# Interactions of White-tailed Deer and Vegetation: Implications for Management and Research

## A Review Paper for the National Park Service

**William F. Porter**

State University of New York
College of Environmental Science and Forestry
Syracuse, New York

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# EXECUTIVE SUMMARY

In the past four decades white-tailed deer (*Odocoileus virginianus*) populations throughout the eastern United States have grown from scattered populations of a few thousand individuals to widespread populations numbering in the millions. Much of this increase can be attributed to forest fragmentation and increased agriculture. Today population levels are probably higher than any previously experienced in eastern ecosystems. The intent of this document is to provide a background for NPS decisions on the management of these deer populations. At issue is whether or not deer are conflicting with cultural management, irrevocably changing plant communities, and destabilizing natural ecosystem processes.

A new approach to assessing deer and vegetation in an ecosystem context examines the strength with which a system will move toward equilibrium in the absence of disturbance (*centripetality*). Analyses here conclude that while ecosystems of eastern North America have been dramatically altered in the past 200 years, the long term integrity of these systems is not at risk. The major change is the deer/vegetation equilibrium point: it has increased by 10x - 50x since 1760. The interaction is complex because the eastern ecosystem is frequently disturbed, and deer and vegetation fluctuate out of synchrony with one another. Further complicating the picture are continuing changes in land-use over very long time intervals. As a result, both deer and vegetation are currently moving toward an equilibrium that is itself moving. In the near term deer populations are likely to continue to increase. However, a long term decline is predicted.

The challenge to managing these systems is first defining appropriate goals and objectives. Given that deer and vegetation in eastern landscapes are highly dynamic, concepts such as *ecological balance*, and *deer health*, probably do not constitute reasonable goals for NPS management. NPS will need to link deer and vegetation specifically to management objectives. A much stronger political and scientific foundation will be necessary before we can sustain management programs in the face of certain legal challenge.

Perhaps the strongest message emanating from past research is that the questions NPS is asking have very complex answers. Gaining these answers will require commitment to development of long term databases and a different approach to research. Long term monitoring is an essential base for management. Future research will require comparative studies, modeling and controlled experimentation. NPS, perhaps more than any land-management agency, is in a strong position to implement this approach.

# PREFACE

In the past four decades white-tailed deer (*Odocoileus virginianus*) populations throughout the eastern United States have grown from scattered populations comprised of a few thousands of 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 the elimination of market hunting. During the 1970's, state fish and wildlife agencies responded to increasing deer abundance with harvest programs designed to cap the populations in most areas at less than 10 deer/km$^2$ (25/mi$^2$).

Over the same period of time, deer populations in eastern national parks have grown to levels beyond our experience. The reasons are largely the same. Within eastern national parks, landscapes have been manipulated to create a mixture of forest and grassland that recreate historic scenes or provide recreational opportunity. In combination with the surrounding interspersion of forest and agriculture, these constitute excellent habitat for white-tailed deer. Because harvest of deer has not been part of the management regime in most eastern national parks, the populations have continued to grow. Today, populations in many parks exceed 40 deer/km$^2$ (100/mi$^2$).

The growth of deer populations is causing concern for vegetation, and health and safety of visitors to parks. There is also developing concern that parks represent the last remnants of natural ecosystems in eastern North America. Questions pertaining to natural regulation of deer in these small parks are frequently asked. Given the fragmented environment of the East, and the absence of historical predators, is there an ecological balance, an equilibrium?

The issues pertaining to deer and vegetation, and their management in eastern National Parks are of enormous ecological and social complexity. They present challenges no less difficult than those of elk and vegetation in the West. In recognition of this complexity, the National Park Service (NPS) commissioned a series of efforts to learn about deer and vegetation, and provide this knowledge to decision-makers.

This report is one of the products those efforts. It provides an overview of the current understanding, hypotheses and speculation about this deer populations and their interaction with vegetation, weather, predators and humans. It is intended for use by National Park Service staff as background material for assessing potential conflicts between deer and vegetation, and evaluating management alternatives. It is written primarily for the manager and administrator. While much of the current science is based heavily on modeling and statistical techniques, an attempt has been made to minimize detail and focus on the "take home messages".

The organization of the document is built around four general questions:

**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. I summarize 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 there are numerous studies of deer, or of vegetation, there are few pertaining to 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 I present is extrapolation beyond the current data.

**What have we learned from past NPS studies of deer that provides a solid foundation for management?** Since 1980, more than 20 NPS studies have been completed. These represent an information baseline, but none are sufficiently definitive to make superintendents comfortable with the decisions that must be made today. I argue that the principal message from this past experience is clear: If a management program is to be sustained in the face of certain challenge, stronger political and scientific foundations are essential.

**What are the priorities for research in the future?** Eastern national parks have a special ability to contribute to research on herbivore/vegetation interaction for three reasons. First, parks today hold the highest densities of deer in our experience. Second NPS has the ability to tightly 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. I recommend multi-faceted approaches and experimentation to examine the dynamics of deer and vegetation in eastern ecosystems, and to examine creative management techniques.

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# CHAPTER 1.

## A BRIEF OVERVIEW OF THE ECOLOGY OF WHITE-TAILED DEER

This first chapter addresses the question: what does a superintendent need to know about deer before venturing into deer management issues? I provide a background about the biology of white-tailed deer, one which is intended to be selective rather than comprehensive.

### Habitat Use Behavior

The common characteristic of 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, but 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 forest cover. 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.

Deer show limited tolerance to human development. Populations in northern suburbs of Minneapolis-Saint Paul and in 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 development generally creates a landscape in which the proportion of woody cover and open grassland becomes more equitable. It also precludes traditional forms of sport hunting. As housing density increases, woody cover decreases. Vegetation tends toward individual trees and linear arrangements. Harassment by dogs and people increases, and deer abundance decreases (Figure 1).

Use of forest and fields by deer follows both circadian and annual cycles. Deer show peak activity periods during late evening and early morning. Hours from dusk to dawn are generally spent in fields. Daytime hours are spent in forest cover. This pattern is most pronounced where there is extensive human activity during the day (Marchinton and Hirth 1984).

