White-tailed Deer in Eastern Ecosystems: Implications for Management and Research in National Parks

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Preface

The issues of deer and vegetation and their management in the national parks of the eastern United States are of enormous ecological and social complexity. These issues present challenges no less difficult than those of elk and vegetation in the western United States. In recognition of this complexity, the National Park Service (NPS) commissioned a series of field studies to learn about deer and vegetation through original research. The National Park Service also commissioned several reviews to provide park staff with greater access to this knowledge.

This report is one product of those efforts. What we know about deer and vegetation is examined, with the intent of clarifying the issues and thinking about them in an ecosystem context. Much of our scientific understanding of deer and vegetation is based on detailed studies, with an emphasis on statistical technique. This review attempts to minimize detail and focus on the "take home messages" from the research and on their application to management.

This document is written for the National Park Service as background material for evaluating management alternatives. While this report is intended primarily for managers and administrators, we expect that many people concerned about parks will find this material useful.

Acknowledgements

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Introduction

In the past four decades, white-tailed deer (*Odocoileus virginianus*) populations throughout the eastern United States have grown dramatically (Figure 1), from scattered populations of a few thousand individuals to widespread populations numbering in the millions. Much of this increase can be attributed to changing land-use patterns, active trap and transfer programs, and hunting regulations. During the 1970s, state fish and wildlife agencies responded to increasing deer abundance with harvest programs. These programs were designed to cap the populations at a level that was compatible with agriculture and other human activities, generally less than 10 deer/km^2 (25/mi^2).

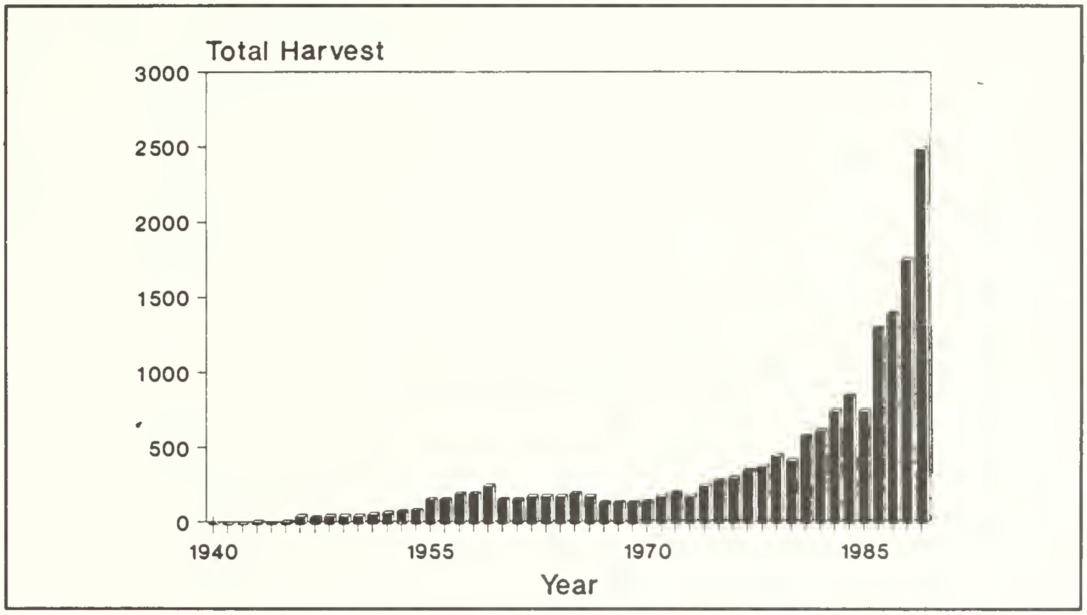


Figure 1. Annual harvest provides indication of growth in a white-tailed deer population in Fredrick County, Maryland, during 1937-89. This growth is typical of that experienced throughout eastern North America over the past 40 years. Redrafted from Hadidian (1991).

Within eastern national parks (those east of the Mississippi River), landscapes have been manipulated to recreate historical scenes or allowed to proceed through ecological succession. The result is a mixture of forest, shrub, and grassland that, in combination with the surrounding interspersion of forest and agriculture, constitute excellent habitat for white-tailed deer. Because deer harvest has not been part of the management regime in most eastern national parks, the populations have continued to grow to densities that are well beyond our experience. Today, populations in many parks exceed 40 deer/km^2 (100/mi^2).

Whether these high deer densities are good or bad is a difficult question to answer. Certainly the growth of deer populations is causing concern for the health and safety of park visitors. The effects of intense browsing by deer on vegetation is causing concern because parks (cultural, recreational, and natural) are becoming increasingly valued as biological reserves containing important remnants of natural ecosystems in eastern North America. Yet, managing deer populations may constitute an unnecessary disturbance of these ecosystems and actually interfere with natural processes.

Eastern national parks range in size from about 0.4 ha to 0.6 million ha (1 acre to 1.5 million acres). Most are in the 400- to 1,600-ha (1,000- to 4,000-acre) size class. Do the natural ecological processes still operate in these parks, particularly with respect to deer and vegetation? Or, does the fragmented environment of the East, and the absence of historical predators, mean that we must impose a new management regime on deer to maintain the integrity of these ecosystems?

The more we grapple with the issues posed by the large deer populations, the more complex the questions seem to become. This report explores the issues associated with large deer populations in parks, attempting to clarify what we know from science and how it can be applied. The report addresses the questions that arise whenever deer and vegetation management are discussed.

What do we know about the behavior and population dynamics of deer? The descriptive information on the behavior and demographic characteristics of deer is extensive. Chapter 1 summarizes our understanding of habitat use, movement behavior, social organization, and demography. This section provides the foundation for the subsequent chapters.

How do deer interact with vegetation within the eastern forest/agricultural ecosystem? While numerous studies of deer, or of vegetation have been done, few address their interaction. Our understanding of deer in an ecosystem context is still in its infancy. We are delving into a realm where the complexity is beyond our experience in science. Much of what is presented in Chapter 2 is extrapolated from current data to provide an answer.

What have we learned from past NPS studies of deer that provide a solid foundation for management? Since 1980, more than 20 NPS studies have been completed. While these studies represent an information baseline, none are sufficiently definitive to provide unequivocal guidance for the decisions that must be made today. The message of Chapter 3 is that political and scientific foundations will need to be much stronger before the National Park Service can sustain deer and vegetation management programs in the face of continuing challenge from public interest groups.

What management alternatives are available and which are the most realistic? While deer populations in some parks should be controlled by management, it is not clear how to accomplish this. We have little direct experience with population management on areas as small as most eastern parks. Chapter 4 provides an overview of approaches that are considered and insight on which have the best potential to work.

What are the priorities for research in the future? Eastern national parks provide a special opportunity to contribute to both applied and basic research on deer/vegetation interaction for three reasons. First, parks today hold the highest densities of deer in our experience. Second, the National Park Service has the ability to regulate the influence of humans on deer and vegetation in national parks. Finally, NPS management is oriented toward the entire ecosystem, rather than a single species. Multifaceted approaches and experimentation are essential to understanding the dynamics of deer and vegetation in eastern ecosystems, and to developing creative management techniques.

In addressing each of these questions, the emphasis is on providing a conceptual background for management planning. References are cited to enable the reader to move efficiently into the scientific literature for additional details, but no attempt is made to provide a comprehensive literature review.

Chapter 1. Ecology of White-tailed Deer

This chapter addresses an obvious and important question: What does a superintendent need to know about deer before venturing into deer management issues? This chapter provides an overview of the ecology of white-tailed deer. This overview is selective rather than comprehensive.

Habitat Use Behavior

The characteristic most common to white-tailed deer habitat throughout the eastern United States is a combination of forest and open field. Areas of woody vegetation, from shrublands to mature forests, provide cover. Deer eat leaves and twigs of woody vegetation, and fruits and nuts, but they prefer to feed in areas with grass or herbaceous vegetation because the quality and quantity of food is higher. Agricultural fields constitute the richest food resource for deer (Harlow 1984, Short 1986).

Deer are fairly tolerant of the amount of (or lack of) forest cover in their habitat. They can survive in areas that are 100% forested and have been recorded to achieve population densities of $10/km^2$ ($25/mi^2$) in the old-growth, mixed northern hardwoods of the Adirondack Mountains of New York. They can also survive in areas with <10% forest, such as the savannas of the Everglades where populations are estimated at 0.25 to $0.40/km^2$ (0.62 to 1.0 mi^2) (Smith 1989).

Deer show limited tolerance to human development. For example, the northern suburbs of Minneapolis-Saint Paul and the parks of the Chicago metropolitan area contain deer populations exceeding $40/km^2$ ($100/mi^2$) (Sillings 1987, Witham and Jones 1987). Low to medium density housing developments generally create a landscape in which the proportion of woody cover and open grassland becomes equal (Figure 2) and also preclude traditional forms of sport hunting. As housing density increases, woody cover decreases. Vegetation tends toward individual trees and linear arrangements. As the number of dogs and people increases, deer abundance decreases.

Deer use forest and fields on daily and annual cycles. Peak activity periods are during late evening and early morning. Hours from dusk to dawn are generally spent in fields. Daytime hours are spent in, or close to, forest cover. This pattern is most pronounced where extensive human activity occurs during the day (Marchinton and Hirth 1986). Daily patterns are also heavily influenced by weather. Deer are able to sense changes in barometric pressure and their activity increases dramatically during the 24 hours preceding the passage of a weather front.

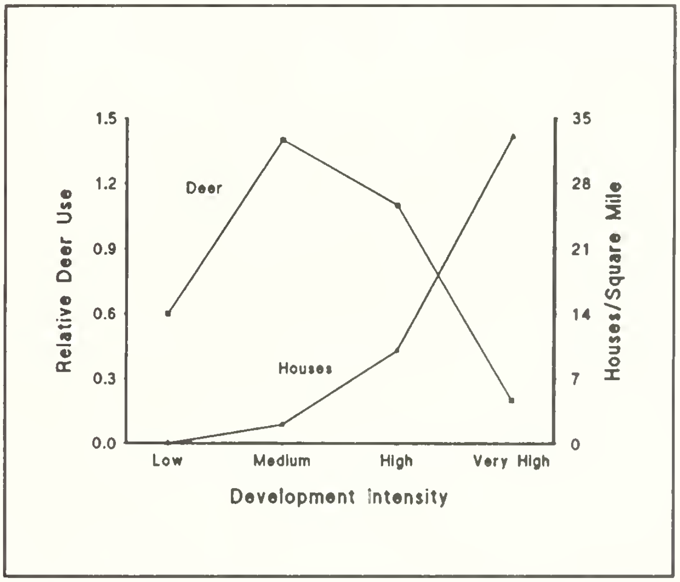


Figure 2. Relationship between deer and human development follows a curvilinear pattern, with optimal habitat conditions occurring at about one house per 60 ha (150 acres) (redrafted from Vogel 1989).

On an annual basis, deer use fields most during the spring and summer. During this period, females are under heavy nutritional stress because of the energy demands of nursing the young. They are attracted to the high-quality food provided by the grasses, forbs, and agricultural crops. By midsummer, the vegetation in fields is tall enough to provide cover as well as food, and deer may spend the entire day in the fields. In northern latitudes, low temperatures and deep snow result in decreased use of fields during winter (Underwood et al. 1991).

Movement Behavior

Deer movement varies seasonally, but the area used by a deer remains the same throughout its life. This area is its home range. During the summer months (i.e., growing season), deer occupy an area of about 200 ha (500 acres), varying from 59 to 520 ha (150 to 1,300 acres). Home ranges are larger in relatively open environments and smaller in forested areas. Home ranges of males are generally two to three times larger than those of females (Marchinton and Hirth 1986).

Home Range - The area traveled by an animal on an annual basis. Sometimes used to refer to the area used seasonally.

The shape of the home range varies, apparently as a reflection of the spatial distribution of cover and food. In general, home ranges are irregular ellipses (Marchinton and Jeter 1967, Hood 1971). In areas of human development, movements become more linear, conforming to the distribution of woody vegetation (Vogel 1989). Social interaction may influence the location of home range boundaries, but little is known about this relationship at present.

In northern latitudes (north of 33^0 north latitude), deer generally have two seasonal home ranges, summer and winter, and migrate between the two. The tendency to migrate is most pronounced where winter snow and temperature are sufficient to significantly restrict activity. Distances of 10 km to 20 km (6 to 12 mi) between summer and winter ranges are common; 50 km (31 mi) appears to be the extreme (Marchinton and Hirth 1986). The distance of the migration appears to vary with climate and individual. Deer move to lowland areas dominated by coniferous forest in most winters because these areas offer better protection against heat loss.

The factor initiating movement to winter ranges and return again in spring is temperature and/or snow depths (Rongstad and Tester 1969, Tierson et al. 1985, Underwood 1990). Biologists have hypothesized that hunting pressure will initiate deer migration to winter range. Rigorous analysis of data at Saratoga National Historical Park does not support this hypothesis (Underwood et al. 1991). Rather, hunting season appears to be seasonally coincident to migration.

Migration between seasonal ranges is less common in southern latitudes. In North Carolina, a seasonal migration appears to be tied to altitudinal variation in spring greenup (Downing et al. 1969). In Alabama, most deer do not migrate, but do show seasonal shifts in the intensity with which they use portions of their home range (Byford 1970). Regardless of latitude, seasonal movements are probably tied to food availability.

The manner in which migration routes are established varies with the sex of the animal. Most females stay near their mother for life, and learn summer and winter ranges from her. Most males (>80%) disperse during their second or third year of life and establish seasonal ranges that encompass those of unrelated females. The males probably establish their traditional summer/winter migration routes by following the females to winter home range. Little is known about dispersing females.

In general, once summer and winter ranges are established, these ranges will be used throughout an individual's life. Evidence suggests that deer will modify migration behavior in response to dramatic changes in food supply (Tierson et al. 1985). However, the fidelity deer show to their home range is strong. In northern latitudes, deer, in some cases, have died of malnutrition on their home range with food accessible in adjacent areas (Severinghaus and Cheatum 1956, Thomas et al. 1964).

Summary: The most common characteristic of white-tailed deer habitat throughout the eastern United States is a combination of forest and open field. Deer use forest and fields on daily and annual cycles. Optimal habitat contains this combination within about 200 ha (500 acres), the average seasonal home range of a deer. In most areas, deer show absolute fidelity to their home range for life.

Social Organization

The core of the social organization in deer is a family group of females. Most females establish a summer (and winter) home range adjacent to and overlapping that of their mother (Tierson et al. 1985, Mathews 1989) (Figure 3). Populations of deer in an area are actually composed of several female family groups. The size of the area occupied by a family group depends on the number of females, but appears to reach a maximum area of 10 km^2 (4 mi^2) (Mathews 1989). Little is known about the social interactions between groups, but family groups do not appear to defend their area against encroachment by other deer in the sense of territorial animals.

