# The Basics of Population Dynamics 

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All forms of wildlife, regardless of the species, will respond to changes in habitat, hunting or trapping, and weather conditions with fluctuations in animal numbers. Most landowners have probably experienced changes in wildlife abundance from year to year without really knowing why there are fewer individuals in some years than others. In many cases, changes in abundance are normal and to be expected. The purpose of the information presented here is to help landowners understand why animal numbers may vary or change. While a number of important concepts will be discussed, one underlying theme should always be remembered. Regardless of whether property is managed or not in any given year, there is always some change in the habitat, however small. Wildlife must adjust to this change and, therefore, no population is ever the same from one year to the next.

Traditionally, wildlife professionals refer to the number of individuals of a particular species within a given locality as a population. They use the term dynamics to describe the shift in the number and composition of individuals over time. For example, white-tailed deer populations rose in South Carolina from 260,000 to 350,000 during 1970, to over 1 million in 2009.

Why is it important to understand, for example, approximately how many deer are in South Carolina or in a particular location? Depending on a landowner's objectives, the goal may be to increase, stabilize, or decrease the population.

Many management objectives can be accomplished by manipulating the habitat. Others may require direct manipulation of the animal population to achieve desired management results. If a landowner is sustaining considerable economic damage from deer browsing on soybeans or disrupting tobacco beds, populations must be manipulated directly by harvesting or removing animals from the population.

In most cases, habitat components and animal space requirements determine the carrying capacity for wildlife. One of the interesting phenomena observed in wildlife species occurs when populations are low with respect to the maximum number of individuals an environment can support. Under these conditions, birth rates (the number of live births per female per year) have a tendency to be high. When a population is at or near the maximum number the environment can support, birth rates are low and death rates (the number of animals in the population dying per year) are high. Both birth and death rates can vary in relation to population numbers. This phenomenon is called density dependence. These concepts are important for landowners and natural resource managers to understand when making decisions affecting wildlife on private land.

## How Many Offspring Can Wildlife Have?

Most people realize that some wildlife species can produce more offspring than others. Bobwhite quail are genetically programmed to lay an average of 14 eggs per clutch. Each species has a maximum genetic reproductive potential or biotic potential.

Biotic potential describes a population's ability to grow over time through reproduction. Most bat species are likely to produce one offspring per year. In contrast, a female cottontail rabbit will have a litter size of approximately 5 . If conditions are good, she may produce a second or even third litter before the summer is over.

Cottontail rabbits have a much higher biotic potential or intrinsic rate of population increase than bats because they can add more members to their population over the same period of time. Animals with a higher biotic potential can respond better to habitat changes or some other type of change more readily than those species with a lower biotic potential.

It is important to remember that with any habitat improvement project, animal numbers will respond only if the most restricting habitat factor (food, water, cover) has been changed. Stated another way, a limiting factor is a basic requirement that is in short supply and that prevents or limits a particular wildlife population in an area from growing.

Limiting factors are often difficult to determine beforehand, even for the most experienced wildlife professional. Part of the art of wildlife management is determining which factor(s) are preventing, for example, white-tailed deer from producing twins or preventing cottontail rabbits from producing 2 or 3 litters of 5 . It becomes apparent that managing wildlife populations is linked to habitat management.

While all wildlife populations sustain varying capabilities for growth in numbers, they all experience environmental constraints or decimating factors. These constraints may take the form of predators, disease, hunting, trapping, weather, or a combination of these factors.

It is important to understand the differences between limiting factors and environmental constraints. A lack of food, cover, or water limits a population. Limiting factors may be a lack of appropriate nesting, brood, loafing, and winter cover for quail or cottontail rabbits to escape the harsh effects of weather or predation. Landowners who choose to reduce the size of individual grain fields in an attempt to reduce soil erosion could also increase the number of bobwhite quail or cottontail rabbits through an increase in the total length and width of hedgerows or field borders (improving cover). This, of course, assumes insufficient cover is the limiting factor for quail and rabbits. In many respects, providing critical limiting factors alleviates or reduces the potentially harmful effects of decimating factors on wildlife.

Decimating factors can depress or reduce populations, but in most cases these factors do not control animal abundance. In some cases, such as severe overhunting of white-tailed deer or waterfowl, the introduction of new parasites or predators, or unusually severe weather, decimating factors can control the size of wildlife populations.