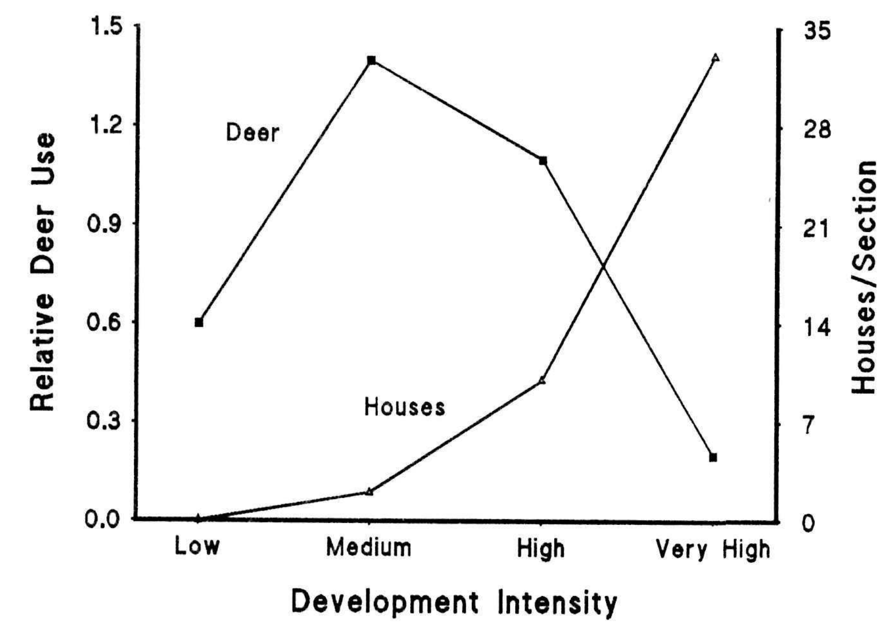


Figure 1. The relationship between deer and development intensity follows a curvilinear pattern with optimal habitat conditions occurring at about one house per 60 ha (150 acres) (redrafted from Vogel 1989).

On an annual basis, deer use fields most during the spring and summer. Females are under heavy nutritional stress because of the energy demands of nursing young and 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.

Circadian and annual behavior patterns are heavily influenced by weather. Deer are able to sense changes in barometric pressure. Activity increases dramatically during the 24 hours preceding the passage of a weather front. In northern latitudes, low temperatures and deep snow result in decreased use of fields (Underwood et al. 1990).

**Movement Behavior**

The movement of deer varies seasonally, but the area used by a deer remains the same throughout its life. The area traversed by an individual through the year is termed its home range. During the summer months (i.e., growing season) deer occupy an area of about 200 ha (range, 59 to 520 ha). Home ranges tend to be larger in relatively open environments and smaller in forested areas. Home ranges of males are generally two to three times larger than females (Marchinton and Hirth 1984).

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 at present.

In northern latitudes (north of 330 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 to 20 km between summer and winter ranges are common; 50 km appears to be the extreme (Marchinton and Hirth 1986). The distance of the migration appears to be vary with climate and individual. Deer move to lowland areas dominated by coniferous forest in most winters because these areas offer better thermal cover.

The mediating 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). It has been hypothesized that hunting pressure will initiate migration of deer to winter range. Rigorous analysis of data at Saratoga National Historical Park (NHP) does not support this hypothesis (Underwood et al. 1990). 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 show only seasonal shifts in the intensity with which they use portions of their home range (Byford 1970).

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. They follow these animals to winter home range. Little is known about dispersing females.

In general, once summer and winter ranges are established, these will be used throughout an individual's life. There is evidence to suggest that deer will modify migration behavior in response to dramatic changes in food supply (Tierson et al 1985, Lewis and Rongstad 1990). However, the fidelity deer show to their home range is very strong. There are cases where deer have starved to death on their home range with food accessible in adjacent areas (Severinghaus and Cheatum 1956, Thomas et al. 1964).

**SUMMARY: The common characteristic of white-tailed deer habitat throughout the eastern United States is a combination of forest and open field. Use of forest and fields follows both circadian and annual cycles. This combination must occur within about 200 ha, the seasonal home range of a deer. In most areas, deer show absolute fidelity to their a 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 2). 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 of 10 (Mathews 1989). Little is known about the social interactions between groups, but it does not appear that family groups 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. 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. 1990).

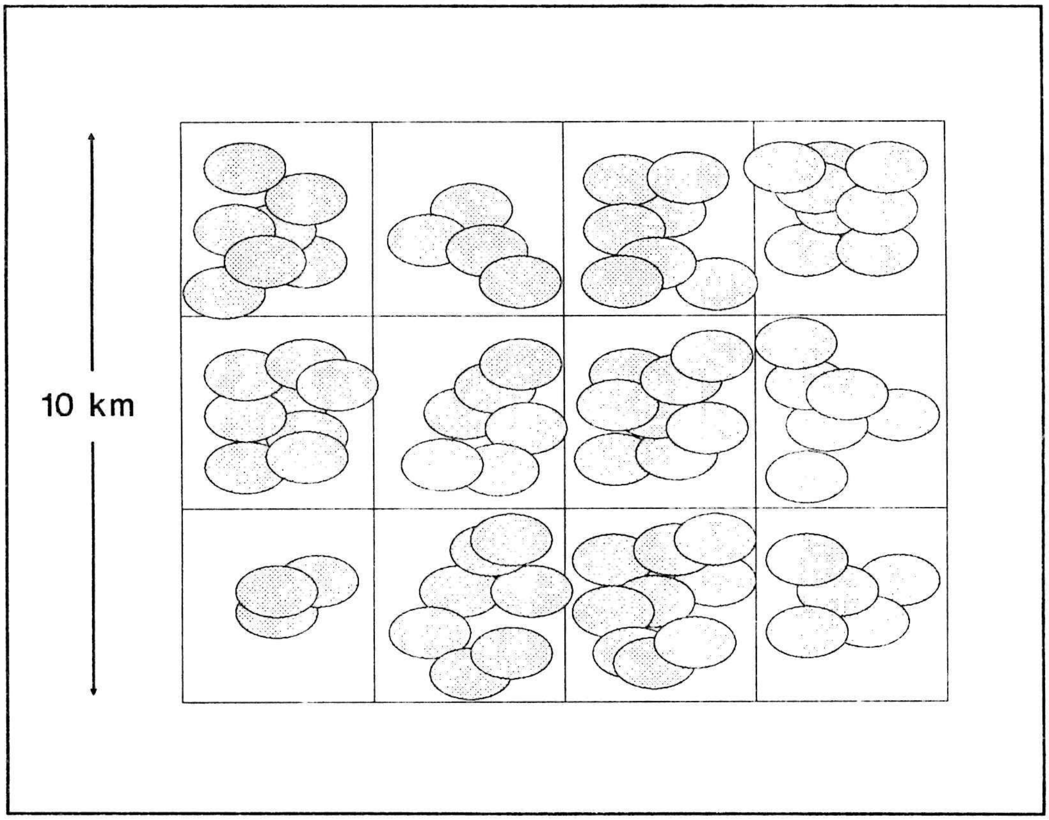


Figure 2. Over a period of years, each generation of female offspring establish home ranges that overlap those of their mother and expand out like the petals on a rose (after Mathews 1989). A population is composed of a series of these family units.

**Demography**

The question of greatest interest to the public is, how many deer do you have on this park? Superintendents of these parks are most likely ask, is the population on 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.*** -- On average, deer produce between zero and three fawns/female/year. Most females two years and older produce two fawns each year, but triplets are not uncommon. Younger females produce a single fawn.