While deer are social throughout the year, the size and composition of social groups vary. Females with fawns are relatively solitary during spring and summer. As fawns grow older, they are more frequently observed with the mother. Larger aggregations occur during the fall and winter, and are probably family units, or multifamily congregations. The largest groups are observed in fall and early spring, when deer are concentrated in open fields where green vegetation is abundant (Storm et al. 1989, Underwood et al. 1991).

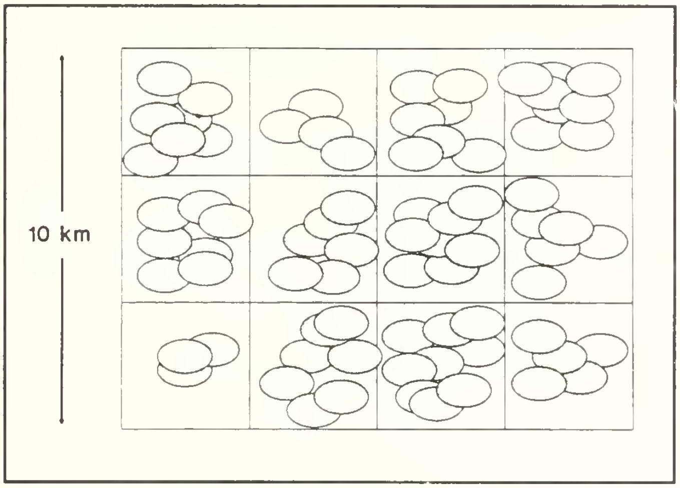


Figure 3. Hypothesized spatial arrangement of home ranges (ovals) of female deer distributed over an area. A grid of 3.3 x 3.3 km (10 km^2) cells is superimposed for scale. Over a period of years, each generation of female offspring establishes home ranges that overlap those of their mother and expand out like the petals on a rose (after Mathews 1989). A population is composed of a series of these family units.

Demography

The question of greatest interest to the public is, "How many deer do you have in this park?" Superintendents of these parks are most likely to ask, "Is the population in this park still growing, and if so, how large is it likely to get?" The answers to these questions fall into the realm of demography. Abundance of deer is determined primarily by four factors: reproduction, survival, carrying capacity, and time.

Reproduction. Two measures are commonly used to assess reproductive performance in deer. Natality is the average number of fawns born per year. White-tailed deer produce between zero and three fawns/female/year. Most females two years and older produce two fawns each year. Younger females produce a single fawn. The number of fawns that survive to sexual maturity is referred to as recruitment, and a 40% to 60% recruitment rate is common.

Variation in reproductive performance (number of young produced by a female of a given age) appears to be related to food resources, the length of the growing season, and genetics. The estrous cycle in deer, like most mammals, is regulated by accumulation of fat reserves and daylength (photo period). Forests, in comparison to agricultural environments, provide lower quality food resources. Northern latitudes, in comparison to southern latitudes, provide a shorter growing season. As a result, deer in northern latitudes grow more slowly and have less time to accumulate fat reserves. Consequently, in northern forests, age of first ovulation is generally delayed until 1.5 or 2.5 years of age. A similar delay occurs in areas where the deer are malnourished as a result of intense competition for food resources. In the southern Midwest agricultural environments where deer populations are held relatively low by hunter harvest, age of first reproduction is 0.5 years. (Table 1).

Recruitment - Number of fawns born per female that survive to sexual maturity (or a designated point in time).

Because reproductive performance is determined by physical growth, biologists have established an index to predict reproduction. Males face the same challenges from growth as females, and antler development is directly related to nutrition. Measurement of the antler beam diameter 2.5 cm (1 inch) above the pedicel on 1.5 year-old males is a good index to nutritional quality of the range, and consequently to reproductive performance of females in the same population. This is a relatively easy statistic to obtain from deer harvested during fall hunting seasons and is frequently used to predict reproduction in a local or regional population (Taber 1958, Severinghaus and Moen 1983).

Survival. In regions where the environment fluctuates widely, fawn survival is the most important determinant of population change. In early summer, new fawns may represent one-half of the entire deer population. If survival is high, the population can double in one year.

Mortality is greatest during the first month after birth, when 30% (reported range, 8% to 100%) of fawns may die (Porath 1980, Mathews 1989). A principal cause of mortality is predation. Abandonment is probably a common cause of mortality when females come into the spring with physical reserves exhausted.

Table 1. Reproductive performances of white-tailed deer in eastern United States.

Study Area	**Dominant Vegetation**	**Fawns**	**Yearlings**	**Adults**
Adirondack Mountains, New York (Severinghaus and Moen 1983[1])	Forest	0.03	0.92	1.54
Northern Michigan (Harder 1980)	Forest	0.06	1.25	1.75
Cape Cod National Seashore (Porter et al. 1991b)	Forest/Sand Dune Community	0.11	1.06	1.61
Saratoga National Historical Park (Underwood et al. 1991)	Forest/Grassland	0.03	0.86	1.37
Gettysburg National Military Park (Storm et al. 1989[2])	Forest/Grassland	1.00	1.70	1.70
Cumberland Island, Georgia (Miller 1989)	Forest/Grassland	NR[3]	1.00	1.70
Western New York State (Severinghaus and Moen 1983[1])	Forest/Agriculture	0.32	1.48	1.81
Ohio (Statewide) (Nixon 1971)	Agriculture/Forest	1.29	1.87	2.04
Iowa (Statewide) (Harder 1980)	Agriculture/Forest	0.74	1.66	2.10

[1] Estimated from antler beam diameter on yearling males.

[2] Value for Fawns corresponds to Storm and other's yearling class; values for Yearling and Adult correspond to Storm and other's adult class.

[3] NR is Not Reported.

The ultimate source of much of the overwinter mortality is nutrition. The keys to survival are the quality of summer food, the length of the time high-quality food is available, and the number of deer competing for that food. Deer accumulate fat reserves during the summer months and use them to survive the winter (Mautz 1978). Drought and frost reduce the quality of food, and snow restricts access to food. During this period deer exist on a negative energy budget, expending more energy per day than they gain. Because fawns allocate much of their energy to growth, their fat reserves are smaller, relative to adults. Thus, fawns are less able to cope with long periods of negative energy budgets than are older deer. Few deer actually die of starvation in the sense of having nothing to eat; most die of malnutrition (i.e., they are unable to get a sufficient quantity of quality food).

Where sport hunting occurs, it is the dominant mortality factor for adult deer. Many states regulate hunting to achieve an annual harvest of 30% to 40% of the females and up to 60% of the males in the fall population (Creed et al. 1984). Under these conditions, deer generally do not live beyond 2.5 years.

Where sport hunting does not occur, the life expectancy increases once a deer reaches 1.5 years, especially for females. Females in northern latitudes commonly live to 12 years and can live to 16 years (Masters and Mathews 1991). Coyotes and dogs kill adult deer year-around (Brundige 1990, Underwood 1990), and in more urban environments, automobiles are the dominant cause of mortality (e.g., Cypher et al. 1985, Storm et al. 1989).

Carrying Capacity. The third determinant of population abundance and growth is carrying capacity. Suppose we have a deer population growing in an area where predators and hunter harvest are not significant mortality factors, as is the case in most eastern national parks. As the population grows, competition among deer for food resources becomes increasingly intense and a series of changes begin to occur:

1. declining abundance of plant species that are preferred by deer as food
2. declining survival of fawns
3. delayed age of first reproduction
4. increasing parasite loads (in southern latitudes)
5. declining average body weight among adults
6. increasing mortality among adults

Ultimately the survival of fawns exactly equals the mortality of adults and the population ceases to grow. A relatively simple mathematical model captures this pattern of growth:

$$dN/dt = r(1-N/K)$$

dN/dt is an expression for the *change in deer abundance per change in time*. For our purposes, this is the number of deer added to the population each year after subtracting the losses. The ability of the deer population to reproduce, or the *intrinsic growth rate*, is represented by r. N is the *population abundance*, and K is the upper limit to population growth. The mathematical formulation $1-N/K$ causes the growth curve to be S-shaped and symmetric. Deer populations appear to grow in a symmetric (logistic) fashion (McCullough 1979) (Figure 4).

The term "carrying capacity" causes frequent confusion because two distinct definitions are used: *ecological carrying capacity* and *economic carrying capacity* (Caughley 1979, Macnab 1985). Both concepts begin by defining carrying capacity for deer in relation to the nutritional conditions of the environment. Both agree that higher carrying capacities occur in environments where higher quality food resources are present in greater abundance and for longer duration. They diverge in their interpretation of the changes (1 through 6, mentioned earlier) that occur as the population grows.

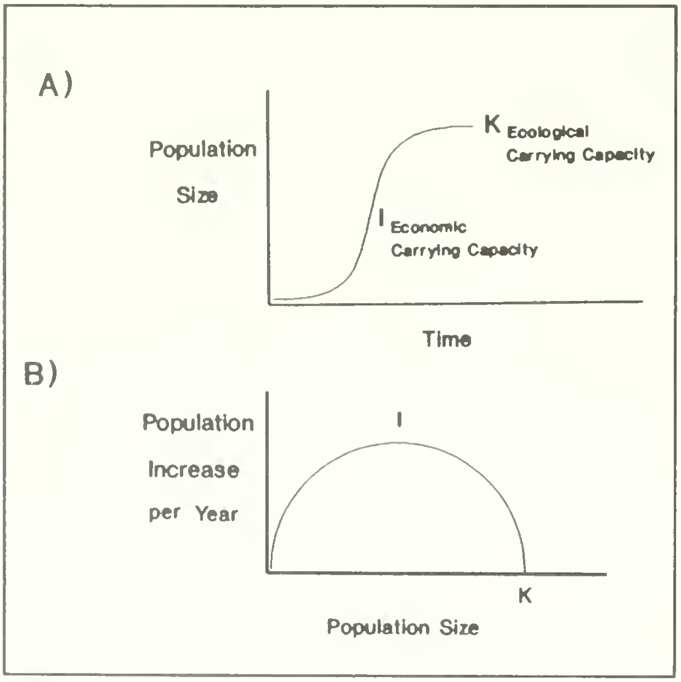


Figure 4. Idealized growth of a population to ecological carrying capacity (K). Economic carrying capacity is a population density that is one-half K, designated I (following McCullough 1979). The growth follows a classical S-shaped (here it is logistic) function $dN/dt = r(1 - N/K)$. (A) Plot of population growth against time. (B) The same growth pattern plotted as the number of individuals added to the population as a function of population size. Note that as the population approaches K, recruitment declines steeply.

Most ecologists view the changes as part of the normal interaction between deer and vegetation. When the browsing and grazing of the vegetation removes exactly the quantity of food resource produced each year, and the few fawns that do survive exactly replace the adults that die each year, the deer and vegetation have reached an equilibrium. This is *ecological carrying capacity* (Caughley 1979) (designated *K* in Figure 4).

However, many wildlife managers argue that these changes in vegetation and deer are not normal but are indicators that the population has exceeded carrying capacity. They maintain that equilibrium is achieved when deer populations are producing the maximum number of offspring per year, are exhibiting high average body weight, and are causing little or no change in the plant community. This is *economic carrying capacity* (designated I in Figure 4) and occurs at about 50% of ecological carrying capacity (*K*/2) (Caughley 1979).

K - Ecological Carrying Capacity. Herbivore abundance when removal of vegetation by browsing and grazing exactly equals the food resources produced annually by the plant community, and fawn survival equals adult mortality.

This philosophy is attractive to state conservation agencies because it corresponds with their values. The goals of most state deer management programs are to maximize recreational hunting opportunities and minimize landowner complaints. At *K*/2, deer populations achieve maximum sustainable yield for harvest. Most deer populations managed through hunting are held below *K*/2 to ensure minimal impact on vegetation.

From an ecological perspective, neither type of carrying capacity is constant. Although textbooks portray *K* as a stationary point, it is not. If we think of *K* as the quantity of the vegetation on the landscape and its nutritional quality, we realize that *K* (and *K*/2) fluctuates. For instance, in years of drought or unusually long winters, *K* is lower than normal. The more widely (and unpredictably) *K* fluctuates, the more difficult it is to manage a population either for a sustainable yield (economic carrying capacity) or to predict ecological carrying capacity (Figure 5).

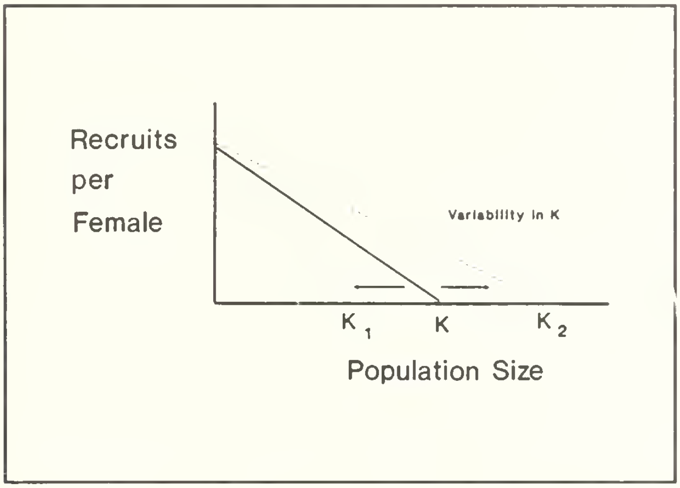


Figure 5. Recruitment (fawns surviving to one year) per female declines with increasing population density. In fluctuating environments, we get a long-term average *K* with variation around this average. K_1 represents the lower bound of ecological carrying capacity typical of the environment, and K_2 the upper bound. Note that the slope of the recruitment rate line can change from one year to the next as *K* shifts up or down.

Regardless of the position of *K*, the population is always responding to it, growing toward it. However, populations cannot respond instantly to changes in *K*, and thus will be above or below *K* at a specific moment in time. The time lags created by this inability to adjust immediately are crucial to understanding deer in an ecosystem context.

Time. In reality, large fluctuations in environmental conditions determine abundance in most deer populations. Unusually favorable conditions may occur for several years. *K* increases, allowing a deer population to erupt (grow rapidly), and the population is quickly above its long-term average equilibrium density.

However, *time* is more critical when deer populations decline. A drop in abundance by > 50% within a span of one or two years is known as a "population crash." In northern latitudes crashes are caused by severe winters. In the central Adirondacks, three successive severe winters resulted in a drop of the deer population from an estimated 12/km^2 (30/mi^2) to 2/km^2 (5/mi^2) (Underwood 1990). A single severe winter at Saratoga National Historical Park caused an 18% drop in an otherwise growing population.

Population Crash - A decline in a population of > 50% in one or two years.

In southern latitudes, disease has caused similar crashes. Epizootic hemorrhagic disease appears to cause the most significant declines and is widespread (Trainer and Karstad 1970). The population crash at Cade's Cove, Great Smoky Mountains National Park, during the early 1970s can probably be attributed to this disease (Wathen and New 1989). In coastal environments, direct mortality from hurricanes may cause major declines (O'Connell and Sayre 1989).

