How to Manage Deer Populations

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Management of wildlife involves the manipulation or control of habitats, populations and people to meet specified goals. The white-tailed deer (Odocoileus virginianus) has probably been studied more than any other species of wildlife. As with all species, habitat is the basic requisite for the occurrence and abundance of deer and has long been studied (Harris 1977). More recently, the characteristics, attitudes and desires of recreational users of the deer resource have received increasing attention (Langenau 1979). The dynamics of deer populations have been less understood, but the recent contribution of McCullough (1979) provides a conceptual basis of the processes that regulate deer numbers. Considered collectively, these studies indicate that the white-tailed deer is extraordinarily adaptable to habitat conditions and not only survives, but thrives, under all manners of harvest strategies. Consequently, deer populations can be managed to achieve a wide variety of goals.

However, the white-tailed deer may be, in a relative sense, our most mismanaged game species. Deer management has traditionally been guided by the value judgement that herds should be maintained at near maximum size to provide maximum harvest. The purpose of this paper is to demonstrate how this judgement is contrary to all reasonable management goals that involve harvest. The problem arises from a lack of understanding of the factors that regulate population numbers and how these factors are affected by harvest.

Basic Principles

To understand the dynamics of a population, we need to know how many animals it contains, the rate at which it is increasing or decreasing, the rate at which it produces young, and its rate of loss through mortality. Properties such as these are called parameters; estimates of parameters are called statistics.

Estimating the Number of Animals

Determining the number of deer in a population is a difficult and sometimes impossible task. It is rarely easy to define the area occupied by the population, and numbers are constantly changing as animals are born, die, and move into or out of an area. The wildlife literature is replete with census methods and techniques for estimating population levels. The ideal situation for census exists in the open habitat of South Texas where deer herds are often contained within fences, and animals are counted by helicopter survey (Brothers and Ray 1975). Other methods of direct counts include spotlighting (Progulske and Duerr 1964), drive counts (McCullough 1979) and various strip census techniques (Overton 1971). Population numbers can be accurately determined by reconstruction if all mortality can be accounted for (Downing 1980, McCullough 1979). Track counts (Tyson 1959), pellet counts (Cochran and Stains 1961) and capture-mark-recapture techniques (Caughley 1977) have also been used to estimate population levels. The accuracy of these methods is affected by season, weather conditions, terrain, habitat type, age-sex structure of the herd, and the abilities of the observer.

Rate of Increase

The simplest measure of a population’s rate of increase is the ratio of numbers in 2 successive years. The finite rate of increase ($\lambda$) can be expressed as

$$\lambda = \frac{N_{t+1}}{N_t}$$

with $N$ representing population numbers and $t$ representing time. When $\lambda$ is greater than 1, the population has increased; when $\lambda$ equals 1, the population has not changed; and when $\lambda$ is less than 1, the population has decreased.

For most population studies, the rate of increase is expressed as the exponential rate of increase ($r$) where $\lambda = e^r$. This expression results in simplified algebra and provides a more logical interpretation of rate of increase. When $r$ is positive, the population has increased; when $r$ is zero, the population has not changed; and when $r$ is negative, the population has decreased. The exponential rate of increase can easily be calculated by the relationship $\ln(\lambda) = r$.

Reproductive Rates

The rate at which does conceive and bear young is influenced primarily by the quality of their diets (Verm 1969). Under good conditions, the average number of fawns born per doe increases, the number of does failing to conceive declines, and maturity is reached at an earlier age. A deer is described as a fawn its first year, yearling its second year, and adult the
third and later years of its life. Does bred as adults typically show higher reproductive rates than those bred as yearlings and fawns (Jacobson et al. 1979), and reproductive rates should be expressed by age to be meaningful. Reproductive rates may be inferred from embryos, luteal bodies in the ovaries (Kirkpatrick 1980), prevalence of lactation (Scanlon and Urbston 1978), and fawn per doe ratios at the time of census (Brothers and Ray 1975). The results of each method have slightly different interpretations as they represent different points of time in the life of the animal.

The sex ratio of fawns at birth appears to be nearly balanced with a slight preponderance of males. Verme (1965) and McCullough (1979) suggest that diet may affect the sex ratio of newborn fawns with the proportion of males increasing as nutritional quality decreases.