Variation in reproductive performance appears to be related to food resources and growing season, and genetics. The estrous cycle in deer, like most mammals, is mediated by accumulation of fat reserves. Forests, in comparison to agricultural environments, provide lower quality food resources and shorter growing seasons. As a result, deer grow more slowly and have less time to accumulate fat reserves. Consequently, age of first ovulation is generally delayed until 1.5 or 2.5 years of age (Harder 1980) (Table 1).

Because reproductive performance is determined by physical growth, biologists have established an index to predict reproduction. Males face the same challenges to growth as females and antler development is directly related to nutrition. Measurement of the antler beam diameter one 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 during fall harvests 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 size in one year. However, in most populations, fewer than 30% of the fawns survive to one year.

Mortality is greatest during the first month after birth when 30% (reported range, 8 - 100%) of fawns may die (Porath 1980, Mathews 1989). Principal causes of mortality are predation by bears and coyotes (Mathews and Porter 1988). Abandonment is probably a common cause of mortality when females come into the spring with physical reserves exhausted.

The ultimate source of much of the overwinter mortality is nutrition. The keys to survival are the quality of summer food and the length of the time high quality food is available. Deer accumulate fat reserves during the summer months and use these 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 least able to cope with long periods of negative energy budgets.

Where sport hunting occurs, it is the dominant mortality factor for adult deer. Many states regulate the harvest to achieve an annual harvest of 40 to 50% of the females and up to 60% of the males in the fall population (e.g., Creed et al. 1984). Under these conditions, deer generally do not live beyond 2.5 years.

Table 1. Comparison of reproductive performance of white-tailed deer in eastern North America. Values are fetuses/female produced by fawns (0.5 yrs old at time of conception), yearling (1.5 yrs) and adults ($\geq$2.5 yrs).

| Study Area | Fawn | Yearling | Adult |
|---|---|---|---|
| **Adirondack Mountains, New York**<br>Severinghaus and Moen 19831 | 0.03 | 0.92 | 1.54 |
| **Harriman Park, New York**<br>Severinghaus and Moen 1983[1] | 0 | 0.41 | 1.30 |
| **Western New York**<br>Severinghaus and Moen 1983[1] | 0.32 | 1.48 | 1.81 |
| **Cape Cod National Seashore**<br>Porter et al. 1991.[1] | 0.11 | 1.06 | 1.61 |
| **Saratoga NHP, New York**<br>Underwood et al., 1990 | 0.03 | 0.86 | 1.37 |
| **Gettysburg NHP, Pennsylvania**<br>Storm et al., 1989[2] | 1.00 | 1.70 | 1.70 |
| **Ohio (Statewide)**<br>Nixon, 1971 | 1.29 | 1.87 | 2.04 |
| **Cumberland Island, Georgia**<br>Miller, 1989 | NR[3] | 1.00 | 1.06 |
| **Northern Michigan**<br>Harder, 1980 | 0.06 | 1.25 | 1.75 |
| **Crane Depot, Indiana**<br>Kirkpatrick et al., 1976 | 0.20 | 1.53 | 1.94 |
| **Iowa (Statewide)**<br>Harder, 1980 | 0.74 | 1.66 | 2.10 |

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

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

[3] NR is Not Reported.

Where sport hunting is not a factor, 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 1990). Coyotes and dogs kill adult deer year around (Brundige 1990, Underwood 1990), and in more urbanized environments, automobiles are the dominant cause of mortality (e.g., Storm et al. 1989).

***Carrying Capacity.***--The third determinant of population abundance and growth is carrying capacity. This is a straightforward, but frequently confused concept. Confusion arises because there are two distinct definitions of carrying capacity in common usage: ecological carrying capacity and economic carrying capacity (Caughley 1979).

Both definitions begin by defining carrying capacity for deer in relation to the nutritional conditions afforded by the environment. Higher carrying capacities occur in environments where high quality food resources are present in greater abundance. As a deer population grows, it consumes more and more of the annual production of quality food resources. Ultimately, competition among deer for these food resources is sufficiently intense that changes begin to occur:

1) Abundance of plant species that are preferred as food declines.
2) Survival of fawns declines.
3) Age of first reproduction is delayed.
4) Parasite loads increase (in southern latitudes).
5) Average body weight among adults declines.

The definitions diverge in the interpretation of these changes. Most ecologists view these changes as part of the normal fluctuation in deer and vegetation. When grazing removes exactly the quantity of vegetation biomass produced each year, the deer and vegetation have reached an equilibrium, *ecological carrying capacity* (Caughley 1979, designated K in Figure 3). Only a few fawns survive and exactly replace the adults dying each year; the population is static (McCullough 1979).

Many wildlife managers argue that these changes are not normal, but are indicative of a population that has exceeded carrying capacity. They maintain that equilibrium is achieved when deer populations are producing the maximum number of offspring per year, exhibit high average body weight, and are causing no change in the plant community. This occurs at about 50% of ecological carrying capacity (K/2).

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 license sales and minimize landowner complaints. At K/2, deer populations achieve maximum sustainable yield for harvest. This is *economic carrying capacity*, (Caughley 1979, designated I in Figure 3). Most deer populations are managed below K/2 to insure minimal impact on vegetation.

Confusion also arises because carrying capacity is not constant. Textbooks portray K as a stationary point. It is not. If we think of K as the nutritional quality and quantity of the vegetation on the landscape, we must conclude that K (and K/2) fluctuates. For instance, in years of drought, K is lower than normal. The more widely K fluctuates, the more difficult it is to manage a population for a sustainable yield.