The importance of time to the question of abundance depends on two factors: the population growth rate and the frequency of crashes. For example, in areas where the growth rate is 1.25 (lambda, λ), a population will need about six years to recover from a single 70% reduction. If it drops from 1,000 deer to 300, and then grows at a constant rate, it will be 375 after one year, then 469 (yr 2), 586 (yr 3), 732 (yr 4), and 915 (yr 5).

In reality, the time to recovery is frequently much longer. Females aged three to nine years produce most of the young each year (Table 1) and are most likely to raise these young to maturity. The loss of a large portion of the population means the loss of many females in prime reproductive age classes. The subsequent population growth rate will be lower than average. The effect is prolonged because heavy losses in the younger age classes mean that few animals survive to become the prime reproductive females of the future.

λ - Lambda - Rate of growth in a population from one year to the next. Calculated as a ratio:

$$\frac{\text{Abundance This Year}}{\text{Abundance Last Year}}$$

Summary: Abundance of deer is determined by four factors: reproduction, survival, carrying capacity, and time. Fawn survival is the most important determinant of population change from one year to the next. When the biomass of food resources removed by deer equals that produced, and the number of fawns surviving exactly replace the number of adults dying each year, the deer and vegetation have reached equilibrium, or *ecological carrying capacity*. This is often confused with *economic carrying capacity*, an equilibrium set by management at which the population shows peak reproductive performance, maximum body weight, and the vegetation shows little change. Time since the last major disturbance may be the most important influence on abundance in most deer populations.

Chapter 2. Deer and Plant Communities from an Ecosystem Perspective

"a plant - herbivore system is not just a vegetation suffering the misfortune of animals eating it. Rather it is an interactive system with massive feedback loops. . . ." (Caughley 1989:8)

Beginning in the mid-1980s, the questions of greatest interest to the National Park Service were those pertaining to the effects of deer on vegetation. While many eastern parks were established to preserve a variety of cultural and recreational resources, these parks were increasingly important as remnants of natural ecosystems. The questions seemed to converge with those confronting managers of natural resource areas. They evolved from what to do about "vegetation damage" in particular parks, to what constitutes "natural" (and unnatural) fluctuation in deer and vegetation.

While this chapter presents deer as a component of the ecosystem process, much of what is presented is not a summary of established fact. We simply do not understand the interaction of deer and vegetation within eastern ecosystems well. These systems are complex, and understanding deer/vegetation relationships has generally proven intractable to traditional investigative approaches. This chapter provides a point of departure for future discussion.

Plant Communities

When venturing into deer/vegetation interactions, we are immediately drawn into the realm of plant ecology. This discipline is built on three premises. First, plant communities are assemblages of species with relatively predictable composition. Second, plant communities are dynamic--they change through time. Third, some communities change more slowly than others, the time scale ranging from one year to centuries.

Succession. One of the great ecological contributions in the past 100 years has been the discovery that the process of change in plant communities is generally predictable. Given information on general climate, soil, and moisture conditions, and the proximity of seed sources, we can often predict the sequence of species that will dominate a site. With additional information on the kinds of disturbance to expect, and the frequency of its occurrence and its intensity, we can forecast the general character of the vegetation over long periods.

The composition of a community at any point in this sequence is determined by the ability of each plant species to compete. Not all plants are equally adapted to growing throughout the ranges of environmental conditions present in the eastern United States. Each species varies in its tolerance and efficiency under given sets of conditions. As plants grow, they alter the conditions on a site in ways which prove to be detrimental to their own reproduction. As a result, they eventually give way to different species which are better suited to the new conditions.

Succession - Predictable sequence of change in plant (and animal) species composition through time on a given site.

The rate at which species composition changes is an important characteristic of succession. The rate of change is dependent on the longevity of the species on the site, and frequency of disturbance by outside forces. Because most species do not reproduce in their own shade, they dominate a site only as long as the first wave of colonizers can live.

In eastern landscapes, change occurs most rapidly when sites are dominated by herbaceous vegetation. Change occurs most slowly when the sites are dominated by mature trees. In the absence of disturbance, eastern forests reach a composition of species that will persist for long periods of time, perhaps centuries. Some communities are composed of the species that can reproduce effectively in their own shade and are in a relative steady state. Many ecologists hypothesize that these long-lived communities constitute the equilibrium condition of the system.

Long-term equilibrium conditions are not common on a local site (<5,000 acres), however. Fires, hurricanes, droughts, and ice storms influence eastern forest systems, periodically driving species extinct or transporting species into novel environments. Given that it takes several centuries to reach an equilibrium condition in eastern forests and major disturbances are likely to occur at least once a century, equilibrium is seldom achieved, and if it is, it does not persist long.

If we take a little different perspective, a different kind of equilibrium may occur. Large parks (>40,000 ha, or 100,000 acres), such as Great Smoky Mountains National Park, may be thought of as composed of hundreds of smaller sites that are in various successional stages. Some have not been disturbed for several hundred years, and others have been disturbed within the past year, but most of the sites are in some intermediate stage for succession after disturbance. Changes are occurring on nearly every site within this mosaic. However, the pattern of change is such that when considering the park as a whole, the proportion of the land area in each of the stages remains relatively constant, and the landscape is considered in equilibrium.

In considering deer/vegetation issues, we must remember the following:

1. The composition of plant communities on most local sites is constantly changing.
2. These changes are driven by processes that operate over long periods of time, by human standards.
3. The current composition reflects events of the past, perhaps the conditions that occurred 100 years ago, more so than the conditions of the present environment.
4. The size of the area is an important determinant of the kind of equilibrium to expect.

Herbivory

Herbivores such as deer add another dimension to the process of change in plant communities because they alter the competition among plant species. Browsers and grazers are selective in their diet. The degree of selectivity varies, but the point is that not all that is green is equally preferred. As a consequence, those plant species not eaten may have a distinct advantage in the competition. Insects probably consume more plant biomass than any other group of organisms, and outbreaks of species such as gypsy moth (*Lymantria dispar*) can have dramatic impacts. For purposes of this discussion, however, we will assume that the influences of insects are relatively constant and focus our attention on the effects of mammalian herbivores.

We know something about the interaction of mammalian herbivores and vegetation from range management studies in western North America, Australia, and Africa. Extensive studies allow us to predict which plant species will increase in the community and which will decrease as a result of varying levels of herbivory by domestic livestock.

However, applying range management approaches to predicting deer/vegetation interactions in the eastern forests is probably not feasible. We do not have sufficiently detailed information. Eastern forests are composed of species with long, complex life cycles, and science is still working on the basic biology of many of those species. Further, food preferences of deer not only differ from those of livestock, but appear to vary from one place to another for reasons that are not yet clear.

Influence of Deer Density. One deer will have some effect on vegetation. As deer densities increase, the effect on the most preferred plant species will increase. If deer populations continue to build, the influence on less preferred plant species will also begin to increase.

Some evidence shows that deer have driven plant species extinct, locally (Bratton 1979). However, it is unclear whether total elimination of plant species by deer is a rare or common phenomenon. Too few monitoring programs have been in place long enough to document this kind of change.

Much stronger data exist to show that deer can have a substantial influence on species dominance within plant communities (e.g., Beals et al. 1960, Tilghman 1989). In the Adirondacks, for example, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) are dominant members of the overstory (Behrend et al. 1970). The understory contains many maple and birch seedlings. The sapling class, however, is heavily dominated by American beech (*Fagus grandifolia*) because, in contrast to maple and birch, beech is not a preferred food item for deer and thus is allowed to grow. The current maple/birch overstory is hypothesized to have developed at a time when deer populations were low. The future overstory is likely to be dominated by beech.

In other cases, deer may be affecting the rate of change in the plant communities. At Saratoga National Historical Park, the usual successional sequence involves invasion of abandoned fields by ash, cherry, and maple (*Fraxinus spp., Prunus spp., Acer spp.*). Indeed, seedlings of these species are common in grassland areas. However, these are preferred food items for deer and browsing does not allow growth above a few centimeters height. Only clonal species such as dogwood (*Cornus spp.*) can tolerate the browsing and invade the open fields. The dogwood persists for about 30 years and is eventually overtopped by ash, cherry, and maple. Tree seedlings appear to be able to grow in the center of these dogwood clones because deer cannot reach them (Austin 1991, Underwood et al. 1991).

In the extreme, browsing by deer may preclude usual successional sequences. Areas of Cumberland Island in the South and Pennsylvania in the North provide good examples of this. On Cumberland Island, browsing is suppressing live oak (*Quercus virginiana*) (Bratton and Kramer 1991). In Pennsylvania, there is almost no woody understory, and when the overstory of cherry and maple is removed by timber harvest, the sites become dominated by grasses and ferns (Marquis 1981).

Diversity. The effects of deer are frequently related to plant diversity. Diversity is a way of quantitatively measuring change in plant communities. Ecologists have developed mathematical techniques for expressing the diversity of a plant community as a numerical index. Comparison of the index values from one time to the next allows us to objectively assess change.

The equations are not important here, but the underlying concept is. Most diversity indices are a combination of two factors. First, richness defines the number of different species present. More species means greater richness. Second, equitability defines the proportional relationships among the species. For instance, if a simple community contains three species, and there are exactly the same number of individuals of each plant species growing in the locale, the proportional distribution is 1:1:1. Equitability is at maximum.

Diversity - An ecological measure composed of two factors: richness (number of different species) and equitability (proportional distribution of abundance among species).

Some people use diversity to mean only species richness. Others use it to mean both richness and equitability. Defining how we are using the term is essential in applying it to a characterization of change in plant communities. Deer affect species diversity primarily through altering species equitability in the community.

Summary: Key to understanding deer/vegetation interaction is recognizing that plant communities are dynamic. The successional process of change is relatively predictable in eastern ecosystems. Deer alter the relative abundance of plant species because they are selective in their diet. This influences which species are dominant (equitability). The influence of deer on species richness is less certain.

Natural Regulation

The concept of natural regulation is central to the question of deer and vegetation management. Natural regulation has been the historical foundation to NPS wildlife management objectives in the large western parks because of the strong orientation to preserve ecological processes (Leopold et al. 1963, Cole 1971, Houston 1982). Current trends suggest that ecological processes will play a more prominent role in managing eastern parks because of the increasing interest in the biological reserves of parks (Agee and Johnson 1988). If the role of eastern parks includes preserving natural ecosystems, the defense for a decision to undertake active management will require that the National Park Service be able to substantiate that natural regulation is not occurring in deer/vegetation interactions.

Considerable debate continues about natural regulation in the literature and a brief summary may be helpful. The disagreements on key issues are largely a matter of perspective. New ways of thinking offer powerful approaches to assessing whether or not natural regulation is likely to occur in a given setting.

Natural Regulation - The natural control of a population such that abundance increases to some limit and then, in the absence of disturbance, remains constant.

Feedback Loops. If a population is to grow to some limit and then remain constant, a mechanism must be present to regulate growth. Negative feedback between population size and continued growth is essential. For deer, this may be as simple as:

deer population growth → increased competition for food resources
increased competition → decreased nutrition
decreased nutrition → decreased reproduction and increased mortality

This is a negative feedback loop because an *increase* in deer abundance ultimately results in a *decrease* in reproduction. In practical terms, we test for natural regulation by looking for a decline in the number of six- to eight-month-old fawns per female in the late winter population as abundance increases (Figure 5).

Issue #1: Science vs. Values. Much of the debate about natural regulation can be attributed to a failure to differentiate ecological conditions from human values. Yellowstone National Park provides a good example. Houston (1982) argues that elk populations are limited primarily by winter food supplies and weather. Given a series of mild winters, the populations will expand and alter species equitability in the plant communities.

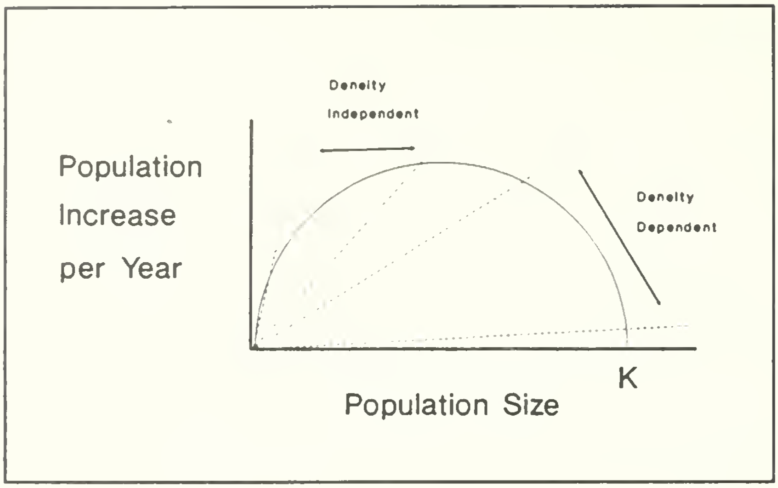
Others contend that the grazing and browsing of large populations of elk have caused a deterioration of plant communities in the Yellowstone-Teton area from historical conditions (e.g., Weinstein 1979, Kay 1990). They interpret this change in condition of the plant community to mean that the elk population is above carrying capacity and, consequently, that the changes in vegetation are abnormal.

The debate is more complicated than this, but the issue is straightforward. The argument is actually ecological carrying capacity versus a value judgment. To adopt ecological carrying capacity means we are willing to accept changes in the plant community that are associated with periodically large population of herbivores. To classify some changes as a "deterioration of the system" means we are accepting a value system. Where ecological carrying capacity specifies a set of conditions, economic carrying capacity (or any other population goal) specifies a set of *desired* conditions and thus imposes a value system (Underwood and Porter 1991).

Issue #2: Density-Dependent vs. Density-Independent Factors. Density-dependent factors regulate population growth if an increase in population density causes a decrease in the growth rate of the population and vice versa (Chapter 1). Environmental forces that operate on growth in a manner which is not influenced by the density of the population are called density-independent factors

The premise for an S-shaped growth form in a population is that natural processes set an upper limit to population abundance and that population growth toward this limit is regulated by density-dependent factors. Skeptics argue that this growth pattern is evident only under laboratory conditions and has not been demonstrated in populations growing under natural conditions (e.g., Hall 1988).

The crucial test is to experimentally reduce a population density and look at the response of the population. If a population grows in a sigmoid pattern and is between *I* and *K* on the growth curve (Figure 4), a reduction in density should result in an increase in recruitment (survival of young to sexual maturity) during the following year. McCullough (1979) used this approach on the George Reserve in Michigan and concluded that density-dependent regulation does function in white-tailed deer. Similar findings have been noted for other ungulate species (Sinclair 1977, Houston 1982).