Decimating factors serve to offset a population's biotic potential and keep the numbers in balance with what the land is capable of supporting. The greater the constraints, the lower the
level of a particular population. Stated another way, a population may be depressed (by hunting, predators, or disease) to a level at which there are no factors limiting population growth. As the population size dwindles, environmental constraints exert less pressure on the population, and the population increases. This increase proceeds according to the species' biotic potential until such point that food, cover, or water become limiting.

## Dispersion, Dispersal, and Density

Wildlife do not recognize legal boundaries like humans do. Instead, wildlife move throughout areas according to the existence of natural or man-made boundaries (waterways, roads, or fences) and changes in the availability of suitable habitat. Consequently, a given animal may be present on a specific landowner's property only part of the time.

Animals tend to choose the best locations where they can find food, cover, and water. In so doing, animals concentrate in numbers in some habitats at the expense of other habitats. Dispersion refers to the location or pattern of animals in space, whether horizontally or vertically (Figure 1). The latter (vertical dispersion) is often ignored but is extremely important when examining the suitability of a habitat for songbirds. Wildlife populations distribute themselves over the landscape in 2 patterns of dispersion: clumped and uniform. All other distributions fall somewhere in between. Wildlife that form clumped distributions are often very social and live in family units. This is the
 most common type of dispersion because the animals are responding to the restricted availability of habitat. Common examples of clumped dispersion include a covey of bobwhite quail; a roosting colony of starlings, grackles, or blackbirds; or a coyote family unit (mated pair, pups from current year, and possibly yearlings).

Other wildlife species, such as groundhogs, tend to be very asocial during much of the year and spread out more evenly or uniformly across the habitat (they are said to exhibit uniform dispersion). Very often these species are highly territorial. A territory is formed when an individual, mated pair, or social group of animals uses an area exclusively and actively defends this area against other members of the same species.

Regardless of the typical dispersion pattern a species takes, animals are constantly shifting around and looking for improved conditions. The pattern never remains constant. This is especially true when newborns grow and begin to move out on their own. Movement of animals from one location to a new, permanent site is called dispersal.

The movement and positioning of animals throughout a landscape strongly influences population density. Density refers to the number of animals present on a defined area at a point in time. It is
an indication of how effective a particular property is at supporting a population of a wildlife species.

Wildlife biologists estimate the white-tailed deer population in South Carolina to be over 1 million. A measure of density would show one deer per 26 acres. Density is perhaps the most frequently obtained measurement of wildlife populations.

When wildlife professionals discuss the dynamics of a population, they are usually referring to the changes in density that are recorded from year to year. There is a problem with using density, because it never remains constant. It changes throughout the year due to births, deaths, and the movements of animals in and out of the population. As a result, we are never certain that any time-specific measure of density is an accurate reflection of a population's performance.

Density is usually estimated from a count of animals on a portion of the total area. This is then expanded to the entire site. If conditions and manpower permit, all of the animals are observed and counted across the area, presumably without error. This is referred to as a census and is a more refined version of determining population size.

Often, it is just more efficient and cost effective to record animal signs (droppings, tracks, vocalizations) and use this as an indication of the abundance of a species. The latter approach is called an index of population size. An index is easier to obtain but does not yield a numerical value for the population. It only provides a relative idea of how common the animals are on a given property.

If obtained properly, a measure of density can be a useful tool for evaluating the success of habitat management practices for increasing the population of a particular species. It is important to do an index before and after modifying a site if you want to accurately measure the effectiveness of a habitat management prescription.
Care should be used to ensure that the index is obtained when: 1) the population is most stable (not changing due to births or frequent dispersal movements); and 2) similar conditions exist (same time of year, time of day, and weather conditions).

## Wildlife Population Parameters

One of the easiest and most convenient methods of estimating or predicting population growth, decline, or stability is to measure the proportion of young to old in a population. This measure is called the population's age ratio. This information can then be depicted graphically in an age pyramid (Figure 2). Age ratios are commonly used to compare changes in a single population between years or within the same year for different populations. Wildlife agencies have used this method to estimate increases in white-tailed deer in the past. Computer

models and simulations can also more accurately reflect this information.
Recent information suggests age ratios may not reflect actual changes in populations. However, age pyramids can allow a private landowner to take a quick look at the number of young versus old animals in the population and dispell several myths concerning the stockpiling of wildlife.