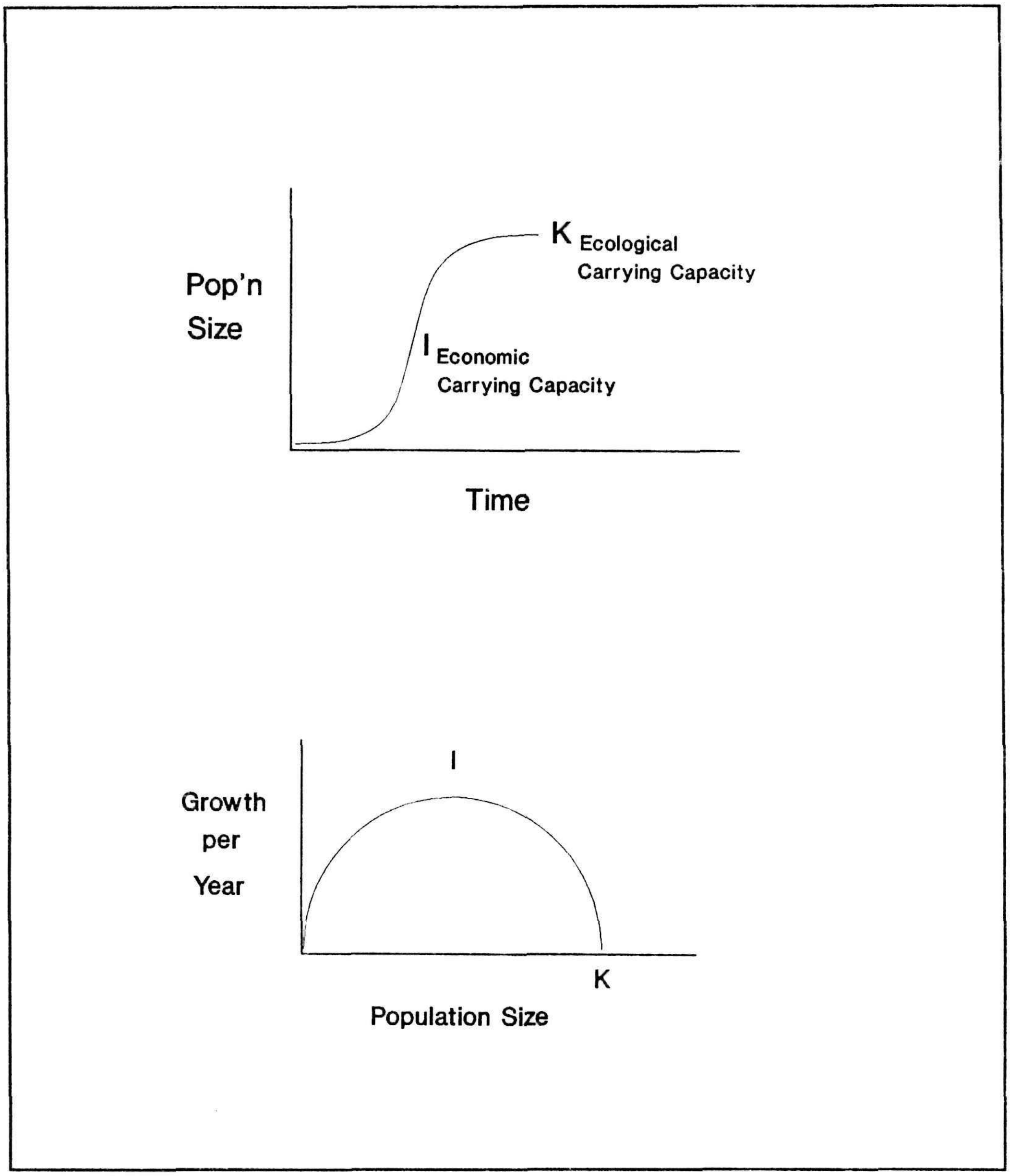


Figure 3. Idealized growth of a population to ecological carrying capacity (K). Economic carrying capacity is a population density that is one half K, designated I (following McCullough 1979). The growth follows a classical logistic function $Dn/dt = r(1 - N/K)$. Above is a plot of population growth against time. Below, the same growth pattern is plotted as the number of individuals added to the population against the population size.

Carrying capacity is an especially important concept in fluctuating environments. Regardless of the position of K, the population is always responding to it because as a population builds toward K, recruitment of young per female declines (Figure 4). However, populations do not respond instantly to changes in K, and this allows them to be above or below K at a specific moment in time . As we will discuss below, these time lags are crucial to understanding deer in an ecosystem context.

***Time.*** -- In reality, episodic events may be the dominant factor determining abundance in most deer populations. When populations decline by > 50% within a span of one or two years we refer to this as a "population crash". These crashes are common to white-tailed deer. In northern latitudes these 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 NHP caused an 18% drop in an otherwise growing population.

In southern latitudes, disease has causes 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 during the early 1970's can probably be attributed to this disease (Wathen and New 1989). In coastal environments, hurricanes may cause major declines (O'Connell and Sayre 1988).

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 ($\lambda$) is 1.25, a population can recover from a single 70% reduction in about five years. If the frequency of severe winters is once every three years, the population will be in a continual state of recovery.

In reality, the time to recovery is much longer. The loss of 70% of the population means loss of many females in prime reproductive age classes (3 - 9 yrs). The loss of these animals means the growth rate will be lower than average until these age classes are filled by animals from younger age classes. Because the heaviest losses in a major crash are in the younger age classes, there are few animals to move into the prime reproductive age groups. Finally, as discussed above, deer populations over large areas are composed of small family units. Loss of every member of a family unit in a crash means that a new female will have to disperse into the area before that area will be repopulated. Thus, episodic events with a period of 10 - 15 years are sufficient to keep a deer population in a constant state of recovery (Underwood 1990).

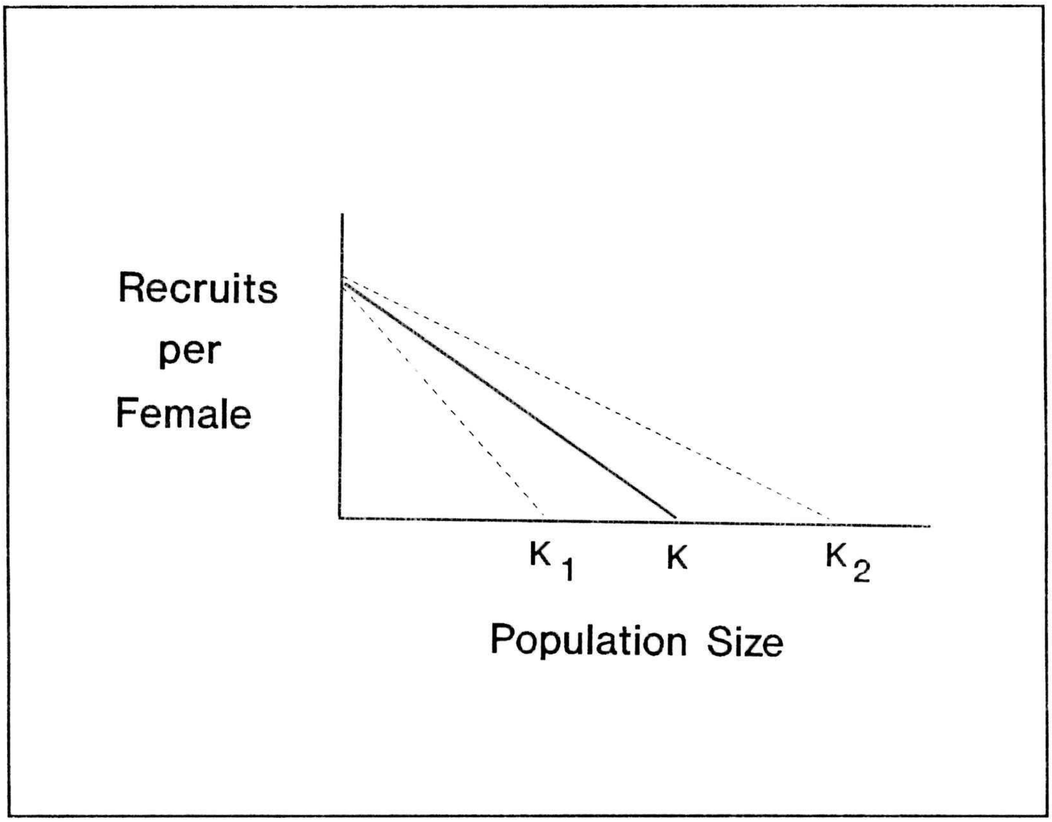


Figure 4. Recruitment (fawns surviving to one year) per female declines with increasing population density. In fluctuating environments, we get a series of lines. K1 represents the lowest K typical of the environment and K2, the highest.