The essence of this debate is the factor of *time*. Populations in many environments do not have enough time to grow to *K*. It is not that *K* is inapplicable. The populations are just disturbed so frequently by external forces such as severe winter or drought (density-independent factors) that they are constantly in a state of recovery (e.g., Dusek et al. 1989). When recovering populations are low on the growth curve (near or below *I*), density-dependent regulatory processes are difficult to discern (Figure 6). Both density-dependent and density-independent factors are operating in these circumstances.

Figure 6. Hypothetical model of range of population sizes over which density-dependent and density-independent processes affect recruitment of young. Frequent influence of density-independent factors can keep the population in a constant state of recovery, masking density-dependent processes.

Issue #3: Presence vs. Absence of Herbivores. Exclosures show us that plant community composition is dramatically different in the absence of deer. This difference has been the chief argument for reducing deer populations in national parks. Yet, as Caughley (1989) observed, if we were to place an exclosure in the midst of the Serengeti savannas of East Africa, an ecosystem where herbivores have existed in large numbers for millennia, we would consider the vegetation growing inside the exclosure to be an aberration in that system.

We know that changes in plant communities are shaped by successional processes. To compete, plant species are continually adapting to the physical and biotic conditions of the environment. While the role of white-tailed deer in the long-term dynamics (centuries or more) of eastern plant communities is not fully understood, two points are clear: (1) deer constitute one of the biotic factors influencing successional patterns and (2) the degree of influence varies with their population density.

The basic issue hinges on the definition of "normal." If deer populations are eliminated or held artificially low, is the successional process normal? Are plant communities arising in the midst of widely fluctuating abundances of deer normal? The difficulty is that "normal" has not been defined in scientific terms, but rather in terms of value systems. Science has yet to be able to cast the question of what constitutes ecological norms for a given system in terms that are rigorous enough to be tested. Until we are able to formulate and test these ideas as hypotheses, this debate adds little to our understanding of the ecosystem.

Issue #4: Presence vs. Absence of Predators. Here the argument is not if regulation occurs, but how. The issue is that hunting by Native Americans (and later, European settlers) and large predators held herbivore populations in check. Because man has removed the large predators and eliminated hunting, deer populations are able to grow to densities never before experienced (Kay 1990, Warren 1991). The plant community has not evolved to cope with these high densities, and thus the browsing is detrimental.

Here there are two critical questions: (1) Can predators limit herbivore populations? (2) Did they do so historically? The answer to the first question is yes and no. Certainly predators can limit ungulate populations under some circumstances, but in general, they appear to be a secondary influence (Connolly 1978, Ballard 1991). Deer populations frequently increase until some other factor limits growth. The role of predators and Native Americans, historically, is difficult to evaluate. It falls into the realm of ecological paradigm, a plausible scenario, but one which probably can never be tested.

Issue #5: Stable vs. Unstable System. Associated with regulation is the concept of stability. Stability can be thought of as an ecosystem's *resistance* to disturbance, or its *resilience* (ability to return quickly to equilibrium) following disturbance. Whether or not stability is desirable is an interesting question, but the concept of stable systems seems to be attractive because it more easily meshes with our management philosophy of preserving resources in constant states. The hypothesis is that the unusually high deer populations are causing significant change in the system and that this must mean the systems are less stable.

Stability - The ability of an ecological system to resist change, or to return quickly to a relatively constant state.

Attacked head-on, this hypothesis proves to be elusive. We have difficulty defining the space and time intervals within which stability should be measured. An astute observer once noted that the robins go extinct in an apple tree several times a day (Smith 1975). How is this different from the loss of a tree species from a park and its subsequent return after a century?

We also have difficulty defining how much change is required to deem a system unstable. If a plant species becomes extinct, is this an indication that the system is no longer stable? How do we distinguish between stable systems that are fluctuating and unstable systems that have lost their ability to move back toward the equilibrium?

Another approach to the question has been through measuring diversity. The rationale is that diversity is equated with ecosystem stability: the more diverse a community, the more resistant it is to change, or resilient to disturbance. Early work suggested a direct relationship between diversity and stability. More critical analyses dispute this simple relationship. Stability appears to be a complex relationship involving the diversity of species, the number of species with which they interact, and the intensity of this interaction (May 1972, Jeffries 1974, Pimm 1982).

Summary: The concept of natural regulation is important because it is the current foundation to NPS wildlife policy. The crux of the issue is whether or not deer are affecting long-term stability of plant communities. Traditional approaches have largely failed to help us evaluate this issue because they frequently confuse value systems and scientific inference. They hinge on defining "normal" and "stable" and, as yet, we have no rigorous, scientific basis for defining these terms.

Ecosystem Behavior

At the heart of the regulation debate is concern for the long-term viability of the natural ecosystem. The common denominator of the debate is the question of whether the system is moving toward an equilibrium or irreparable breakdown. The concept of *resilience* in plant/herbivore interactions is the true issue.

We know that deer and vegetation of the eastern United States are seldom in a state of constancy. They are disturbed continually by a variety of powerful outside forces. Consequently, the system is seldom, and perhaps never, at equilibrium. The important question is, how strong is the tendency for the system to move toward equilibrium (Caughley et al. 1987)? No work has been done to address this question. What follows is a speculative analysis to answer the question, drawing on studies in other areas.

For a system to move toward equilibrium, a feedback loop must exist between herbivore populations and plant biomass: increased consumable plant biomass → increased herbivore populations → decreased consumable plant biomass → decreased herbivore populations → increased consumable plant biomass, etc. Three qualities add complexity to this simple relationship. First, forest understory plants vary widely in their response to browsing by deer. This makes it difficult to predict how given densities of deer will affect vegetation. Still, if the environment is relatively constant, we can expect biomass of vegetation and deer to achieve relative constancy.

Second, inherent to the system is fluctuation in annual moisture and temperature conditions. In the eastern United States, seasonal drought and winter reduce food quality. The degree of reduction is variable, but the change is often sufficient to affect the population dynamics of deer.

Third, the annual fluctuations occur *within* the context of the long-term changes due to succession, and the powerful forces that disrupt succession. Large perturbations result from hurricanes and fires. These factors alter the deciduous forest so greatly that frequently the system does not return to its predisturbance condition for decades or centuries.

We might think of all of this environmental fluctuation in terms of *K*. Favorable conditions push *K* up, unfavorable conditions push it down. A series of years with favorable conditions can cause a deer population to grow. When favorable conditions are followed by severe conditions (e.g., drought-induced decrease in *K*), the deer population is caught above the new *K*. The population is likely to crash.

Succession causes fluctuation in *K* on a longer time scale and can have greater impact. Vast numbers of species move into and out of the communities. The changes in plant biomass and species composition associated with succession mean changes in nutritional conditions for deer. *K* is moving up and down with forest development, compounding the effect of annual variation in weather. Deer populations are thus growing toward an equilibrium target that is itself moving and may be moving in two directions at once, at different rates (Figure 7).

Deer cannot respond instantly to changes in vegetation. Following a hurricane or fire, the regeneration of a forest results in more than 100 times the increase biomass of seedlings and saplings per year. Deer populations are able to grow by a maximum of 2 times per year. Nutritional conditions would support many more deer, but a population response takes more time.

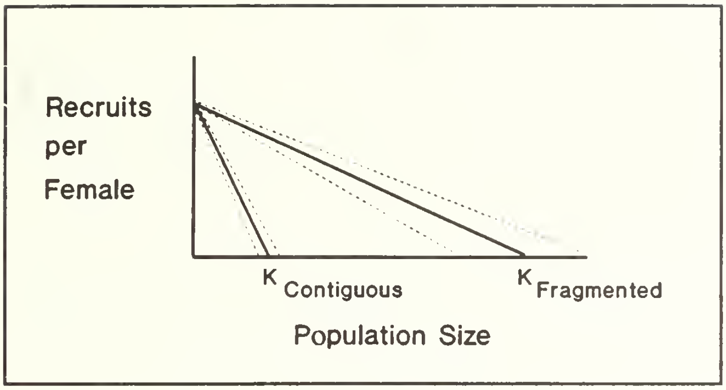


Figure 7. In eastern forests, succession causes changes in carrying capacity for deer, a moving equilibrium. The equilibrium is highest in early successional communities interspersed with mature forest (a fragmented condition) and lowest in mature, contiguous forests when trees exceed the height deer can browse.

These time lags add still more complexity to the recovery process. Once the forest moves into the large sapling stage, biomass production within the reach of deer declines and nutritional conditions drop to low levels. Prior to this point, the deer population was growing toward a higher *K*. *K* is now lower and the deer population is well above it. This condition leads to the inference that the population has "over-shot" *K*. It will take a few years (perhaps a decade) for the population to adjust to the new conditions.

In short, the deer/vegetation systems of the eastern United States are disturbed frequently by external forces. Plant communities and deer populations are frequently out of synchrony. Both deer and vegetation conditions at any moment are more a product of the conditions of past years than those of the present. The major perturbations common to the eastern United States, and succession, inject long time lags into the system. These time lags loosen the feedback loop, but do not alter the basic processes necessary for centripetality.

The implications are clear. Deer will have the greatest effect on vegetation when their populations are "caught" above *K*. When such a condition occurs, competition for food will be high and deer will feed on a broader array of plants. The intense browsing will deepen the trough of plant biomass production in the understory, particularly among species that are preferred food items. The probability for complete loss of a plant species is highest when deer are above *K*.

Summary: Because vegetation and deer populations respond to disturbance on different time scales, deer are seldom at *K*. Changes in weather and successional development of vegetation cause variation in *K*. Deer populations are not able to respond quickly to changes in *K* and thus are frequently out of synchrony with vegetation conditions. The probability for significant loss of a plant species is highest when deer populations are high and *K* is declining rapidly.

Application to Human-Dominated Landscapes

The argument is often made that many ecological processes no longer operate in eastern forests. Predators have been removed, hunting by Native Americans is absent, the forest has been fragmented, and agriculture and urban development have dramatically altered natural processes. Eastern parks exist within this human-dominated landscape. Do feedback loops still function in these systems?

Predators. Removing predators is considered by many to be the cause of the dramatic increases in deer populations. There is probably only limited truth in this assertion. If predators take an increasing proportion of the herbivore population as it grows larger, they will have three impacts: (1) they will reduce the long-term average biomass of the herbivore population, (2) they will reduce the peaks of the fluctuations, and (3) they will reduce annual recruitment of young. By reducing recruitment of young, predation will lengthen the time it takes the herbivore population to recover from a trough. This lengthens the time interval during which the population is below the long-term mean abundance (Figure 8).

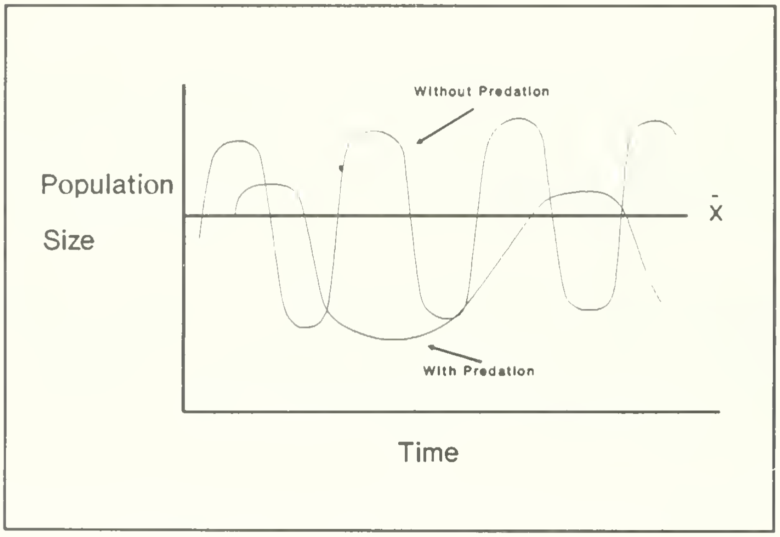


Figure 8. Theoretical model comparing deer population fluctuation with and without predators. The effect of predators is to reduce the amplitude of fluctuation, reduce the peak of the growth, and lengthen the interval between oscillations.

There is still considerable uncertainty about the role of predators in regulating populations of herbivores (e.g., Peterson 1988). Perhaps the clearest conclusion to date is that the presence of predators will allow greater long-term vegetation change. Because predators lengthen the time during which deer populations are in the low portion of the cycle, many plant species may achieve growth that would otherwise not be possible. For instance, tree seedlings in old fields in the East require five to eight years to grow to a height at which deer can no longer limit growth (Underwood et al. 1991). The presence of predators may provide this "window of opportunity." The 200- to 400-year-old forest stands we see today may be a product of this window of opportunity, their species composition reflecting a time period of low deer populations.

In a broader sense, are eastern ecosystems which include predators likely to be moving towards equilibrium? If the relationship between predators and deer is similar to that between deer and vegetation, predators are part of a feedback loop:

> increased numbers of predators → decreased numbers of deer → decreased numbers of predators → increased numbers of deer, etc.

The equilibrium will continue to be determined by vegetation conditions and, under most conditions, predators will *respond to* deer population fluctuation, rather than *cause* it. However, the presence of predators will likely reduce the amplitude of fluctuation. Depending on the degree to which predators affect fluctuation of deer abundance, they may or may not be important in maintaining the eastern forest ecosystem.

Substitutions for Predation. Does the mortality associated with sport hunting or auto/deer collisions substitute for the absence of predators? Yes and no. While hunters show a preference for taking males, the harvest of females provides a potential for regulating population growth in deer. Under current hunting regimes in most states, the *proportion* of females harvested increases with increases in population density and declines as populations decline. Thus, managed sport hunting that involves significant harvest of females acts in a regulatory manner similar to that of predators.

Interestingly, there is some question as to whether or not the hunting regulates deer populations too tightly. Managed deer populations often fluctuate only ± 10%. If eastern plant communities have coevolved with widely fluctuating deer populations, tight regulation of the population may actually be counter to conditions required for normal succession.

Automobiles do not substitute for predators in an ecological sense. The number of auto/deer collisions increases with increasing deer populations, but the *proportion* of the population removed does not. This form of mortality reduces population size, but because it does not change proportionally to the population, auto/deer mortality is not regulatory.

Influence of Agriculture. Changes in the landscape appear to have a far greater impact on the system than the loss of predators. Fragmentation of the eastern forest with pastures, hayfields, and crops dramatically increased food resources for deer between 1760 and 1860. Modern agriculture is even more productive and increases nutritional conditions for deer during both summer and winter. Deer/vegetation equilibrium levels in 1960 were probably 10 to 50 times those of 1760 (Figure 9).