**Mortality**

Mortality patterns of mammals suggest a "U-shaped" relationship between mortality rate and age (Caughley 1966). A relatively high rate of mortality occurs during infancy, followed by a low rate at puberty and an increase thereafter. Bucks are generally more susceptible to mortality than does even in areas where hunting is not a factor (Cowan 1950, McCullough 1979). Survival of newborn fawns declines as the quality of diet for the doe decreases (Langenau and Lerg 1976). Estimation of age-specific mortality rates has long been attempted by use of life tables based on the distribution of ages at death from a sample of the population (Caughley 1977, Downing 1980). If the sample is obtained by shooting, the distribution is often biased by hunter selectivity and behavioral differences by sex and age. The population's rate of increase must also be known to accurately estimate mortality rates. Most accounts of deer mortality assume that the population is stable in numbers and distributions of sex and age.

A basic premise of harvesting game is that hunting mortality is substituted for natural mortality. This assumption seems reasonable only if harvesting occurs before the period of greatest stress, and if natural mortality is related to density. The usual relationship between hunting mortality and natural mortality is more dearly implied by examination of the isolated rate of harvest \( h_x \), the rate at which individuals die if no natural mortality occurs; and the isolated rate of natural mortality \( n_x \), the rate at which individuals die if no hunting mortality occurs. They are related to the total rate of mortality, \( q_x \), by

\[
q_x = h_x + n_x - h_x n_x.
\]

The implication here is that both hunting and natural mortality occur simultaneously and throughout the same period. For example, consider a herd of 1,000 deer in the fall, of which 250 will die by the following fall if no hunting occurs. If 100 deer are harvested, the total mortality rate would be 0.325 \((q_x = 0.10 + 0.25 - 0.1 \times 0.25)\).

**Carrying Capacity and K-Selection**

Two fundamentally different strategies of survival have been recognized in organisms (Dasman 1981). K-selected species are adapted to live in relatively stable habitats at or near carrying capacity \( K \) which is defined as the population size where births are exactly matched by deaths. This strategy favors evolution of strong competitive ability, large body size, long life span, low reproductive rate and high parental care. By contrast, r-selected species are adapted to live in temporary or uncertain environments. Typically, they are small, have short life expectancies, produce large numbers of offspring and provide little parental care. They tend to show boom or bust population responses. White-tailed deer are a K-selected species and most insects are r-selected species.

Growth of K-selected populations is often described by the logistic equation:

\[
\frac{\Delta N}{\Delta t} = r_m N \left(1 - \frac{N}{K}\right) \quad \text{where},
\]

\[
N = \text{total population}
\]

\[
\tau = \text{time}
\]

\[
r_m = \text{maximum rate of increase}
\]

\[
K = \text{carrying capacity or maximum number of animals that habitat can support}
\]

\[
\Delta N = \text{change in population size per unit of time}
\]

\[
\left(1 - \frac{N}{K}\right) = \text{environmental resistance to population growth}.
\]

Population growth as described by the logistic model exhibits a characteristic "S" or sigmoid shape. The basic assumption of the model is that the rate of increase decreases as a linear function of population size. This implies that the amount of available resources per individual decreases in direct proportion to the increase in the number of individuals. For white-tailed deer, nutrition acts to regulate population growth. McCullough (1979) found that the growth of the George Reserve deer herd resembled logistic growth, but that rate of increase decreased as a curvilinear function of population size, not in direct proportion. The logistic model overestimated population size during the early years and underestimated it in later years. The time required to achieve K-carrying capacity was estimated at 14 years when this level was actually achieved in only 8 years.

Other models than the logistic exist that better describe population growth of white-tailed deer (Caughley 1977), but for the sake of simplicity, we will use the logistic model to illustrate some basic principles of managing deer populations by harvesting.
Principles of Harvesting

A hypothetical deer population that conforms to logistic growth will be used to illustrate some basic principles of harvesting. Assume that we have a 7,000-acre tract of land under deer-proof fence and that K-carrying capacity for deer is 1,000 animals (one deer per 7 acres). Our goal in managing this herd is to provide a sustained yield (SY), a crop that can be taken year after year without forcing the population into a decline. For a given population size, SY will equal the number of deer that would be added to the population if no harvesting occurred (Table 1). Note that SY is not unique and that there is a large number of possible SY values, each corresponding to a different management treatment. Management for harvest by sport hunting logically aims at defining the treatment which produces the maximum sustained yield (MSY) or maximum revenue or recreational value (the optimal sustained yield, OSY).