**SUMMARY: Abundance of deer is determined primarily by four factors: reproduction, survival, carrying capacity and time. On average, reproduction in deer varies between zero and three fawns/female/year. In regions where the environment fluctuates widely, fawn survival is the most important determinant of population change. When vegetation biomass removed by grazing each year equals that produced, and the only fawns surviving replace the adults dying each year, the deer and vegetation have reached an equilibrium, ecological carrying capacity. Time since the last major disturbance may be the dominant factor determining abundance in most deer populations.**

# CHAPTER 2.

## DEER AND PLANT COMMUNITIES FROM AN ECOSYSTEM PERSPECTIVE

Beginning in the mid 1980's the questions of greatest interest to NPS were those pertaining the effects of deer on cultural resources, specifically vegetation. However, it became obvious that while eastern parks were established to preserve important cultural resources, these parks were increasingly important as natural ecosystems. In the past year, the questions 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 eastern ecosystems well enough to provide a tight overview. These systems are complex and have generally proven intractable to traditional investigative approaches. This chapter is intended to provide 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. Many of the concepts in plant ecology are still being tested and debated. However, we can identify three premises on which this discipline is built. First, plant communities are assemblages of species whose composition is relatively predictable. 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 contributions of ecology in the past 100 years has been the discovery that the process of change in plant communities is predictable within broad limits. 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, we can forecast the general character of the vegetation over long periods.

The composition of the community at any point in this cycle is determined by the ability of a each plant species to compete. Not all plants are equally adapted to growing throughout the ranges of environmental conditions present in North America. Each species varies in its tolerance and efficiency under given sets of conditions. As plants grow, they alter the conditions on a site; eventually they give way to species better suited to the new conditions.

The rate of change 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 at 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 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 thus in a relative steady state. Many ecologists hypothesize that these long-lived communities constitute the steady-state or equilibrium condition of the system.

Long term dominance is not common, however. Fires, hurricanes, droughts, and ice storms impact the eastern forest systems frequently. They profoundly change the character of the plant community and thus equilibrium is seldom achieved.

The important message here is that the composition of plant communities in eastern landscapes is almost constantly changing. The current composition reflects events of the past, more so than current conditions. However, it is the knowledge of the current conditions and successional sequence that allows us to predict the direction of future change.

**Herbivory**

Herbivores 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 species not eaten may have a distinct advantage in the competition.

Much of what we know about the interaction of herbivores and vegetation comes from range management in western North America. Extensive studies allow us to predict which species will increase in the community and which will decrease as a result of varying levels of herbivory.

However, applying range management approaches to predicting deer and vegetation interactions in the eastern forests is probably not feasible. We simply 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.

***Impacts and Deer Density.*** -- One deer will have an ecological impact. As deer densities increase, the impact on the most preferred plant species will increase. If deer populations continue to build, the impact on less preferred plant species will also begin to increase.

There is little direct evidence of deer driving plant species locally extinct. However, it's unclear whether total elimination of species by deer is a rare phenomenon or a consequence of the lack of monitoring programs in place long enough to document this kind of change.

Much stronger data exist to show that deer have a substantial influence on species dominance within plant communities (e.g., Beals et al. 1960). In the Adirondacks, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) are dominant members of the overstory (Behrend et al. 1970). The understory, however, is heavily dominated by American beech (*Fagus grandifolia*), a species that is not a preferred food item for deer. The current 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 NHP, browsing by deer allows clonal species such as dogwood (*Cornus spp.*) to invade open fields, and precludes development of ash, cherry, and maple (*Fraxinus spp., Prunus spp., Acer spp.)*. The dogwood persists for about 30 years, and then is overtopped by ash, cherry and maple (Underwood et al. 1990).

In the extreme, browsing by deer may be preclude normal successional sequences. Areas of northern Pennsylvania provide good examples of this. There is almost no woody understory and when the overstory of cherry and maple is removed, the sites become dominated by grasses and ferns.

***Diversity.*** -- The impacts 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 single numerical value. Comparison of the value 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.

Some people use diversity to mean only species richness. Others use it to mean both richness and equitability. Thus, defining how we are using the term is essential in applying it to a characterization of change in plant communities.

Deer impact species diversity primarily through altering the equitability of species in the community.

**SUMMARY: Key to understanding deer/vegetation interaction is recognition 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. It has been the historical foundation to NPS wildlife management policy in the West because of the strong orientation to preservation of ecological process. If current trends continue, preservation of ecological resources will evolve to an equal footing with cultural resources in eastern parks.

Given the current political climate, any management action involving wildlife will be challenged. The substance of the challenge is likely to emanate from the history of NPS actions which, since the Leopold Report, have been largely predicated on natural regulation. If the role of eastern parks includes preservation of natural ecosystems, the defense for a decision to undertake active management will require that NPS be able to substantiate that regulation is not occurring in deer/vegetation interactions.

There continues to be considerable debate about natural regulation in the literature and a brief summary may be helpful. The disagreements on key issues are largely a matter of perspective, but it is important to recognize this. New ways of thinking offer powerful approaches to assessing whether or not natural regulation is likely.

***Issue #1: Science vs. Values*** -- Much of this debate can be attributed to confusion of ecological inferences and value systems. Yellowstone provides a good example. Houston (1982) argues that elk populations are controlled primarily by winter weather. Given a series of mild winters the populations will expand, and as a consequence, alter species equitability in the plant communities.

Chase (1986) contends that plant community composition has deteriorated from historical conditions as a result of grazing/browsing by elk. This change in the plant community suggests that the population is above carrying capacity and therefore not regulated.

The debate is more complicated than portrayed here, but the essence doesn't change. The argument is actually ecological versus economic carrying capacity. The issue here is not regulation, but whether we are willing to accept changes in the plant community that are associated with fluctuations in the herbivore population. To deem changes as a "deterioration of the system" implies the issue is one of value rather than science.

***Issue #2: Density Dependent vs. Density Independent Factors.*** -- The premise for a sigmoid growth form in a population is that natural processes set an upper limit to population abundance. Detractors argue that this growth is evident only under laboratory conditions and has not been demonstrated in natural populations.

The real 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 that the effects of population density on recruitment or survival are difficult to discern.