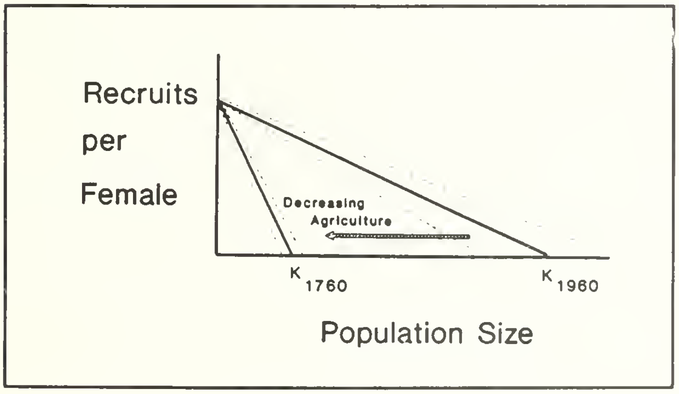


Figure 9. Ecological carrying capacity has increased dramatically in the past 200 years as a result of forest fragmentation and agriculture. *K* can be expected to decline as the amount of land in agriculture decreases in eastern United States.

If we can assume that the current forest/agricultural landscapes will remain relatively constant, then the landscape of today may be more strongly centripetal than that of the past. Agricultural environments are a primary source of nutrition for deer in the eastern United States and thus have great influence on the feedback loops. Agriculture precludes the normal successional process, and consequently, the deer/vegetation system moves from a cycle of decades or centuries to a cycle that is annual. While crop rotation can cause local variation in food resources over a span of several years, the long-term successional change is absent. The general pattern is one of reduced fluctuation in food resources, and consequently, deer populations.

However, much of the eastern United States landscape is not constant. It has been changing dramatically for much of this century. The feedback loops affecting this change are not ecological, but economic. Agriculture is declining in the East and significant portions of the landscape are reverting to forest through succession. Near urban areas, forest/agricultural landscapes are being developed for housing and industry. Both of these trends are likely to continue into the next century (National Research Council 1982, Joyce et al. 1990), and carrying capacity for deer will decline.

These land-use changes represent more than perturbations of the system. They constitute major changes in equilibrium. Prior to 1760, deer populations were being driven toward a target that was moving as a result of disturbance and succession. However, there was a relatively constant equilibrium point to this process. Today, the equilibrium point is moving because of human actions, as well.

Decline of Sport Hunting. The changing societal values regarding sport hunting will further alter the behavior of the system. Sport hunting in the East is diminishing. While this has no effect on *K*, we can expect increased average deer populations and higher peaks to population fluctuations. In the absence of hunting, regionwide deer populations could reach abundance levels now seen on many national parks--more than 10 times current levels.

Implications. This analysis suggests that because of the dramatic shifts in the equilibrium, we can expect significant changes in plant communities. However, the analysis also suggests that regulation and stability are still inherent qualities of the system. Where forest/agricultural landscapes are constant and crop rotation is relatively consistent, the system is on a stable, annual cycle. Deer populations will continue to fluctuate, but with a much higher mean value than in the past, at least over the next 20 to 30 years.

Predicting the equilibrium point is obviously challenging in this dynamic environment. The pace of change and the intensity of human development is difficult to predict. Further compounding the challenge, local landscapes are fluctuating out of synchrony with one another. Future trends in deer populations will probably vary on a scale as small as a few thousand hectares.

In the next 10 years, we can anticipate further increases in deer populations. Even in areas where they are not subject to hunting, deer have yet to reach *K* (e.g., Underwood et al. 1991). However, given continuation of the trends in agriculture (decreasing) and intensity of urban development (increasing), the long-term (next 50 years) trend for deer in eastern North America is downward (Figure 9).

A manager should be most concerned where the environment is highly dynamic. Rapidly changing landscapes mean sudden changes in *K*. When deer populations are caught well above *K*, the potential effect on vegetation is greatest. Much of the impact will be manifest in changes to long-term equitability of plant species. Those species unable to tolerate the highs of the fluctuations in deer populations may be gone by the time appreciable decline in *K* occurs and may have to be restored by active management.

Summary: While landscapes in the eastern United States have been dramatically altered by forest fragmentation and agriculture, centripetality still functions. *K* has increased by at least 10 times between 1760 and 1960. In the short-term, deer populations are likely to increase because they have yet to reach the current *K* and because hunting is projected to decline. If losses of plant species occur because of browsing by deer, the losses are most likely to occur in landscapes undergoing rapid change. In the long-term, deer populations can be expected to decline throughout the eastern United States.

Chapter 3. Management Application

The analysis in Chapter 2 suggests that the deer populations of today probably do not pose a serious threat of disrupting essential ecosystem processes. However, these populations will cause significant changes in plant species composition as a result of a much higher equilibrium, at least in the near term. The crucial question becomes, can we accept the changes? This question cannot be answered with science. The answer must be a value judgment and therefore belongs in the realm of management.

This chapter describes how the background material previously presented may be applied to deer and vegetation management in a specific park. This chapter first discusses the importance of setting clear objectives and then outlines the specific information that a park must obtain before considering management action.

Formulating Goals and Objectives for Management

The first requisite for management is to formulate a set of clearly articulated objectives. This step seems obvious, but has proven troublesome in discussions of deer problems. The reasons for the difficulty stem from two sources: distinguishing between goals and objectives, and formulating reasonable objectives.

Goals and Objectives. Goals represent general targets. They may not ever be entirely accomplished, but they represent a direction for management. For instance, the goal in most historical parks is to create a landscape that helps the visitor visualize the historical event to the maximum degree possible. We may never know when we have achieved the landscape condition that maximizes interpretive quality. We know only that this is where we are headed.

Generally, there are multiple goals. For instance, in addition to maximizing interpretive capabilities, parks also seek to maximize visitor safety, and minimize maintenance costs.

The distinction between goals and objectives is in their specificity. Where goals are general targets, objectives are specific actions to be undertaken to enable us to move toward the goal. For example, one of the goals in Everglades National Park is to maintain a naturally functioning ecosystem, minimizing the disturbance caused by man. To accomplish this, the historical flow of water must be restored. One immediate objective is to modify the irrigation practices that are disrupting the historical flow.

In contrast to statements of goals, statements of objectives allow us to evaluate whether or not we have accomplished them. This is the crucial test. With each objective, we should be able to identify a criterion for testing whether or not we have accomplished the objective.

Reasonable Objectives. For management to be successful, it must have objectives that are not only clear, but objectives that can be sustained in the face of challenge from a great diversity of conflicting value systems. There are two anchor points for coping with challenges, one political and the other scientific.

Goals and objectives are inherently value-driven. They reflect society's interests and aspirations, as translated by the political process. Reasonable goals seem relatively easy to articulate. Most people will agree that preserving historical scenes or ecological processes are appropriate goals. The difficulty arises in translating these into objectives. In casting objectives we add definition to the goals. While goals are perceived as shades of grey, objectives tend to be viewed as black and white.

The Yellowstone fires of 1988 provide a classic example. The goal of management is to minimize interference by man in natural processes of the Yellowstone ecosystem. The management objective associated with this goal is to let fires burn when they meet specific criteria. During the summer and fall of 1988, the goal was almost universally accepted. The management objective was not.

The National Park Service sustained its fire management policy, in part because the policy was securely anchored politically, and in part because the National Park Service was able to muster substantial scientific evidence in support of its position. Politically, the management goals and objectives had been carefully communicated and reviewed within all levels within the National Park Service. There was broad understanding and "ownership" of the policy. Scientifically, the Park Service was able to provide data and experts to support the hypothesis that fires burning large portions of this ecosystem were part of, and perhaps essential to, the normal cycle.

Objectives for Deer and Vegetation Management. A comparison of three National Park System units, Saratoga National Historical Park, Gettysburg National Military Park, and Fire Island National Seashore, provides an interesting illustration of the difficulties in formulating objectives. Deer are perceived to be a problem in all three parks. At Saratoga, a five-year study concluded that there were no grounds for active management of deer at the present time. At Gettysburg, a study recommended substantial reduction in the deer population. At Fire Island National Seashore, a harvest of deer was attempted but halted before completion because of public opposition.

The goals at Saratoga and at Gettysburg are nearly identical, and the deer population densities are similar. The goals are to restore the landscape to its form at the time of the battles fought in 1777 and 1863. Both studies showed that deer are significantly affecting vegetation.

Why then do the recommendations for management differ? At Saratoga, the park wants to restore the vegetation, but has yet to determine what the vegetation looked like in 1777. In the absence of clearly defined descriptions of the desired vegetation pattern, it is not possible to determine whether or not deer are in conflict with park objectives. Once the historic vegetation base map is completed, specific management objectives can be formulated and criteria established to identify when deer are in conflict.

At Gettysburg, knowledge of the historical landscape is nearly complete. Agricultural crops were part of the historical scene at both the military park and the Eisenhower National Historic Site, and it is clear that deer on the southern units of the park are precluding growth of corn. Because the objective is clear, and because the linkage between deer and failure to achieve the objective is established, the park is in a position to formulate a management plan that can be anchored to science.

One of the goals of Fire Island is preserving coastal forest ecosystems. Some interest groups suggest that the objectives should be cast in terms of ecological *balance* or maintaining the system at equilibrium, as measured by the *health* of the deer herd, or some index of *damage* to the flora caused by deer. Such an approach ultimately proves to be illogical.

When we emphasize balance or equilibrium, we imply that our goal is some constant state. Yet eastern systems such as Fire Island are rarely at equilibrium or any other constant state under natural conditions. Perturbation by hurricanes and other disturbance factors and continual recovery *is* the normal condition. Preserving the coastal forest ecosystems means allowing changes to occur.

Although health of the deer herd can be written into objectives (e.g., minimum body weight or antler size on yearling males), it is not a logical objective within the context of the eastern ecosystem. Periodic malnutrition is a normal ecological condition for deer, and death, while it may conflict with the value

Although health of the deer herd can be written into objectives (e.g., minimum body weight or antler size on yearling males), it is not a logical objective within the context of the eastern ecosystem. Periodic malnutrition is a normal ecological condition for deer, and death, while it may conflict with the value systems of some people, is a normal part of ecosystem function.

Similarly, measuring vegetation *damage* implies that a "picture" is the desired goal. Yet, if we consider ecosystem processes, some fluctuation in deer populations, including periodic crashes, may be essential to the dynamics of succession. To argue for some constancy in the plant community is not consistent with a goal of preserving this kind of ecosystem.

The practical solution is to formulate clear objectives that are consistent with the goals of the park. At Gettysburg, that goal is to enhance interpretive qualities of the landscape, and growing farm crops is consistent with the goal. If deer prevent corn from growing, or create conditions in the plant community that are beyond the normal cycle of change, we have a clear conflict between deer and management (Figure 10).

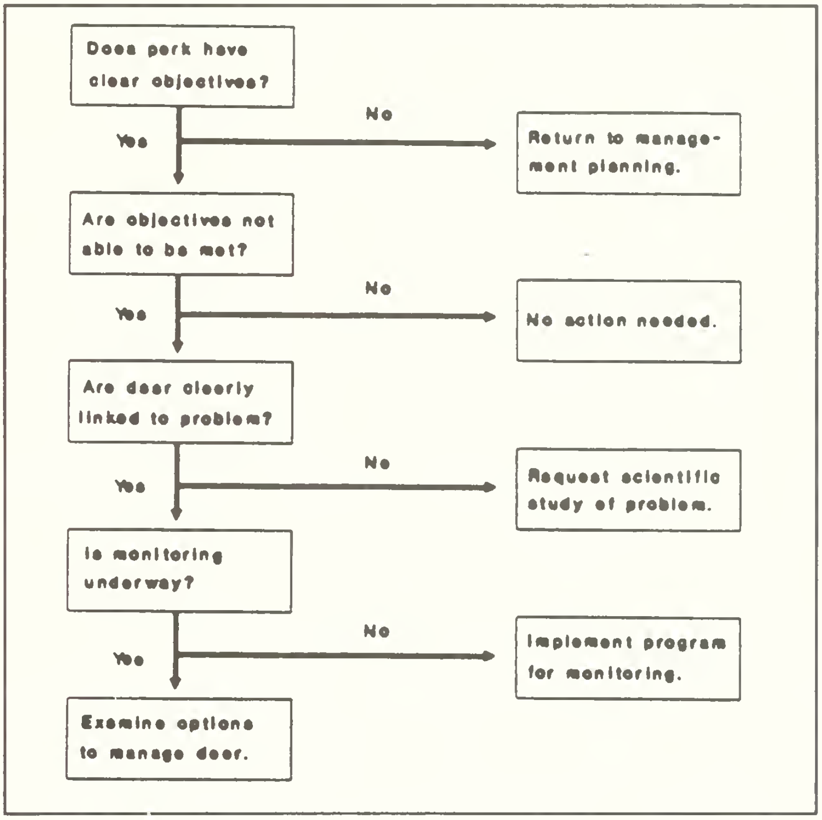


Figure 10. General flowchart of the preliminary steps in deciding when to initiate a program to control deer population abundance.

Summary: Management is inherently value-driven. To sustain management actions we need to clearly define goals and objectives that are solidly anchored politically and scientifically. Manipulation of deer requires a clear identification of deer as a source of conflict with management objectives. Given that deer and vegetation in eastern landscapes are highly dynamic, concepts such as *ecological balance* probably do not constitute reasonable approaches for NPS management. Neither are the arguments that deer are in *poor health* or *damaging* the vegetation.

Long-Term Monitoring Programs for Management

The foundation for management is monitoring. To formulate objectives and implement management programs, we need information on the resources present in a given park. To ensure timely implementation of management programs that perpetuate desirable conditions, we need to know how resources are changing.

The irony in eastern ecosystems is that change is perhaps the only constant. Change adds complexity to management, occurring at regular or irregular intervals, and on time scales ranging from days to decades. Different resources change on different time scales. We can cope with this complexity only if we can predict the probability that change will occur, and the rate and direction of change, for each resource.

The capability to predict change requires that we first be able to describe it. This is the intent of monitoring. Long-term data sets enable us to see subtle, as well as bold, patterns of change (e.g., Magnuson 1990, Swanson and Sparks 1990). Effective monitoring requires careful attention to decisions about what variables are important to measure, when and how to measure them consistently, and how to record and manage the data.

For our purposes, the intent of monitoring is to predict how various resources will change when deer populations change. Four variables of primary importance in monitoring deer and vegetation interaction are abundance and recruitment rates of deer, and plant species richness and equitability.

Abundance of Deer. Abundance is important because it provides a reference point with which to associate the condition of other resources. Long-term monitoring of abundance helps us understand the forces that cause change and also helps us predict how the population will change in the future.

Effectively monitoring abundance of deer requires a sound statistical design, but monitoring need not be expensive. Our purpose is to compare population size from one time to the next. We do not need an absolute estimate of deer populations (although estimates are sometimes helpful in dealing with the public). We need only a relative measure, an index of abundance.

An example of a simple index is the number of deer seen along a given stretch of road during a specified period of time each year. We know that the number of deer seen is some function of actual abundance. The challenge is ensuring that the function between the number of deer seen and their true abundance is constant. In practical terms, this proportion of the population being tallied expresses our ability to detect deer. It doesn't matter whether our survey technique is able to detect 10% or 99% of the total population. As long as the function is a constant, our index will provide a means of comparing populations from one year to the next.