Although there can be exceptions, wildlife populations are likely to decline if they are top heavy or support a much larger number of adults than yearlings. This decline, over time, can be attributed to the small number of new individuals moving into the reproductive segment of the population. In contrast, a population that is essentially young will have a greater proportion of yearlings. The population will likely increase as maturation of the yearling class expands the reproductive segment of the population.

Assessments of population age structure are most often applied to long-lived species (whitetailed deer) and generally require extensive efforts to obtain the complete age distribution for the population of animals.

With relatively short-lived species (e.g. muskrats, quail, cottontail rabbits, woodcock, mourning dove), the information is more readily obtained but will be useful only into the next year because of the high death rates and rapid turnover of the populations.

Age pyramids for small game show that a large percentage of the population never makes it to age 3. This tells the landowner and manager that you can't stockpile game (by not hunting in hopes of having a larger breeding population in the spring) unless there is sufficient habitat to support the animals. It also provides another important lesson: it is difficult to increase small game bird populations by stocking pen-raised birds (most of these birds will usually die over the first winter) unless the habitat is present to support a larger population. If the habitat is present, the birds may be present.

Sex ratios are another feature of populations that wildlife managers examine carefully, because a disruption in the proportion of males to females can dramatically affect the reproductive success of a population. Sex ratios are most often expressed as the percentage of males in the population or the number of males per female. Sex ratio information is commonly used by wildlife agencies when managing big game herds. Agencies manipulate the ratios of bucks to does removed from the population each year in an attempt to yield the maximum number of animals that can be harvested. They must also maintain a sufficient number of bucks in the population to ensure a complete reproductive effort by does the following year.

For a polygynous species, like white-tailed deer (one male can breed with several females), sex ratios are skewed or shifted to favor females in a harvested population. For a monogamous species, like Canada geese or coyotes (one male breeds with one female), a balanced sex ratio (50:50) is required for maximum production of offspring. For example, if the sex ratio is shifted to 40 males per 60 females in Canada geese, the population will exhibit only 66 percent production. In the case of a monogamous species, a sex-specific hunting season could devastate a population. However, even unharvested wildlife populations do not normally maintain an even sex ratio.

Although data do not always support the following generalizations, many studies have shown that most mammals give birth to slightly more males than females; whereas, for birds the pattern is reversed, with more females born than males. Later in life, these trends tend to move toward a more even or $1: 1$ ratio.

## Mortality Factors

Common to all living creatures are the events of birth and death. Few, if any, animals in the wild die from old age. Instead they succumb to one of many factors that affect the members of their particular species. Mortality refers to the inherent loss of individuals from a population through death. Mortality is difficult to measure because carcasses are hard to locate. The fate of animals that disperse or move out of a population can seldom be determined.

Consequently, it is more practical to measure survivorship, or the numbers of animals remaining alive, as these individuals can be located and accounted for. Wildlife species with a high reproductive potential, such as cottontail rabbits, tend to have low survivorship and high mortality at younger ages, therefore offsetting their high reproductive outputs. Animals with a lower reproductive potential, such as white-tailed deer, have higher survivorship of young, compensating for the smaller litter sizes. Frequently, survivorship values or rates are obtained from field data for all age classes in a population. From these values, survivorship curves can be developed for a specific population. These are used to assess the population's potential for growth or decline in a particular habitat.

Several mortality factors (e.g. disease, predation, exposure to severe weather, starvation or malnutrition, accidents, harvest) can be the proximate cause of how an individual animal meets its fate. While the proximate cause may be predation or exposure to severe weather, the ultimate cause may be related to a lack of sufficient cover to escape predators or the effects of adverse weather.

A wildlife population will be subjected to many limiting factors over time that may produce an overall reduction in population size. Because habitat conditions, weather patterns, and populations of predators and prey are constantly changing, some factors that have a significant impact in one year may be less so the following year. Despite these inconsistencies, in many cases the overall reduction in population size from mortality factors across years remains the same.