1. A population that is at K-carrying capacity has no "surplus" animals and must be reduced below K before SY harvesting can occur. Thus, the goals of maximum population size and MSY are contradictory.

2. For each population size below K, there is an appropriate SY.

3. For each level of SY except MSY, there are two population sizes from which this SY can be harvested.

4. When a constant number is harvested each year, the population will adjust itself and stabilize at the size for which that number is the SY. If the number harvested exceeds MSY, the population will decline to extinction.

5. SY must be calculated from the size to which the population is initially reduced and not K.

MSY can be taken from only one population level which is theoretically equal to 0.5 K and harvested at the instantaneous rate,

$$H = 2$$ (see Caughley 1977 for derivation).

For our example, the MSY of 173 occurs at a pre-hunt

<table>
<thead>
<tr>
<th>Prehunt population size N</th>
<th>$\frac{\Delta N}{\Delta t} = SY^2$</th>
<th>Instantaneous harvest rate$^3$</th>
<th>Isolated harvest rate$^4$</th>
<th>Adjusted SY harvest</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>62</td>
<td>0.623</td>
<td>0.464</td>
<td>46</td>
</tr>
<tr>
<td>200</td>
<td>111</td>
<td>0.554</td>
<td>0.425</td>
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<tr>
<td>300</td>
<td>146</td>
<td>0.465</td>
<td>0.345</td>
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</tr>
<tr>
<td>400</td>
<td>186</td>
<td>0.416</td>
<td>0.340</td>
<td>136</td>
</tr>
<tr>
<td>500</td>
<td>173</td>
<td>0.346</td>
<td>0.293</td>
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<td>600</td>
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<td>60</td>
</tr>
<tr>
<td>1000</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

1Assumptions: K-carrying capacity = 1,000 deer, maximum rate of increase is 2 fawns per breeding doe ($\lambda = 2.0$, $r_m = 0.693$), does produce first fawns at age 2 and annually thereafter, sex ratios are equal. Both sexes and all ages are harvested at same rate.

2$\frac{\Delta N}{\Delta t} = SY = \frac{N-K}{N-K}$

3Harvesting occurs throughout year.

4Harvesting occurs in short time period.

Some important principles are apparent from this example:

- A population that is at K-carrying capacity has no "surplus" animals and must be reduced below K before SY harvesting can occur. Thus, the goals of maximum population size and MSY are contradictory.
### Maximum Sustained Yield

Estimates of SY from the logistic model are based on the assumption that harvesting is not selective for age or sex. It is generally accepted that shifting the sex ratio of a deer herd in favor of does should increase the number of bucks recruited and thus increase buck harvest. If recruitment is a function of total population size, then maintaining a population at a fixed size and imbalancing the sex ratio in favor of does should increase SY. The rate of increase ($\lambda$) can be related to mean survival rate ($p$) and mean fecundity rate ($m$) as $\lambda=p+pm$. In our hypothetical herd, $\lambda=1.346$ at 0.5 K. Assuming $p=0.9$ then $m=0.495$. Theoretically, the sex ratio can be imbalanced to increase SY until breeding is impaired (Table 2). Bucks-only hunting is often justified on this basis. However, if does are not harvested, they will increase to K and recruitment will drop. SY of bucks will actually decrease as post-hunt population size increases beyond that appropriate to 0.5K.

The empirical data of McCullough (1979) indicate that population growth is more a function of the number of does rather than population size. Imbalancing the sex ratio at population levels of 0.5 K and beyond actually decreased SY of bucks. These results suggest that achieving MSY of one sex requires simultaneous MSY of the other sex.