Population Index - A measure of population size that is used primarily to assess the magnitude of change from one time period to the next.

Unfortunately, several factors influence detection. Most of these are related to the behavior of deer. For instance, deer are more active in late fall than in midsummer and thus more likely to be seen in late fall. Other factors that influence detectability include time of day, barometric pressure, and precipitation conditions.

These factors add variation to the index, and there are two ways to control this variation. The first is to structure the survey tightly. For instance, conducting the survey every year during the same month controls for seasonal variation in detection rates. The level of activity of deer is the same each November, so comparisons of the number of deer detected in the survey each November allow us to judge the change in population.

It is generally impossible to control for all factors, so a second approach is used in conjunction with structuring the survey. The survey is conducted several times each year under all kinds of conditions. The survey data are then examined using statistical techniques to remove the variation in rates of detection under different environmental conditions. What remains is the variation in the index that is attributable to changes in abundance. Underwood and others (1991) illustrate the application of this technique.

Recruitment of Deer. Recruitment is the number of young that survive to some specified point in time (Chapter 1). Technically, this point in time is associated with sexual maturity, but because we cannot easily judge maturity in the field, recruitment is usually defined as the number of young surviving to late fall or winter. Recruitment is an important characteristic of a population because it is probably the most sensitive to competition for resources. Consequently, recruitment helps us make judgments about the position of the population relative to ecological carrying capacity. Like abundance, recruitment provides an ability to measure the impacts of management actions and predict future changes.

Perhaps the best time to monitor recruitment is during late winter, when some green vegetation begins to emerge in open fields. By this time, most of the mortality that will remove fawns from the population has occurred and the remaining fawns will be recruited into the reproductive population. This is also a good time because deer activity in open areas increases and deer are most visible.

The purpose is to estimate the ratio of fawns to adult females. Deer born the previous year can be distinguished from adults with careful attention and practice. Multiple counts are essential because each count is a sample of the population, and mean and variance are needed whenever the intent is to compare areas or years. A minimum of five counts is necessary to allow any statistical evaluation. Interpretation is relatively straightforward if adult mortality is reasonably constant from one year to the next. If it is not, the analysis becomes more involved.

Plant Species Richness. One of the key measures of plant communities is the number of species present (Chapter 2). The objective of monitoring plant communities is to characterize species richness and document the continuing presence of plant species. To meet this objective a monitoring program should include two components.

First, a park should establish a reference collection of plants found in the park. This collection is essential to scientifically documenting those species that are present in the park at a particular point in time. This collection should consist of a complete set of the flora present at the park and should be professionally mounted and archived.

Second, the park should identify and map the location of rare and endangered species and other species important to the park's management objectives. These other species may be designated because they are sensitive to deer browsing, considered important to the ecosystem or interpretation of the park, or are of value to other management objectives.

The monitoring of these selected species and sites should be conducted yearly. Because the time of development (phenology) of each species varies, the monitoring protocol must include a specific time schedule. The protocol can then be integrated with the seasonal work plans of the park staff.

Plant Species Equitability. This variable measures the proportional distribution of abundance of the plant species in the community (Chapter 2). As such it allows us to discern changes in the community with much higher resolution than presence and absence. Plant ecologists refine this measurement further, characterizing communities in terms of the relative frequency, density, and (in forest communities) dominance of plant species.

This variable requires a more extensive monitoring program. Measuring equitability is best done with a series of sample points in each of the major vegetation types in the park. The number of sample points allocated to each vegetation type depends on the variation of the vegetation within the type. The smaller the variance around the mean estimated from the sampling, the fewer samples needed. At minimum, five samples are needed to estimate the variance, but variance is high for many characteristics of vegetation, and hundreds of samples may be needed.

At each sample point, a series of plots are established. The size and location of the plots vary with the growth form of the plant species. Ideally, these should be measured annually at the same time of year. Plant communities are frequently affected by short-term phenomena, such as human activities, drought, or outbreaks of a particular insect population. This adds variation to our analysis of deer and vegetation interaction. Annual measurement ensures some ability to account for and control this variation.

Implementation. Integrating monitoring into already tight work plans is obviously easier said than done. A superintendent must decide that a solid, scientific basis for management is important to the park. Once implemented, there should be strong resistance to abandoning the program or downgrading the attention given to it in difficult years. Data collections begun in the 1960s are showing that there is nothing as enlightening as a complete, long-term data set, and nothing as confusing as a long-term data set that lacks measurements in some years or contains questionable values.

Careful documentation of the what, where, when, and how measurements are made is essential, because over time many different people will be involved in the data collection. Sample points or deer observation routes should be referenced on maps and marked with permanent stakes in the field. Explicit protocol for measurement and data forms must be standardized.

In most circumstances data will be stored as computer records. In addition to the normal cautions about computer data storage, a couple of procedures should be included in database management. First, to ensure that data are not inadvertently corrupted, an archival copy of the data set needs to be established to which access is limited. Second, as computer hardware and software evolve, this archive must be periodically upgraded to maintain compatibility between the data set and the hardware and software.

It is important to remember, however, that politically, and increasingly scientifically, a picture is worth a thousand numbers. Each sample point should be photographed from the same point at least every five years (see Rogers et al. 1984). Care should be taken to ensure the transparency or photographic material that is used has a long archival life.

Summary: Because ecological processes involving deer and vegetation span decades, long-term monitoring is an essential base for management. An annual index to deer abundance and estimates of fawn:doe ratios in late winter are sufficient for most analyses of deer population change. Vegetation monitoring requires annual measurement of species at permanent sample points to measure changes in species richness and equitability. Pictures at sample points are invaluable.

Chapter 4. Alternatives for Deer Management

Only when a park has clearly determined that high deer densities are in conflict with its objectives and has initiated a long-term monitoring program is an assessment of management alternatives appropriate. This chapter explores the alternatives that are most frequently proposed--examining their ecological effects, chances for success, and costs of implementation.

The chapter begins with an examination of a no action alternative. This alternative serves as a reference for six approaches to controlling deer densities: restoring predators, fencing, hunting on the periphery of parks, live-trapping/removing, and shooting to reduce the population. The order of presentation here follows a loose progression from least to most invasive in terms of management effects on natural ecosystem processes. Traditional public hunting as a means of deer population control is not considered because it is not within the legislative authority of most eastern national parks.

No Action

A decision of *no action* means that the National Park Service will undertake no direct action to influence the abundance or movement behavior of deer in the parks, and will make no attempt to influence management actions by other agencies on lands surrounding the park. Under this alternative, the deer population is allowed to fluctuate in response to environmental changes. An implicit assumption is that there is an upper limit to population growth, and that in the absence of perturbation, deer and vegetation will reach an equilibrium.

Immediate and Long-Term Effects. In the next 10 to 20 years, deer populations in most parks are likely to remain high relative to historical levels. As these populations approach ecological carrying capacity, average weights of individuals and reproductive rates will decline, especially among younger deer (Chapter 1). In some areas, diseases may become epidemic and cause substantial mortality. Browsing will reduce the abundance and distribution of species preferred by deer. Browsing will allow increases in plant species that are not preferred by deer (Chapter 2).

In some areas, a significant portion of the deer population migrates seasonally between a park and private land. Deer that reside in a park for part of the year will continue to affect crops and ornamental plants on adjacent lands. Complaints by surrounding landowners will depend on an understanding and acceptance of NPS management goals. Automobile accident rates will fluctuate with the size of the deer population. The risk of Lyme disease to humans will probably not be affected by changes in deer densities (Telford et al. 1988).

While deer populations are expected to decline over the long-term (>30 years) because K is declining (Chapter 2), they will remain near K. Deer will maintain forest understories in a relatively open condition, and grasses and ferns will dominate in many areas. Some park users will view this condition as aesthetically appealing, and others will find it distressing. Tree regeneration will be limited to species not preferred as food by deer and the mix of tree species dominant in the overstory will change. Consequently, the effects of current deer densities, regardless of how they change in the near future, may persist for many decades. However, no evidence suggests that increased soil erosion or other disruption of basic ecosystem processes will occur.

In many parks, deer populations are unlikely to remain near ecological *K* for long periods. Severe winter weather, droughts, hurricanes, and other forms of disturbance will drive the populations down. During the lows in the population, the plant community will be released from browsing pressure and may change rapidly in composition. If the deer population remains depressed for as few as five years, forest regeneration may attain sufficient height growth to escape the effects of browsing (Behrend et al. 1970, Underwood et al. 1991).

Estimated Costs. Costs of a no action alternative are expected to be minimal. Staff time will be required to handle complaints and to present interpretive programs that will help visitors and surrounding landowners to understand the management objectives of a park. Substantial educational efforts will be required early in a no action management program to dispel misconceptions about deer ecology and NPS management policies.

Probability of Success. The probability of success is mixed. Considerable uncertainty exists about what to expect if the no action approach is chosen. Scientists can make general predictions, and all available evidence suggests that the system will behave according to these predictions. However, specific predictions are difficult because we have no experience with deer populations that are near ecological *K* for long periods of time. The ability to sustain this decision will hinge on acceptance by NPS park, regional, and national office personnel and the general public. This, in turn, will depend on the degree to which the deer populations conflict with management objectives and value systems.

Recommendations. If the no action alternative is selected, concerted efforts should be made to establish close communication with all interest groups inside and outside the National Park Service. NPS fire management policy provides a model (Chapter 3). Recent experience with public meetings on deer management issues suggests that educational presentations and open discussions pay large political dividends (McAninch and Parker 1991). This appears particularly true when efforts are made to include groups with conflicting values in the same meeting. The acrimony often dissolves when the perceptions are confronted with facts. University scientists can be especially helpful at the outset of this process because they are viewed as objective, outside observers who carry the agenda of no interest group. In instances where the public understands NPS goals, deer ecology, and management alternatives, complaint levels have declined appreciably.

Restoring Predators

A decision to restore predators means to actively translocate large predators to a park and establish a free-ranging population. Under this alternative, the deer population is allowed to fluctuate in response to environmental perturbations and predation. The key assumptions are that a viable predator population can be established in a park and that restoration will cause the long-term average density of deer to shift significantly downward.

Immediate and Long-Term Effects. In the short-term, successfully restoring a significant predator population may yield some reduction in the deer population. Plant species that are widespread, but held in check by browsing, will respond quickly. In most eastern parks, forest regeneration and invasion of open fields by woody vegetation will be noticeable within 5 to 10 years. Complaints about deer by surrounding landowners and automobile accidents may decline. However, if *any* livestock are present on lands surrounding a park, conflicts between predators and landowners will likely be an issue.

Long-term changes are much more difficult to predict. Field studies on wolves (*Canis lupus)* and computer modeling support the general patterns of predator/prey interactions outlined in Chapter 2. Wolves could cause a significant long-term reduction in deer populations (e.g., Boyce 1990, Archibald et al. 1991). However, species ecologically suited to most eastern parks, such as bobcat (*Felis rufus*), coyote (*Canis latrans*), and perhaps the red wolf (*C. niger*), are unlikely to produce significant changes in most years. Deer populations will be driven by the same environmental factors that are important in the absence of predators. Periodically, environmental conditions, in combination with predation, will cause a precipitous decline from which recovery by the deer population may be slow (e.g., Theberge and Gauthier 1985, Fuller 1990, Underwood 1990). This will present the "window of opportunity" type of change in the plant community.

Estimated Costs. Costs of this option will be high. Recent efforts to translocate lynx (*Lynx canadensis*) and bobcats yield cost estimates of $2,000 per individual animal released (R. Brocke, pers. comm.; R. Warren, pers. comm.). Releasing one pair of red wolves is approximately $100,000 (M. Pelton, pers. comm.). Obviously, if the restoration is successful, long-term maintenance costs will be small.

A significant investment will be made in staff time. Compliance with state and federal regulations for translocating major predators is involved, especially for species classified as threatened or endangered. Key to gaining authorization is a consensus on methods for controlling individual predators that move outside of a park and cause problems for surrounding landowners (Kellert 1985, Fritz 1990). Prerelease programs of public information and relations will be vital (Warren et al. 1990).

Probability of Success. Probability of success is low. The assumption that a viable predator population can be established is questionable. Success depends on the size of a park and on surrounding land use. Predators are highly mobile species and long-distance movements away from the release site are likely. Most large predators show some degree of territoriality (exclusive use of home ranges) and range over areas >50 km^2 (20 mi^2). Establishing populations large enough to provide minimum genetic variability (LaCava and Hughes 1984) is probably not possible within the boundaries of most eastern parks. Individual animals are likely to move off the park periodically and mortality rates will be high (Fritz et al. 1985). Additional releases may be necessary periodically to establish a population.

Second, the assumption that successfully restoring predators will result in a significant reduction in a deer population is questionable. Studies of the role of wolves, coyotes, and bobcats all show that the scenario in which predators cause a lower, long-term equilibrium population in deer is unlikely (e.g., Connolly 1978).

Finally, if the first two assumptions are met and predators are successful in driving deer populations down to low levels, abundant alternative food resources must be available for the predators. If alternative prey species are few, predator populations will decline with the decreasing deer population. Because of the small size of most parks, and the isolated nature of the predator populations, these population lows may represent serious bottlenecks that significantly reduce genetic diversity. Demographically, the loss of a few individuals in a population that is already relatively small means a high risk for extinction.

Recommendations. If this alternative is under serious consideration, computer modeling work should be undertaken to examine the genetic and ecological questions. The probability of meeting the two major assumptions, and the abundance of alternative food resources, need to be thoroughly examined (e.g., United States Department of the Interior, National Park Service 1990).

Politically, the chances for success will depend on the investment in public education and communication. Management programs need to be crafted to address both the positive (e.g., the presence of predators attracts tourists) and negative (e.g., the presence of predators increases conflicts with neighbors) effects of predators on the park and surrounding landowners. This is best accomplished by drawing the public interest groups and governmental agencies into the planning at the outset. Efforts to reintroduce the timber wolf to Michigan failed because of lack of public support (Weise et al. 1975). In contrast, restoring the red wolf and the lynx enjoyed strong public support because of planned campaigns to inform the public and enlist their assistance (Brocke et al. 1990, Fritz 1990).

Fencing to Control Deer Movements

Selecting this alternative means that fences will be constructed to restrict deer from designated areas, such as small patches of rare plants, forest stands, agricultural fields, and highways. A variety of fencing designs is available (Hawthorne 1980, Porter 1983, Schafer and Penland 1985). Under this alternative, the deer population is again allowed to fluctuate in response to environmental perturbations. The key assumption is that deer represent a conflict in localized areas of a park and that by restricting them from these areas, the problem can be alleviated.