The crucial test is to experimentally reduce a population and look for subsequent increases in recruitment (Figure 4). Compensatory responses are most easily measured in deer populations when the population is between *I* and *K* (Figure 5). Many populations are generally below *I* because of hunting or frequent losses due to severe winter or drought. McCullough (1979) provided definitive evidence on the George Reserve in Michigan in a relatively benign environment. More recently Dusek and Mackie (1989), and Underwood (1990) have demonstrated density dependent growth under widely fluctuating conditions.

***Issue #3: Presence vs. Absence of Herbivores.*** -- Exclosures show us that plant community composition is dramatically different in the absence of deer. This has been the chief argument for reduction of elk populations in Yellowstone. Yet, as Caughley (1989) observed, if we were to place an exclosure in the midst of the Serengeti, we would consider what was growing inside the exclosure to be an aberration in that system.

We know that changes in plant communities are shaped by successional processes. We also know that the successional process itself is being shaped by evolution of plant species. To compete, plants are continually adapting to the physical and biotic conditions of the environment. Large herbivores constitute one of the biotic influences to which plant species have been adapting for millennia. Science has discovered a wide variety of adaptations that plants use to defend against herbivory and compete in its presence.

The basic issue hinges on the definition of "normal". It leads to a variety of interesting questions: 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 the issue has yet to be cast in terms of testable hypotheses. Until it is, this debate adds little to our understanding of the ecosystem.

***Issue #4: Stable vs. Unstable Systems.*** -- Associated with regulation is the concept of stability. Stable systems seem to hold a lot of attraction because they more easily mesh with our management philosophy of preserving cultural resources in constant states. The hypothesis is that the unusually high deer populations are causing the system to become unstable.

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). Further, we have difficulty defining how much change is required to deem a system unstable. If a plant species becomes extinct, is this an indication 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 the notion that diversity is equated with ecosystem stability: the more diverse a community, more resistant to change, or resilient to disturbance. Early work supported the relationship between diversity and stability. More recent work disputes it.

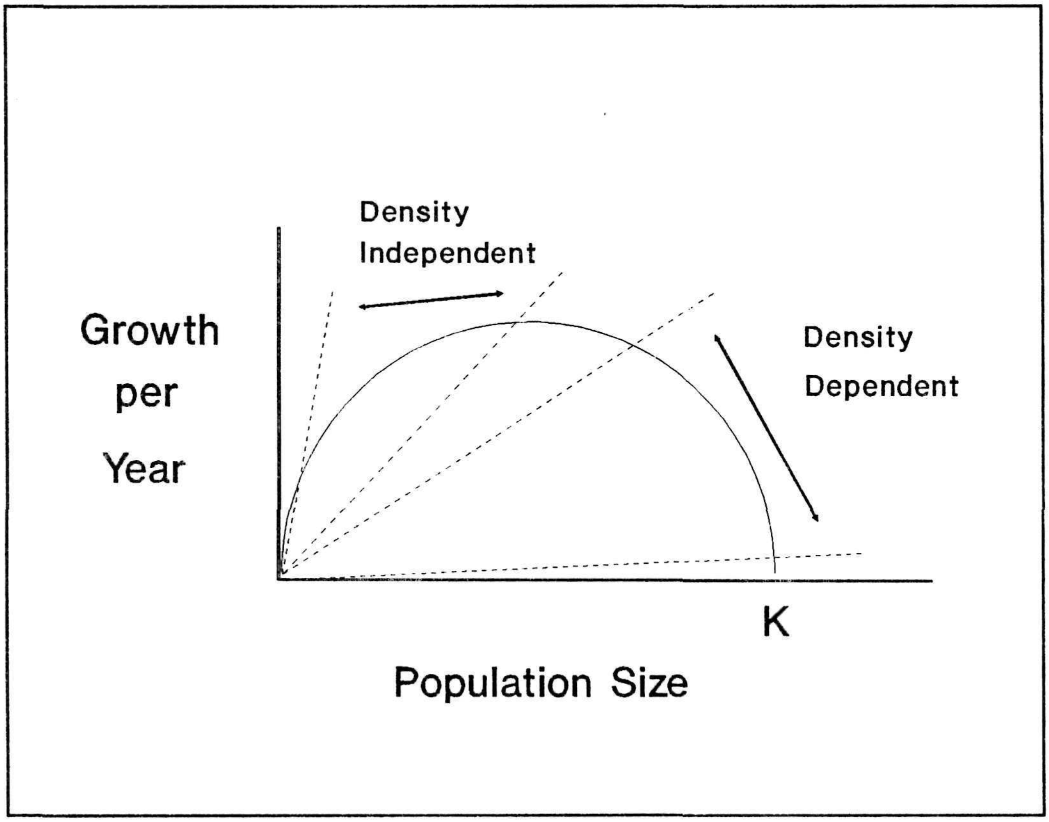


Figure 5. Hypothetical model of the range of population sizes over which density dependent and density independent processes affect recruitment of young. Frequent influence of density independent factors keeps the population in a constant state of recovery, masking density dependent processes.

**SUMMARY: The concept of natural regulation is important because it has been the historical 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 of defining "normal" and "stable" and, as yet, we have no rigorous, scientific basis for defining these terms.**

**Centripetal System Behavior**

At the heart of the debates about regulation is concern for the long term viability of the natural ecosystem. The common denominator to all of the debate is the question of whether the system is moving toward an equilibrium or toward chaos. The concept of *centripetality* provides a powerful approach to assessing this risk because it allows us to determine whether or not the system has an equilibrium.

We know that herbivore/plant systems of eastern North America are seldom in a state of constancy. They are buffeted constantly by a variety of outside forces that are both powerful and multidirectional. Consequently, the system is seldom near equilibrium. The important question is, how strong is the tendency for the system to move toward an equilibrium? This tendency is referred to as *centripetality* (Caughley et al. 1987). Where centripetality is weak or not present, the integrity of the system is at risk.

Is the system of deer and vegetation in eastern North America centripetal? 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 centripetality to exist, a series of conditions must be met.

1. **A feedback loop must exist between plant growth and accumulation of biomass:** Increased growth → increased biomass → decreased growth → decreased biomass → increased growth, etc.

2. **A feedback loop must exist between herbivore populations and plant biomass:** Increased plant biomass → increased herbivore populations → decreased plant biomass → decreased herbivore populations → increased plant biomass, etc.

**Australian Grasslands: An Example of Herbivore/Vegetation Interaction**

Caughley et al. (1987) examine long term records and models of Australian grasslands with kangaroos. The dominant feature in this system is variation in rainfall. The grass responds rapidly to increased rainfall and, because rainfall is highly variable, the annual variation in plant biomass is high. Fluctuation occurs unpredictably, but frequently.

