particular area is simply unsuitable for the welfare of the species; but most often the application of suitable controls on key factors will result in a desired change in the population being managed.

Population Models

When wildlife managers predict how many mallard ducks will be present in the fall population, based upon sample counts of breeding ducks and the number of prairie ponds in the spring, they are using a model. Similarly, an estimate of the number of deer present obtained by sampling and counting pellet groups (droppings) left by the deer is another example of the use of a model. A model, as defined by Walters (1971) is any physical or abstract representation of the structure and function of a real system.

In the past decade, attempts have been made to construct models of everything biological from cellular physiology to entire biomes. These models are simulation models that trace through a period of time the changes that take place in a system, given some beginning conditions and some circumstances that effect changes in those conditions. Populations of animals lend themselves reasonably well to the methods of simulation modeling. Owing to the speed with which they perform calculations and the convenience they offer for altering variables at various stages in the operation of a model, computers offer wildlife biologists new opportunities to simulate populations of animals under study and to predict the effects of various management procedures. The basic tools for doing so are an understanding of FORTRAN or Pascal computer language and several years of data for a population, including age structure, sex ratios, birth rates, death rates, immigration, emigration, and environmental conditions that influence these factors.

Computer models have been developed to simulate wolf (*Canis lupus*)–moose (*Alces alces*) populations on Isle Royale (Jordan et al. 1971) and the projected recovery of whooping cranes (*Grus americana*) (Miller and Botkin 1974). An excellent example of a model was constructed to simulate a population of mule deer in Colorado (Medin and Anderson 1979). These authors noted that a model has three basic values: (1) it forces the researcher to think about population dynamics in new ways (conceptual value); (2) the researcher must become aware of the usefulness of various types of information necessary to construct an accurate model, and therefore of the information necessary to understand population functions (developmental value); and (3) the model may be useful in predicting future courses of the modeled population or the effects of manipulation of the population by adjusting rates of exploitation or by altering the environment (output value).

The model of the mule deer population studied by Medin and Anderson utilized the following variables gathered over several years of study: vegetation available as food, weather, food consumption, nutrients in food, other animals as predators or competitors, age, sex, and number of deer present, natural mortality rates, hunter harvest, age structure in hunter harvest of deer, birth rates through ovarian and fetal analysis, and the condition of the deer. Only one environmental variable, the amount of precipitation in the April–July period, seemed to have a significant effect on birth rates; it did so by affecting the amount of nitrogen available in winter forage. The density of deer in winter had an inverse influence on their birth rates. By calculating functions for these variables and feeding them into a computer, Medin and Anderson were able to simulate closely the dynamics of the deer population over five years for which reliable data were available. The assumption is then that the model might be projected into the future, given a reasonable assortment of May–July precipitation values. The authors also tested the effects of different harvest strategies on the model (Fig. 5-7). Then the authors asked some "what if" questions of their model and obtained results depicted in Fig. 5-8.

The student can readily see the value of a population model provided the model is reasonably realistic. Biologists who develop models also can recognize the frequent inadequacies of field data and assumptions of cause and effect of variables used in the model. A population model should be only one of many forms of information the wildlife manager may use. At this point in development of population models, an attitude of informed skepticism seems appropriate.

The Human Population

It is not possible to consider management of wildlife populations without also considering management of the human population. In 1983, there were about 4.7 billion people on the earth and this number has been increasing at a rate of 1.8 percent per year. At such a rate (which has prevailed over the past several decades), a doubling of human numbers will occur in 39 years (Population Reference Bureau 1983). Each day more than 200,000 people are added to those already on the earth. Only six of the 170 nations of the world show zero or negative growth rates. The 1983 U.S. population of 234 million has been growing at a rate of 0.7 percent. Hutchinson (1978) observed that a glance at a newspaper suggests that many people behave as if there was no carrying capacity, no upper limit, to the number of people that the earth can support.

It is true that over the centuries human inventiveness has periodically increased the carrying capacity of the earth, first by changing from a hunting and food gathering mode of existence to one of agriculture. Later industrialization, mechanization, and rapid transportation permitted people to trade useful items for food, and fewer farmers were needed to produce human food. The "green revolution," the development of high yield grains, further permitted the feeding of even more people. But agricultural production over the past decade has been scarcely keeping pace with population growth, and an estimated 20–40 percent of the people in the world are underfed (Miller 1982).

Most ecologists believe that the carrying capacity of the planet for humans is rapidly being approached, and that resources cannot be produced and processed fast enough to meet the demands of an ever-growing population. In some places, such as India and Bangladesh, the carrying capacity has already been exceeded.