Immediate and Long-Term Effects. Successful fencing will immediately eliminate conflicts with deer on the protected areas. Plant species held in check by browsing will respond quickly. Equitability among plant species will change dramatically within the first 5 to 10 years on many sites. Where the desired vegetation is woody, the fence may be removed after 5 to 10 years, but the boundary effect created by the juxtaposition of the fenced and unfenced plant communities will persist for more than a century. Where the objective is to protect a low-growing or herbaceous plant community, fencing will need to be permanent.

Two significant exceptions to these predictions have been observed. First, those sites dominated by ferns may show no appreciable change because ferns have an ability to chemically inhibit the development of many other species by a process known as allelopathy (Whittaker and Feeny 1971, Putnam and Tang 1986). Second, where oak regeneration is a primary concern, exclusion of deer from oak forest understories may not result in immediate response by oak seedlings. The conditions necessary for regeneration of some species of oak, even in the absence of deer, are still unclear.

Finally, some consideration should be given to the long-term consequences of the complete exclusion of deer. Plant communities in eastern North America have evolved with deer and the presence of some species may be dependent on deer. For example, the browsing by deer may control the development of one species, shifting the competitive interaction and allowing a second species to persist. In this sense, the exclosure may create a condition that is ecologically more aberrant than the large deer populations (Putman 1986, Caughley 1989).

Estimated Costs. Two types of cost must be considered, construction and maintenance. Costs of construction range from $0.04 for single-strand electric livestock fences to $4.00/m for woven wire fences (Hygnstrom and Craven 1988). Costs per meter decrease as the size of the area fenced increases. Exclosures of 0.5 ha (1 acre) using woven wire and treated 4x4 inch posts at Saratoga National Historical Park cost $1,000 each, and required 25 person-days to erect in 1986.

Maintenance will be an annual activity. Woven wire fences require annual attention to maintain tautness, and constant monitoring is necessary in forest sites because of the risk of trees falling on the fence. Electric fences require that herbaceous vegetation be cleared away from the fence to prevent grounding of the electrical charge. Duration of the maintenance activity will depend on the plant species being protected.

Use of "optical fences" created by devices that reflect automobile headlights have been effective in some circumstances in reducing auto/deer accidents (Schafer and Penland 1985). Testing is continuing, and costs will likely decrease as more agencies begin to adopt this approach.

Probability of Success. The probability of success with fencing is mixed. Effectiveness of fencing is highest where the areas from which deer are excluded are small. Single-strand livestock fences will probably work only on small areas (<2.0 ha, 5 acres) where food resources outside the fence are abundant and should be tried first (Porter 1983, Hygnstrom and Craven 1988). Exclosures consisting of 3-m-tall fences surrounding 0.5 ha to 2.0 ha (1 to 5 acres) will probably be successful in most circumstances. As exclosures get larger, or stretches along highways get longer, there is increased disruption of deer behavior and a greater probability that the deer will jump the fence. Excluding deer from larger areas or highly preferred food resources may require a taller fence.

Fencing along highways is unlikely to stop seasonal migration by deer. Physical barriers to movement will concentrate deer into narrow migration corridors across highways and may present significant problems. The "optical fence" design offers an attractive alternative because it does not concentrate migrating deer but does reduce accident rates. Again, each situation will require some experimentation to determine benefit:cost ratios.

Depending on the location and configuration of the fence, the fence material and posts will create significant visual impact. Within 5 to 10 years, differences in vegetation inside and outside the fence will create a visual impact. Auto/deer collisions may be eliminated along some areas of highway.

A variant of fencing is treatment of specific plants with chemical "deer repellents." Testing to date does not show repellents to be effective (Hygnstrom and Craven 1988, Swihart and Conover 1990).

Recommendations. Close cooperation between resource managers and interpreters will enhance the prospects for this alternative's success. Objectives for plant community composition need to be articulated as specifically as possible. For instance, does it matter what species of tree regenerates? The answer could influence the type and duration of the fence to be constructed. Areas to be fenced need to be identified and their size determined with an eye to keeping them as small as possible.

Where fences will present an obstruction to viewsheds, planners should consider irregular-shaped exclosures, avoiding straight linear stretches of fence with square corners. Planners should also explore the influence of the long-term boundary effect created by a fence and consider measures to mitigate this, if necessary.

Hunting on the Periphery

This approach means removing deer through legal hunter harvest on areas immediately surrounding a park. This approach entails managing deer removal within the context of the current hunting season, or expanding bag limits, extending hunting seasons, or holding special hunting seasons. To be an effective management tool, hunters must focus on removing females. The approach assumes that a significant proportion of the deer reside outside of a park and become vulnerable to hunting during a part of the year because of seasonal movement behavior.

Immediate and Long-Term Effects. In the short-term (5 to 10 years), a significant increase in hunters removing deer on the periphery will reduce deer densities and their browsing impacts on vegetation. The effect will be greatest near a park's boundaries, decreasing toward the center. This gradient may exist where the distance between park boundaries and the park center is as short as 2 km (1.2 mi) (Underwood et al. 1991).

Significant changes in deer abundance will result in an increase in the average size deer and, subsequently, an increase in reproductive performance. Visibility of deer will decline as the population is reduced. These effects are likely to be gradational within a park, as well.

Probability of Success. The probability of success with hunting on the periphery is mixed. Successfully implementing this alternative is not within the purview of the National Park Service. A park must rely on the cooperation of state wildlife agencies and adjacent landowners to achieve its objectives. Thus, the probability of success is dependent on good rapport and close agreement between NPS management objectives and those of its neighbors.

Efficacy also depends on the vulnerability of the deer. Deer are vulnerable only if they are outside of the park boundaries during the hunting season. In areas where deer spend summers off the park and winters on the park, migration between seasonal ranges can occur over a broad range of dates. Those deer that migrate prior to the opening of the hunting season are obviously less vulnerable.

Additionally, many deer show short migrations between seasonal ranges (<2.0 km, 1.2 mi) and others have home ranges that overlap the park boundary. Consequently, the ability to reduce the deer population will depend on hunter access. The configuration of the park boundaries and management objectives of surrounding landowners will influence this access to the deer population.

In the long-term (>20 years), the utility of this alternative is questionable. It is hypothesized that migration behavior is learned. Some animals in the population have learned to migrate long distances and others have learned to migrate short distances. Hunting on the periphery may serve only to eliminate those individuals whose migratory patterns make them vulnerable. Ultimately, the portion of the population not vulnerable may grow, compensating for the loss of the long-distance migrants, and the population on a park will remain unchanged.

Estimated Costs. Costs will be minimal except for enhanced boundary enforcement during the hunting season. Staff time will also be necessary to work with state wildlife agency personnel to arrive at an appropriate harvest quota.

Recommendations. Planners must consider balance between effective deer population control and political sensitivities. From an ecological perspective, the greatest impact on the deer population can be obtained by harvesting animals near the boundary of a park, and efforts should be made to concentrate hunter pressure on lands immediately adjacent from a park. However, the negative response to the "firing line" experience of Yellowstone National Park must be recognized and management programs formulated to avoid this type of hunter behavior (Houston 1982). Computer modeling using geographic information systems will be able to provide much more definitive answers to the questions about the efficacy of this approach and hunter management for a particular park.

Live-trapping and Removing

Adopting this approach means that the National Park Service will reduce deer populations to desired levels and maintain them by live-trapping and transferring of animals out of a park. This option assumes that there are individuals or agencies willing to take large numbers of deer on a continuing basis.

Immediate and Long-Term Effects. Successfully reducing deer populations that are near *K* will yield a substantial increase in plant biomass. Plant species that are widespread, but held in check by browsing, will respond quickly. In most eastern parks, forest regeneration and invasion of open fields by woody vegetation will be noticeable within 5 to 10 years. As the deer population declines, the average size and reproductive performance of individual animals will increase. Complaints about deer by surrounding landowners and automobile accidents will decline. Visibility of deer within the park will decrease.

Estimated Costs. Based on experience from a variety of studies using rocket-nets, Clover traps, Stephenson box traps, and dart guns, average costs for capturing a deer are approximately $400 to $800 per deer, depending on personnel costs (Ismael and Rongstad 1984, O'Bryan and McCullough 1985, Adirondack Ecological Center unpublished data). Transportation and veterinary costs are additional. As the deer population is reduced, costs per deer removed will increase because deer will become more difficult to catch.

A significant reduction and control of the deer population will require a removal of >40% of the female segment of the population. During the first several years, this means moving >200 animals in many parks. This represents an annual expenditure of >$120,000.

Probability of Success. The probability of success with live-trapping and removal are low. First, the assumption that individuals or agencies are willing to take large numbers of deer on a continuing basis is questionable. Deer populations are high throughout much of the eastern United States. Without suitable recipients, a translocation approach will falter. Second, the implicit assumption that survival rates will be high for deer trapped and released is probably unfounded. Mortality rates of 3% to 5% of the deer during capture are to be expected (Underwood et al. 1991, Adirondack Ecological Center unpublished data). Mortality rates >70% within the first year appear to be common for translocated deer (Jones and Witham 1990).

Reproductive Intervention

This alternative means undertaking action to deliver contraceptive drugs to females to reduce the recruitment of young. This approach assumes that an effective drug can be found soon to control fertility in deer, that it can be delivered to deer in free-ranging populations, and that enough females can be treated to inhibit reproduction sufficiently to control population growth.

Immediate and Long-Term Impacts. Short-term impacts (5 to 10 years) will be minimal because this approach does not remove any animals. Given the long life expectancy of deer in unhunted populations, little change can be expected in most park populations. Beyond 10 years, the population will decrease more rapidly as many of the deer born prior to the treatment reach senescence and die.

Once a population declines to about *K/2*, significant changes in vegetation will begin to occur. The pace of change in vegetation will depend on the degree of prior vegetation depression and time lags such as those associated with invasion of seeds. The average body size of deer will increase and the reproductive performance of untreated females will increase. In some latitudes, females six months of age will begin showing high fertility unless treated (e.g., McCullough 1979). Visibility of deer will decline as the population is reduced.

Estimated Costs. Costs are unknown at present because this approach is still in the experimental phase with free-ranging deer. If treatment of the deer requires live-trapping or darting the animal, minimal costs will be approximately $600 per animal. Total costs will depend on the number of deer that need to be treated and the frequency with which treatments need to be applied. Modeling suggests that 70% of the females in a population must be treated. Assuming effective contraception will last two years (Plotka and Seal 1989), costs will be similar to live-trapping, about $600/deer.

Probability of Success. The probability of success with reproductive intervention is presently low. A successful technique for implementing this approach is not currently available. There are currently two major challenges. First, biologists are still searching for a drug that is specific to deer and will not affect reproductive systems in organisms that consume deer (i.e., predators, scavengers, and humans). Second, a delivery system is needed that will enable animals to be treated efficiently, and allow easy identification of animals once they have been treated.

Direct Reduction by Shooting

A decision to reduce the deer population by shooting means employing NPS personnel to kill a specified number of female deer throughout a park on an annual basis.

Immediate and Long-Term Effects. Successfully reducing deer populations away from *K* will result in significant increases in plant biomass. Plant species that are widespread, but affected by browsing, will respond quickly. In most eastern parks, forest regeneration and invasion of open fields by woody vegetation will be noticeable within 5 to 10 years. Some highly preferred species of plants may not show dramatic increase unless the deer population is reduced to very low numbers. The average size and reproductive performance of the deer will increase. Complaints about deer by surrounding landowners and automobile accidents will decline. Visibility of deer within the park will decrease most under this alternative because deer will develop a wariness toward humans.

Probability of Success. The probability of success with reducing by shooting is mixed. Ecologically and economically, this alternative is effective and efficient. Politically, it attracts considerable negative sentiment from groups with such diverse values as animal rights activists (opposed to killing) to hunting organizations (opposed to a park being closed to public hunting). Success will depend on drawing these groups into a constructive dialogue, and educating the public about the management objectives, conflicts, and alternatives.

A modification of this approach is a selective removal of family units of deer from areas where conflicts are most severe. This technique has not been tested, but modeling suggests that deer could be eliminated from areas as small as 400 ha (1,000 acres) for 10 to 15 years with a one-time removal of 12 to 20 individuals (Porter et al. 1991a). This modification may provide an important compromise solution that would be acceptable to the varied public interest groups.

Estimated Costs. Principal costs will be personnel to shoot deer, and to process and dispose of those animals removed. Given average reproductive rates, to hold a population constant at some lower density will require an annual removal of approximately 25% to 50% of the females, depending of conditions in a park. Costs of shooting deer over bait were $74/deer in a Wisconsin study (Ismael and Rongstad 1984). As deer populations decline, costs per deer removed will increase because deer will be more difficult to find and shoot.

Chapter 5. Future Research on Deer and Vegetation in National Parks

If park programs to manage deer and vegetation are going to have a solid anchor in science, we must change our approach to obtaining the data. The research projects of the past 10 years have given us little more than glimpses of the knowledge we need. Clearly, we are most comfortable when our management is based on well-established cause-and-effect relationships. However, determining cause-and-effect relationships requires the scientific rigor of modeling and experimentation, and these are often expensive enterprises, both financially and politically. This chapter outlines the five components of research administration that should be considered as the National Park Service strives to maximize the return on its investment in research.

Long-Term Data Bases

A key deficiency to past studies of deer and vegetation in the East is their lack of perspective on long-term change. This is abundantly clear in comparing these studies with the classic large herbivore studies of the past three decades.

The major studies of large herbivore interaction on Isle Royale (Peterson 1988), the Serengeti (Sinclair and Norton-Griffiths 1979), Yellowstone, and Australia all show the same basic pattern. Herbivores and vegetation are definitely linked through a feedback loop, but the relationship is difficult to discern because the herbivores and vegetation fluctuate on different time scales. These studies were largely successful because they had more than 20 years of data available to the analysis and could sort out the complexities.

Accumulating useful 20-year data sets within the traditional NPS framework seems unrealistic. Certainly, maintaining a funding commitment and administrative focus for intensive, long-term research is difficult. However, continual intensive research is not necessary for meeting the information needs of deer/vegetation management programs. The ideal approach may actually be one which weds long-term monitoring with periodic intensive research.

Monitoring provides the time perspective on key variables that is lacking in traditional research designs. Only a few variables may need to be monitored, so the effort is inexpensive relative to research. Periodic research efforts ensure in-depth analyses of these data by bringing scientists with state-of-the-art statistical and conceptual approaches into the effort. The research efforts also broaden the data base because they often focus on an array of variables that are different from, but complementary to, those being monitored.

The National Park Service may be in a better position than other land-management agencies to use an approach which links monitoring and research. National parks are among the few places where the potential for continuity of management allows examining natural processes. Parks are better protected from capricious change than most areas and can allow long-term dynamics to occur. Many parks have been sites for projects studying deer or plant communities. These studies provide solid historical data bases on which monitoring and future research can build. Finally, monitoring fits well within the structure of the park system because most parks have skilled ranger and resource management staff to implement monitoring programs.

Integrative Studies

In the past, most of the eastern deer projects have focused almost entirely on either deer or vegetation. The studies have been important because they have helped us better define the questions. Unfortunately, they have not provided the answers.