Kangaroos respond to changes in plant biomass but the relationship is complicated by response time. If kangaroo populations are relatively low when favorable conditions occur, it takes several years for the populations to build. Once they achieve high levels, they persist in spite of low rainfall/plant production. Thus density of kangaroos at any one time does not reflect current food conditions, but rather reflects past conditions.

Kangaroos also influence plant biomass, but again the relationship is complicated by time scales. Increased rainfall results in grass production that overwhelms the kangaroo populations. Grazing will reduce the amplitude of the peak but will not control vegetation growth. Under drought conditions, kangaroo populations, having increased during previous years of favorable conditions, are well above the new K. Feeding by this large population deepens the trough of the fluctuation in plant biomass. Ultimately, the reduced plant biomass leads to reduced kangaroo densities.

Conditions #1 and #2 are met because feedback loops are evident at both the plant and plant/herbivore levels. The grassland is centripetal even in the absence of herbivores. The feedback loop involving vegetation and herbivores is weaker, but nonetheless present. Any perturbation of either the grassland or the kangaroos will result in short term change, but the system will continue to move toward an equilibrium when conditions are constant.

**Applications to Native Forests of Eastern North America**

The difference between the Australian system and that of 18th century eastern North America (i.e., prior to extensive agricultural development) is not one of ecological process, but complexity. We know that plant communities will not add biomass unendingly. The feedback loop described in condition #1 is evident. We also know that deer populations will not grow unchecked, and that they interact with vegetation in a manner described by condition #2.

The contrast in complexity, however, is striking. In both the Australian and eastern North American systems, annual changes in weather fluctuate irregularly, affecting growth of both vegetation and kangaroo/deer populations. However, additional forces of change are super-imposed in eastern North America. Perhaps greatest is the complex sequence of successional change that occurs on a time scale of centuries in eastern North America.

***Similarities with the Australian Paradigm.*** -- In mature forests, the feedback loop involves the plants in the understory. In a general sense, the older trees become superfluous in the herbivore/vegetation loop. The deer/vegetation cycle in the understory is much like that of the kangaroos and grasses:

> Increased numbers of deer → decreased biomass of vegetation in the understory → decreased numbers of deer → increased biomass of vegetation, etc.

If the environment is relatively constant, we can expect biomass of vegetation and deer to achieve relative constancy.

Inherent to both Australian and North American systems are fluctuations in annual moisture and temperature conditions. In eastern North America seasonal drought and winter reduce food quality. The degree of reduction is variable, but in many years the change is sufficient to affect the population dynamics of deer.

We might think of this environmental fluctuation in terms of $K$. Favorable conditions push $K$ up, unfavorable conditions push it down. Like the Australian system, 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 $K$. The population is likely to crash.

***Differences with the Australian Paradigm.*** -- The chief difference between the Australian system and that of eastern North America is the complexity of the changes occurring in the vegetation. In eastern North American, seasonal and annual fluctuations in $K$ occur <u>within</u> the context of the long term changes due to succession, and the large forces that disrupt succession. Large perturbations result from hurricanes and fires. These factors alter the plant community so greatly that, frequently, the system does not return to its pre-disturbance condition for decades or centuries.

The intervening period is marked by profound changes in plant growth and the vast number of species moving 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 move 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 moving and may be moving in two directions at once, at different rates (Figure 6).

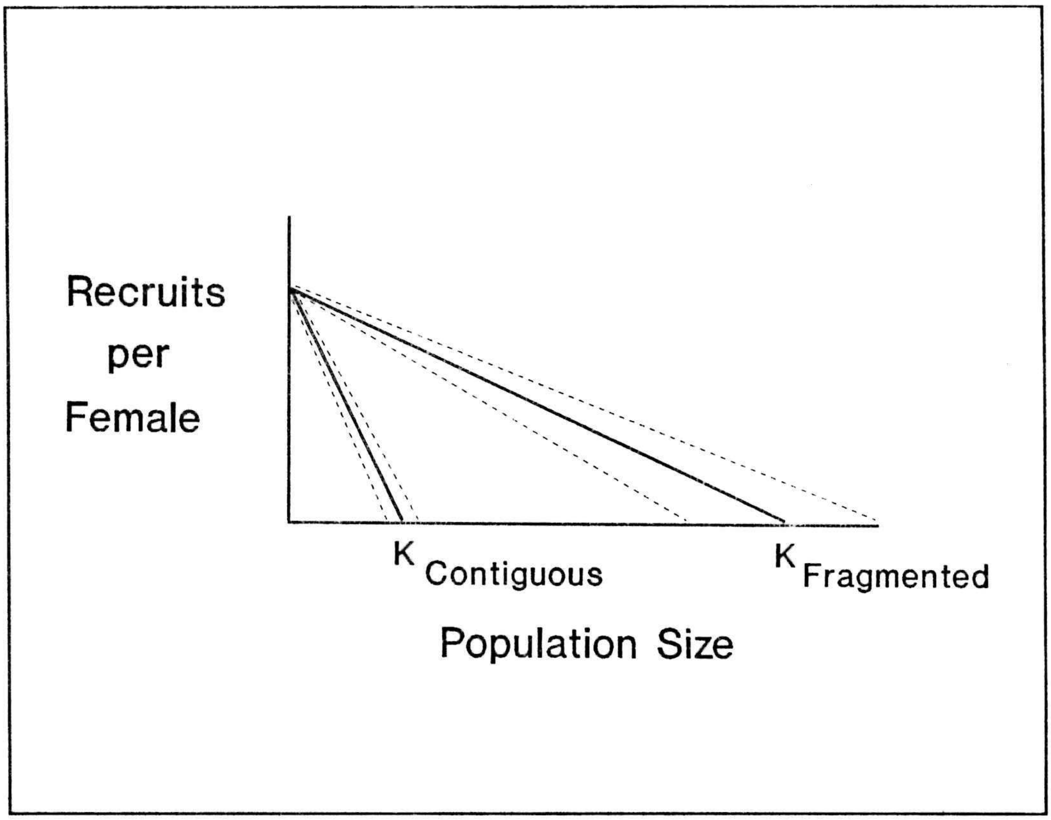


Figure 6. In eastern forests, succession causes changes in carrying capacity for deer, a moving equilibrium. The equilibrium is highest in young, fragmented forests and lowest in mature, contiguous forests when trees exceed the height deer can browse.

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

These time lags add further complexity to the process the recovery. Once the forest moves into the large sapling stage, biomass production within the reach of deer declines and nutritional conditions drop to very low levels. Prior to this point, the deer population was growing toward a much higher *K*. *K* is now much lower and the deer population is caught well above it. It will take a few years (perhaps a decade) for the population to adjust to the new conditions.

In short, like the kangaroo/grassland system, the deer/forest systems of eastern North America are constantly buffeted by external forces. Plant communities and deer populations are frequently out of synchrony. Both deer and vegetation conditions at any moment have more to do with the conditions of past years than those of the present. The major perturbations common to eastern North America, and succession, inject long time lags into the system. This loosens the feedback loop, but does not alter the basic processes necessary for centripetality.