In effect, the specific causes of death tend to balance or compensate each other. Wildlife professionals call this phenomenon compensatory mortality. Stated another way, one type of mortality largely replaces another kind of mortality in animal populations, while the total mortality rate of the population remains constant. For example, bobwhite quail have great difficulty surviving severe weather conditions at the northern limits of their range. When winters are extremely cold, many animals die from exposure, and fewer animals will be taken by predators. During mild winters, many quail survive only to fall prey to a host of predators because of finite amounts of escape cover. The overall effect is that approximately the same number of quail are supported by the habitat from year to year. Habitat to a large extent,
determines the number of animals that can survive in a population, or animals that produce a "surplus." This surplus is removed by mortality.

Perhaps a more specific example with bobwhite quail will help. Let's assume that total mortality on a bobwhite quail population is 70 percent; 70 percent of the total population will die in the first year. In the first year when the weather is severe, 20 percent of the population is lost to predators and 50 percent of the population dies from exposure. The total mortality rate for the population is 70 percent.

In the second year when predation removes 60 percent of the population, only 10 percent of the population is lost to exposure for a combined total mortality rate of 70 percent.

Wildlife managers employ the concept of compensatory mortality when establishing hunting and trapping regulations. In compensatory mortality, hunting and trapping serve to replace the natural mortality factors operating on a population, and keep the population density in balance with what the habitat can effectively support.

In the quail example, the population was hunted, and 30 percent of the population was removed. In this situation, predators removed 10 percent of the population, and 30 percent of the quail died from exposure. The total mortality rate remained unchanged at 70 percent.

The portion of a wildlife population that is capable of being removed is called the harvestable surplus, that portion of the population that would invariably die from other causes. Data suggest that species with a high reproductive potential can have a larger percentage of the population harvested in any one year than species with a low reproductive potential, because their higher reproductive outputs will replenish the loss of animals more quickly.

Muskrats are a perfect example. When large numbers of muskrats are removed by trapping, the population responds in these ways:

- the length of the breeding season is increased so more litters are produced,
- the number of offspring produced per litter increases, and
- surviving muskrats are less susceptible to disease or predation.

Regardless of which species we are talking about, man must regulate the removal of animals because all populations have a harvest level at which the mortality factors are no longer compensatory but additive. This means one kind of mortality is added to the other sources of mortality.

Additive mortality can be detrimental and lead to population decline. Back to the quail example: we know approximately 70 percent of the population will die every year, whether we hunt the population or not. If hunting pressure is heavy and a large percentage of quail are killed, pushing the total mortality above 70 percent, this would be considered additive mortality.

One important note: regulated sport hunting has never resulted in a species being placed on the endangered or threatened species list. Commercial, market, or unregulated hunting has
been responsible for, in some cases, the extinction of a wildlife species, such as the passenger pigeon.

## What Keeps Wildlife Populations in Check?

Up to now, we have discussed a variety of concepts that describe some facets of wildlife populations. We have yet to address the underlying theme behind population management: the concept of carrying capacity.

On any particular tract of land, there will be a unique array of vegetative cover types and landforms that are arranged in a given pattern that provide habitat for some wildlife species. An individual animal must find food, cover, and water within reasonable proximity to survive on that tract of land. The spatial arrangement and quality of habitat will ultimately determine how many members of a species can exist on the property. This is a simplified version of carrying capacity, the maximum number of animals an environment can support under stable, steady conditions without causing destruction of the habitat. Over the period of a year, a population will experience births, deaths, and movements of members into and out of the area. All of these characteristics of a population are related to a greater or lesser degree to habitat suitability.

Habitat quality serves to regulate or maintain wildlife populations at fairly stable numbers from year to year. As the habitat is manipulated or permitted to slowly change on its own, the carrying capacity of the area will become different. Consequently, the population will respond with an increase or decrease in size. Such changes are predictable but usually only in a very coarse manner.

Problems can and do arise, however. Disease outbreaks or drought, for example, can seriously deplete population numbers. It may take several years to restore the population to its original density. When such catastrophic events occur, few wildlife populations have the capacity to withstand them.

As a final comment, it should be noted that some forms of wildlife tend to track or stay fairly close to the carrying capacity set by their habitat. Other species fluctuate widely around the habitat's carrying capacity. This sometimes depends on how much of the landscape has been changed by man. Knowing in advance how a particular wildlife species will likely respond to habitat alteration is one of the keys to successful wildlife management.