### Trophy Management

Management for trophy bucks has generally been associated with selective bucks-only hunting and resulting populations at or near K-carrying capacity. Brothers and Ray (1975) present evidence that this strategy is not good for optimizing the yield of trophy deer. With the poor nutritional plane of populations near K-carrying capacity, it takes longer to produce a trophy animal than with the relatively high nutritional plane of populations at or below 0.5 K. The SY of trophy bucks is a direct function of the number of bucks recruited and the age at which they die. Since 0.5 K is the population level at which maximum recruitment can be sustained, this is the logical population size on which to base a trophy management plan. Maintaining the female segment at 0.5 K will require substantial harvest of antlerless animals. Invariably, some male fawns will be mistakenly harvested as does. However, if yearling bucks can be protected from harvest until they are trophy class animals (5 1/2 years old, for example), MSY yield of trophy bucks would be realized. If population growth is a function of the number of does, the increase in population size above 0.5 K caused by total protection of bucks from 1 1/2 to 5 1/2 years of age should have little effect on recruitment. The important harvesting considerations are holding the female segment of the population at a level appropriate to 0.5 K and protecting the bucks until they reach trophy age.

In our example, about 73 bucks are recruited at 0.5 K each year. Harvesting at a rate $h=0.293$, there should be 52 yearling bucks added to the population each year. Assuming 90 percent survival annually until these bucks are 5 1/2 years of age allows a MSY of 34 trophy bucks, 21 male fawns, 21 female fawns and 52 adult does.

<table>
<thead>
<tr>
<th>percent Females</th>
<th>Population size (N)</th>
<th>SY</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_1$</td>
<td>Bucks</td>
<td>Does</td>
<td>Bucks</td>
</tr>
<tr>
<td>0.5</td>
<td>250</td>
<td>250</td>
<td>87</td>
</tr>
<tr>
<td>0.6</td>
<td>200</td>
<td>300</td>
<td>114</td>
</tr>
<tr>
<td>0.7</td>
<td>150</td>
<td>350</td>
<td>141</td>
</tr>
</tbody>
</table>

1. $SY (bucks) = N(P_1\bar{p}m - P_1\bar{p} + P_1 + \bar{p} - 1)$ from Caughley 1977.
2. $SY (does) = N\bar{p}_f(\bar{p} + \bar{m} - 1)$ from Caughley 1977.
Conclusions

Managing for maximum population size is not the best strategy, to maximize SY of total numbers, bucks or animals of a specific age. A goal of maintaining a herd at K-carrying capacity implies that the total value derived from the herd is in viewing large numbers of deer or using them to control vegetation. Optimization of yield more closely follows optimization of recruitment which requires managing for a population size near 0.5 K. A herd should sometimes lie managed at less than 0.5 K if the objective is to reduce competition with livestock or control crop predation.

Management for MSY or OSY necessitates harvest of antlerless deer in large numbers. Sportsmen often object to this, especially the harvesting of fawns. The number of deer seen will be less than when populations are near K. The "people" aspect of managing deer for MSY or OSY, even trophy management, may be more challenging than defining the OSY harvesting strategy.

The logistic model assumes that the ability of habitat to support animals remains constant. This is seldom the case in nature as succession, weather and utilization by animals constantly alter the structure of habitats. A model relating the effects of habitat on population growth, the effects of animal populations on habitat and the role of succession is needed to predict the outcome of harvest strategies with great accuracy. Such a model has been proposed (Caughley 1976), but currently we do not understand a single species of wildlife to this degree.

Those interested in managing deer populations will need to collect certain information on the herd. Measures of reproduction, mortality, age structure, sex ratio and herd size are desirable. Much can be inferred from the sex, weight, age and reproductive condition of animals in the harvest. This information should be considered minimal for management. Although it cannot be used to analytically determine a SY, it does provide a basis for judging alterations in harvest strategies. This information greatly increases the wisdom of trial-and-error management decisions. If the size, age and sex structure of the pre-hunt population can be estimated each year, the ability to achieve a management goal is increased substantially.

I hesitate to recommend use of the logistic model to calculate harvest quotas. The principles of harvesting illustrated with the model appear to be logically correct, but knowledge of the rate of increase and the value of K are difficult to determine for a specific habitat. It appears that the best strategy is to attempt to maintain a pre-hunt population slightly above 0.5 K. McCullough's (1979) empirical model indicated that MSY of the George Reserve deer herd occurred at 0.56 K rather than 0.5 K.

Population management is necessary for optimization of deer management goals. Definition of concise goals, let alone development of harvest strategy to achieve goals, is seldom practiced. The white-tailed deer is adaptable and readily responsive to management. The aim of management is to make possible the satisfaction of societal needs within the biological constraints of the resource. If these needs relate to number of animals or yield, management of populations must be considered on the same plane as management of habitats and people.

Literature Cited