The need to feed, clothe, and house the growing billions of people requires both more extensive and more intensive use of the land and waters. In doing so, man competes with other animals. Faced with the

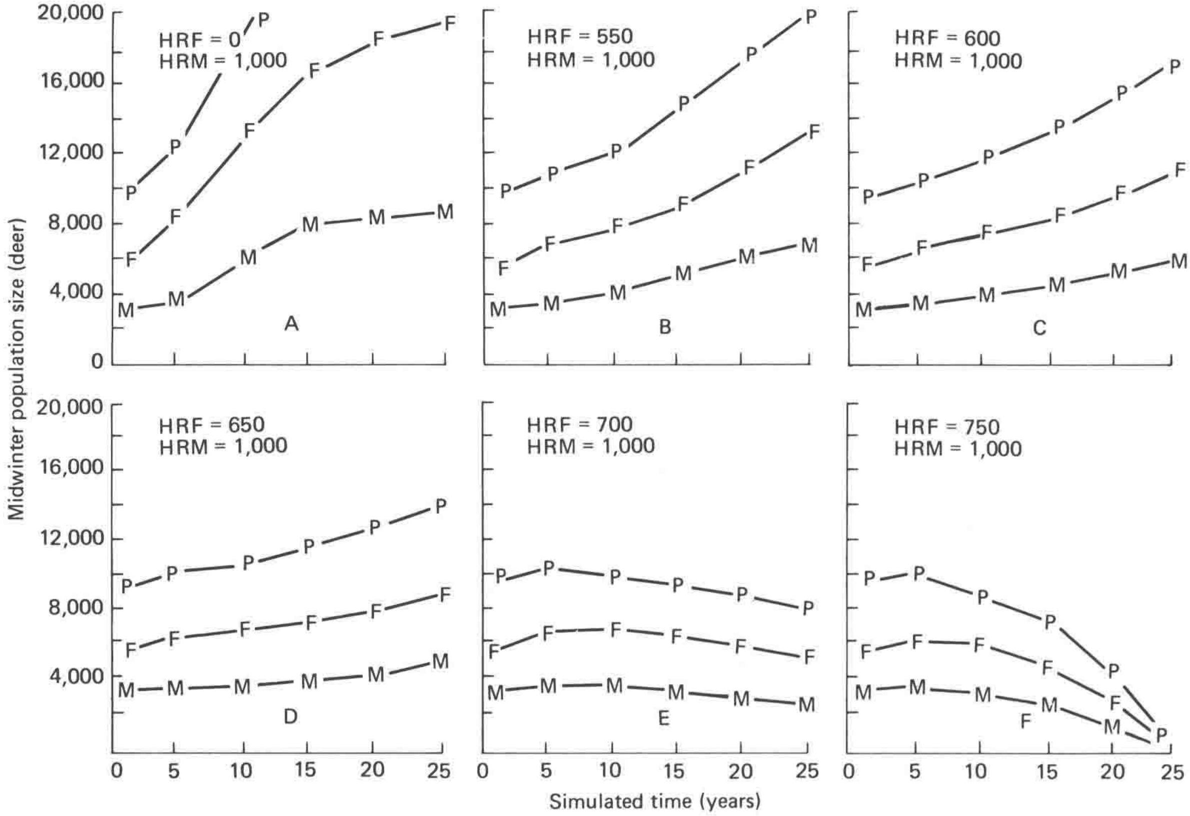


Figure 5-7. Plotted model output from simulated harvest strategies (**P** = total population size, **F** = female population size, **M** = male population size). Annual harvest rate values for females (**HRF**) were varied from 0 (Part A) to 750 (Part F). The annual harvest rate for males (**HRM**) was kept at a constant value of 1000. Data-based harvest rates were assigned for the first three years of simulated time; the harvest rates indicated were operative thereafter. (From Medin and Anderson 1979.)

necessity of raising crops and trees and mining energy sources of all kinds to supply starving people, arguments for providing habitat for wildlife lose their strength; and the wildlife management goal of balancing the needs of other animals and those of humans is weighted by the sheer numbers and "humane" priority of our own species.

The influence of the human population is truly global. Lead from the exhausts of millions of automobiles is found in the Antarctic ice pack, and chlorinated hydrocarbon pesticides are infused from the atmosphere into food chains of the tundra, where pesticides have never been applied. Sulfur and nitrogen oxides emitted from power plants in one country cause acidification of lake and soils in another. The production and use of resources to support humanity affects the resources for other animals, usually to their detriment.

There is no doubt that the human population will stop growing at some point. The question is only whether human numbers will be controlled through such "natural checks" as starvation and territorial defense, or through intelligent application of methods to reduce the birth rate to match death rates, which have been lowered through medical treatment. The future of wildlife as well as that of humans rests upon such a choice.

Summary

Wildlife management involves manipulation of populations; therefore, an understanding of population ecology is essential to wildlife managers regardless of the species being managed. Basic population at-