Again, the classic studies of Isle Royale, Serengeti, Yellowstone, and Australia provide important models. They incorporated multiple studies, each focusing on individual components of the system, but conducted them in close collaboration. Their power arises from the orchestration of these individual efforts to yield a synthesis.

NPS science offices can provide the leadership in formulating, guiding, and maintaining the commitment to an integrated study design. They can facilitate close collaborative relations with outside scientists that will ensure a strong approach to constructing syntheses from a multifaceted monitoring and research design.

Comparative Research

One of the most powerful approaches to synthesis is to compare the results of studies done across broad environmental gradients. The more similar the studies in design, methods, and data sets, the stronger the comparison. This approach was used by the International Biological Program (IBP) in the 1960s, and no other program has ever stimulated as much conceptual development in the realm of ecosystems.

One of the most important contributors to a scientist's ability to identify the underlying patterns is exposure to similar questions in different environments. The more similar the questions, and the broader the gradient of environments, the greater the perspective that can be brought to bear on the analysis of any problem (including deer and vegetation) in a particular park.

The National Park Service is in an excellent position to undertake this comparative approach. National parks are spread across several environmental gradients. The administrative structure is in place to ensure compatibility of field technique and database management, and to facilitate collaboration among investigators at different sites. Finally, because the Park Service technically owns the data, access to combined data bases by various users can be assured.

Modeling

Recent advances in modeling provide techniques that are essential to understanding deer/vegetation interaction from an ecosystem perspective. Traditional analyses are simply not effective in coping with the complexity of this interaction in conjunction with the dynamics of eastern landscapes. Recent texts provide excellent illustrations of the power of modeling in examining ecological feedback loops in fluctuating environments (e.g., Caughley et al. 1987).

Modeling helps focus research. It draws together the existing data, explicitly states the assumptions, and forces us to state clearly and objectively how we think the system behaves. As a result, it is open to scrutiny by others. Modeling can quickly rule out many hypothesized mechanisms of system interaction. Perhaps no other method is more efficient at identifying what we need to know and at providing direction for further research (e.g., Starfield and Bleloch 1986).

Modeling can also help focus management. It forces the manager to articulate the crucial questions. What is fact and what is conjecture can be quickly identified. Alternative approaches to management can then be explored through simulation (e.g., Bunnell 1989). This provides managers with "experience" in how the system is likely to respond to different alternatives. It helps evaluate the merits and risks of each alternative (e.g., Walters 1986).

National parks may provide an ideal setting for modeling. They possess many of the best long-term data sets available today. Collectively, they also comprise a relatively wide range of natural conditions and are less directly impacted by man in comparison to other lands. These features allow testing of models across broad ecological gradients and under conditions where the man's role is tightly controlled.

Experimentation

The key to understanding deer/vegetation interactions is to establish cause-and-effect linkages with certainty. Previous research has been largely descriptive. While this has been helpful in framing the questions, it does not lend itself to rigorous analysis. Long-term monitoring can provide insight into cause and effect, and sometimes provide data for a rigorous test.

The most effective way to achieve this rigor is to conduct the research in an experimental mode. Most often this takes the form of direct manipulation of one component of the system. However, experimental research can also be designed in anticipation of a natural perturbation. The crucial feature is a well-designed combination of treatment and control components.

The National Park Service is one of the few agencies that can conduct the necessary experimental work. Parks offer a high degree of control over impacts of human activity, in comparison to most eastern landscapes. They also offer the opportunity to track experiments for long periods of time because park management programs are more consistent than those on other government lands, or on most private lands. Finally, the Park Service has a system for logistical support and long-term monitoring that is frequently lacking elsewhere.

Summary: Answering the complex questions now confronting management will require commitment to developing long-term data bases. The focus of research needs to be on the process more than the components. Understanding the process will require comparative studies and modeling. Controlled experimentation, involving manipulation, will be essential to applying science to management problems. The National Park Service, perhaps more than any land-management agency, needs to commit to such an approach.

Recommendations for Research Programming

Recommendation #1: Monitoring Should Be Expanded. To obtain the long-term perspectives that are necessary, the National Park Service should implement a strong monitoring system in most of its eastern parks. Resource managers and scientists should work together to decide which variables are to be monitored, and the protocol to be followed for measurement and data management. The variables listed in Chapter 3 provide a starting point for discussion. The Long-Term Ecological Research Program (LTER) of the National Science Foundation provides an example of this approach for a comprehensive monitoring program (e.g., Michener 1986, Franklin et al. 1990).

The National Park Service should require that principal investigators provide full data sets as part of the deliverable product with each study. Data entry and archiving need to be codified. Again, LTER provides a model. Central archiving responsibilities should be assigned to the regional office. With improving communication capabilities through national computer networks, access should be relatively easy. Once the program is in place, workshops should be held for NPS scientists, resource managers, and university cooperators to teach all participants the required measurement procedures and data management protocol.

Recommendation #2: A Coordinated, Interregional Research Program Should Be Initiated. To maximize the potential for addressing ecosystem-level questions, intensive studies should be conducted in a few parks, selected because of their comparative value. Two environmental gradients should be considered in selecting study locations: a north/south latitudinal gradient and a rural/urban gradient. Additional criteria for selecting study sites should be the existence of a strong historical data base pertaining to both vegetation and deer, and a strong local commitment to long-term monitoring.

Studies should run concurrently at each of the sites, and the National Park Service should facilitate interchange of ideas among scientists. A meeting of participants from all study sites should be held annually. The agenda should include workshops on data analysis and modeling techniques taught by those who are applying the techniques to similar problems. The agenda should also include a session in which participants address a specific question each year using a comparative approach, attempting to identify and evaluate new hypotheses through synthesis. Results should be published in an NPS series to broaden communication.

Recommendation #3: Studies Should Be Multidisciplinary, Integrated Research Efforts. Studies at each site should focus on interactions among major components of the ecosystem, rather than the components themselves. At minimum, this should include the soil/vegetation interactions, and deer/vegetation interactions. Getting the necessary expertise will require a small team of investigators headed by one scientist who has the leadership skills to provide oversight.

Recommendation #4: Modeling Should Be Incorporated From the Start. Because the power of modeling is now recognized by most scientists active in plant community ecology, population dynamics, and ecosystems analysis, it will be incorporated regardless of NPS action. The Park Service should play a role in assisting scientists to maintain currency with state-of-the-art techniques. This can be done through annual workshops and by retaining the services of a modeler who can serve as a consultant to each of the projects.

Recommendation #5: Experimental Manipulation Should Be Encouraged. The needs for immediate management action to relieve problems also provide excellent opportunities for experimental research. The National Park Service should consider conducting the management actions within the context of experimental science. In addition, the National Park Service should consider undertaking experiments specifically designed to test promising hypotheses, with the intention that such research would contribute to an increased understanding of the deer/vegetation interactions. The experimentation should be designed to consider the importance of long-time perspectives, opportunities for comparative analysis, and additive effects of a multidisciplinary approach.

Recommendation #6: NPS Research Efforts Should Emphasize Both Applied and Basic Science. While the goal of NPS research on deer and vegetation was originally cast in terms of applied questions, answering the questions has proved difficult because of a lack of fundamental ecological information.

As the National Park Service moves forward, the agency should consider funding not only projects that meet immediate management needs, but also those that allow us to gain a better understanding of the system. It is evident from most fields of science that the best preparation for solving the specific, but unpredictable, problems of the future is pursuit of basic, as well as applied, research.

Recommendation #7: NPS Should Initiate Multifaceted Research. First, the National Park Service needs to begin examining the influence of the surrounding landscape on deer/vegetation interactions. Much of what happens in parks results from conditions surrounding the parks. Comparative studies across both the landscape fragmentation and the urbanization gradients would be especially appropriate. Modeling efforts that link population dynamics and movement behavior of deer with spatial land-use patterns are important. Advances in population modeling and geographic information systems make such efforts tractable.

Second, the National Park Service should undertake direct experimentation of several management alternatives that have been proposed. Of particular importance is the hypothesis that local management of deer populations can be achieved via removing discrete family units (Figure 11). Each experiment should be conducted on at least two parks across the forest fragmentation and deer population density gradients. The immediate needs identified in many of the eastern parks make this effort both important and timely.

Selected Research Questions

A series of more specific questions can quickly be generated to bring sharper focus to research in these general areas. The following list is intended to stimulate this thinking.

Are eastern deer/vegetation systems moving towards equilibrium, given the dynamic landscape? This question is of obvious importance in the context of NPS responsibilities to preserve ecological processes, as well as ecosystem components. Specific hypotheses have been advanced for different environments, but no experimental or modeling work has been done in eastern landscapes.

Will introducing predators affect the population dynamics of deer and the feedback loops of the deer/vegetation interaction? Reliance on predators is a commonly proposed solution to deer problems and is readily addressed using modeling. Coyotes are thought to be increasing in eastern parks. Will an increase in coyote populations affect the period and amplitude of fluctuating deer populations? The recent work modeling the impacts of wolves on large herbivores in Yellowstone would serve as a place to begin such an effort.

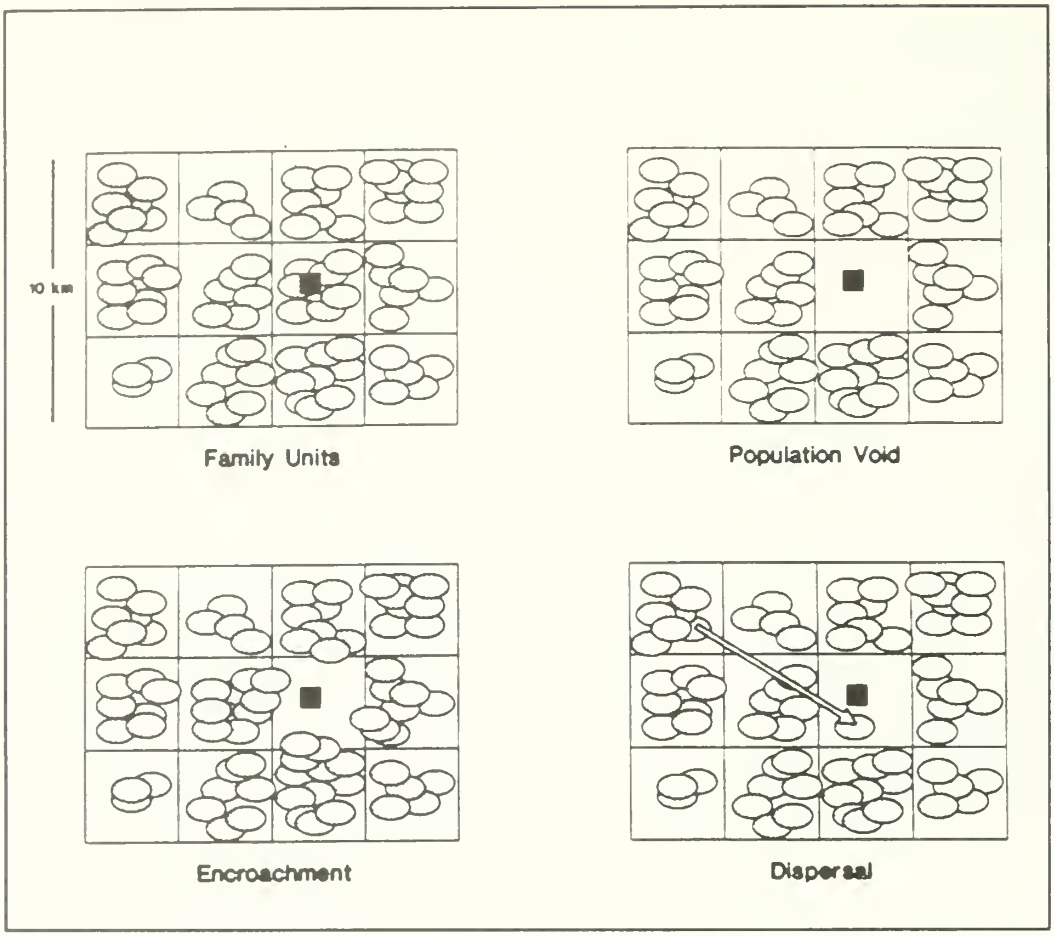


Figure 11. Model of localized reduction of a deer population by eliminating the family unit surrounding a cultural resource (black square). The family unit is removed and the area remains void of deer until encroachment or dispersal causes new growth in that area (from Porter et al. 1991).

At what levels of browse intensity does equitability change significantly? Some levels of browse intensity are likely to increase equitability within the plant community by reducing the presence of a common species that is also highly preferred as a food item. Other levels of browse intensity may reduce equitability by nearly eliminating rare species. The approach used by Underwood et al. (1991) which characterized a gradient of browsing impact could be easily adapted to address this question.

Are we losing plant species as a result of browsing by deer? This question is of importance because of the growing concern for biodiversity, but no rigorous experimentation is available to date. The approach to this question would involve a long-term commitment to monitoring and to some exclosure studies.

Is a fluctuating deer population more desirable if natural ecological process is the management goal? If we think about management in terms of fluctuating conditions, what are the normal limits of this fluctuation? How will plant communities differ at their extremes if deer populations are allowed to fluctuate widely? Are the extreme conditions appropriate in the context of other management goals? How large must parks be to accommodate the full range of variation? Because this is a question of long-term dynamics, modeling is probably the only immediate avenue.

Can we control deer by hunting on the periphery? It is hypothesized that hunting on the periphery of a park would remove migrants, but would have little long-term impact on the population within a park. A first test of this hypothesis could be achieved via modeling.

Can we control browsing impacts using highly selective deer removal? This question is generated by a more complete understanding of social organization and movement behavior of deer. It presents a management alternative that needs to be examined experimentally.

How do changes in landscape pattern influence the behavior and population dynamics of deer? Most eastern parks are small, and vegetation and urban development on lands surrounding parks have significant impact on deer that use a park. Although these surrounding lands are dynamic, we probably can predict changes in their character over the next 20 years and provide a basis for long-term management planning.

How do changes in park size influence deer harvest and, consequently, behavior and population dynamics? This question is corollary to hunting on the periphery because park size influences the portion of the deer population that is vulnerable to hunting mortality factor. It is also corollary to the question of surrounding landscapes because deer in larger parks may be less influenced by surrounding landscape. However, other dimensions include questions of minimum viable populations and genetic diversity as parks become increasingly isolated by urban development. A "natural" experiment has obvious potential as an approach to the question because the many national parks in the East are of such different sizes.

How will changes in the vegetation within parks influence deer population dynamics? Vegetation changes are likely to be less dramatic inside parks in comparison to outside. However, with succession in shrub and forest communities, or perturbations such as hurricanes, changes will occur. These changes will influence deer populations. Predicting the response of deer to changes is tractable with modeling, but predicting the feedback to vegetation requires additional field study. Experimentation could be coordinated with vegetation management.

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