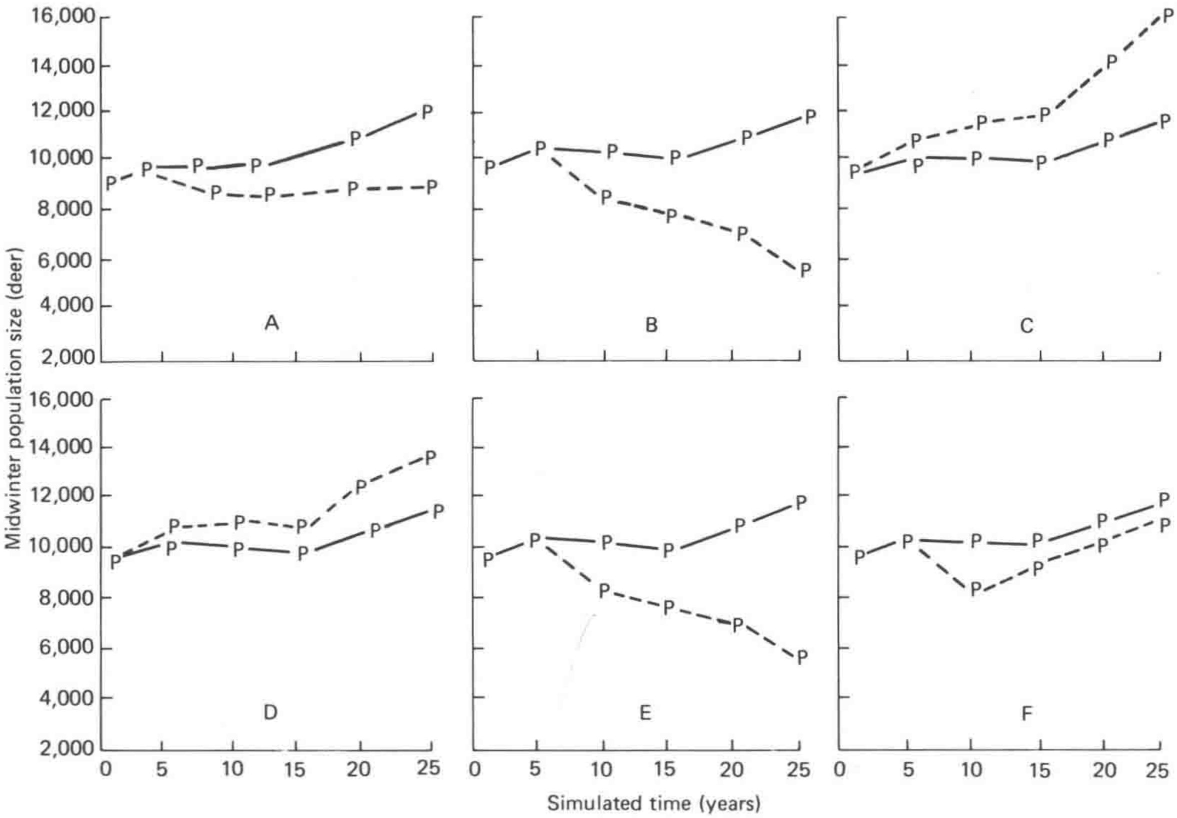


Figure 5-8. Plotted model output that compares a basic simulation run (**HRF** = 650, **HRM** = 1000) with those in which a specific "what if . . .?" question was asked of the model. Solid lines show the basic simulation run; dashed lines show an altered simulation run. **P** represents the total population size. (A) Harvest rate was increased by 50 percent (HRF = 975, HRM = 1500) in Year 9 only and was allowed to operate at the basic rate all other years. (B) Harvest rate was increased by 50 percent for 2 consecutive years (Years 9 and 10) and allowed to operate at the basic rate all other years. (C) Fawns were harvested annually in proportions larger than those existing in the population at the time of hunting (simulating a positive hunter bias with regard to shooting fawns). (D) Periodic harvest removal in which the basic female harvest rate doubled (**HRF** = 1300, 0, 1300, 0, . . . ; **HRM** = 1000) in alternate years. (E) A "catastrophic" year in which the mortality rate of the fawn age group was increased by 50 percent and the mortality rate of all older age groups was increased by 25 percent in Year 9 only; the basic harvest rate was allowed to operate each year. (F) Increased mortality rates were assumed as in Part E, except that the "catastrophic" year was followed by a year of antlered-only hunting (in Year 10); the basic harvest rate was allowed to operate all other years. (From Medin and Anderson 1979.)

tributes include density, sex ratios, age structure, natality, mortality, immigration, and emigration. The logistic equation $\Delta N/\Delta t = rN(K - N)/K$ is useful in illustrating theoretical population growth and the influence of carrying capacity. Factors acting to limit populations in the center of a species' geographic range are usually dependent upon the density of the population. Species at the periphery of their range are frequently controlled by density-independent factors. In practice a wildlife manager must seek reasons for imbalances in birth rates, death rates, immigration, and emigration. The reasons for such imbalances may be sought in the adequacies or inadequacies of food and cover in the environment and how they interact with birth, death, immigration, and emigration. Natality information is frequently easier to obtain than mortality information. Life tables are useful to compare mortality among various populations to locate age classes affected most by mortality.

Organizing the approach to solving a problem of population management involves seeking factors of a variety of sorts that limit growth of populations. Once these are identified, the manager may apply suitable modifications either directly to the population or to its habitat to bring about a desired change in the population. Models, or abstract representations of populations, may be useful to wildlife managers in illustrating which data are necessary to understand population dynamics and to predict the effects of various management measures on a population. Computers make modeling of populations a feasible management technique. The principles of population ecology apply to humans as well as to other species, and the future of wildlife depends as much upon management of the human population as it does on management of other species.