The implications of this are clear. Deer will have the greatest impact on vegetation when their populations are caught above *K*. Such a condition is likely to occur and when it does competition for food is highest and deer feed on a broader array of plants. It will deepen the trough of plant biomass production in the understory, particularly among species that are preferred food items. This is when the probability for complete loss of a plant species is highest.

**SUMMARY: *Centripetality* provides a much stronger approach to assessing the long term integrity of the ecosystem. Deer and vegetation are centripetal, but the relationship in eastern North American landscapes is complex. Because vegetation and deer populations respond to disturbance on different time scales, deer are seldom at *K*. Because changes in vegetation cause variation in *K*, deer populations move toward an equilibrium that is itself moving. The probability for complete loss of a plant species is highest when deer populations are high and *K* is declining rapidly.**

**Application to Man-Dominated Landscapes**

The argument is often made that many ecological processes no longer operate in eastern forests. Predators have been removed, the forest has been fragmented, and agriculture and urban development have dramatically altered natural processes. This is important because many parks exist within this man-dominated landscape. Does centripetality still function in these systems?

***Predators.*** -- The removal of predators is considered by many to be the cause of the dramatic increases in deer populations. The analysis offered by Caughley suggests there is probably only limited truth in this. 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 and thus lengthen the time interval during which the population is below average abundance (Figure 7).

There is still considerable uncertainty about the role of predators in regulating populations of predators (e.g., Peterson 1988). Perhaps the clearest conclusion to date is that the presence of predators in the system 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. 1990). The presence of predators may provide this "window of opportunity". Indeed, the species composition in many forest stands today probably reflects a time period of low deer populations at the time of origin of the stand.

In a broader sense, are eastern systems which include predators likely to be centripetal? If the relationship between predators and deer is similar to that between deer and vegetation, predators are part of a centripetal system:

> 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 track deer population fluctuation, rather than cause it. It is likely, however, that predators will tighten the centripetality (reduce the amplitude of fluctuation).

***Substitutions for Predation.*** -- Does the mortality associated with sport hunting or auto/deer collisions substitute for the absence of predators? Yes and no. 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 does act in a regulatory manner similar to that of predators.

Interestingly, there is some question as to whether or not the population regulation imposed by modern hunting to too strong. In some places the hunting is so tightly managed that the deer populations fluctuate only ± 10%. If eastern plant communities have co-evolved 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, it is not centripetal.

***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 10x - 50x those of 1760 (Figure 8).

If we can assume the arrangement of forest/agriculture will remain relatively constant, then the landscape may be more strongly centripetal than that of the past. Agricultural environments are the primary source of nutrition for deer in eastern North America and thus have the greatest 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. In the absence of these long term successional changes, the fluctuation in the deer populations is significantly reduced.

However, much of the eastern North American 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 the East and significant portions of the landscape are reverting to forest through succession. In urban areas, agriculture is being abandoned to human development. Both of these trends are likely to continue into the next century.

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 itself is moving.

Predicting the equilibrium point is obviously challenging in this dynamic environment. Further compounding the challenge, local environments are fluctuating out of synchrony with one another. Thus, the future trends in deer populations vary on a scale as small as a few thousand hectares.

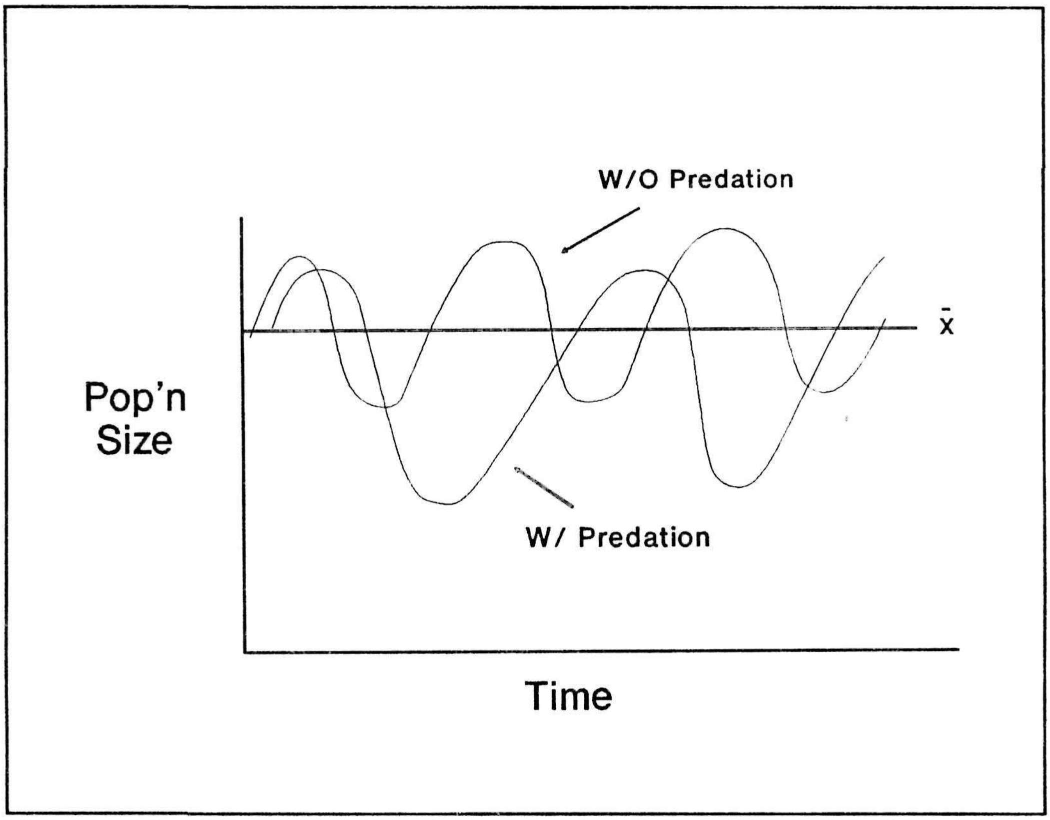


Figure 7. Theoretical model comparing of deer population fluctuation with and without predators. The impact of predators is to is to reduce the peak of the growth and lengthen the interval between oscillations.

It is possible, however, to make a few general predictions regarding regional changes. The long term trend for deer in eastern North America is downward. Given continuation of the trends in agriculture (decreasing) and urban development (increasing), *K* will decline (Figure 9). In the short term, we can anticipate further increases in deer populations. Deer populations have only been growing in the East since the early 1960's. Even in areas where they are not subject to hunting they have yet to reach *K* (e.g., Underwood et al. 1990).

***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*, it will weaken the centripetality in the system. We can expect increased average deer populations and higher peaks to population fluctuations. In the absence of hunting, deer populations regionwide could be expected to reach abundances seen on the national parks, more than 10x current levels.

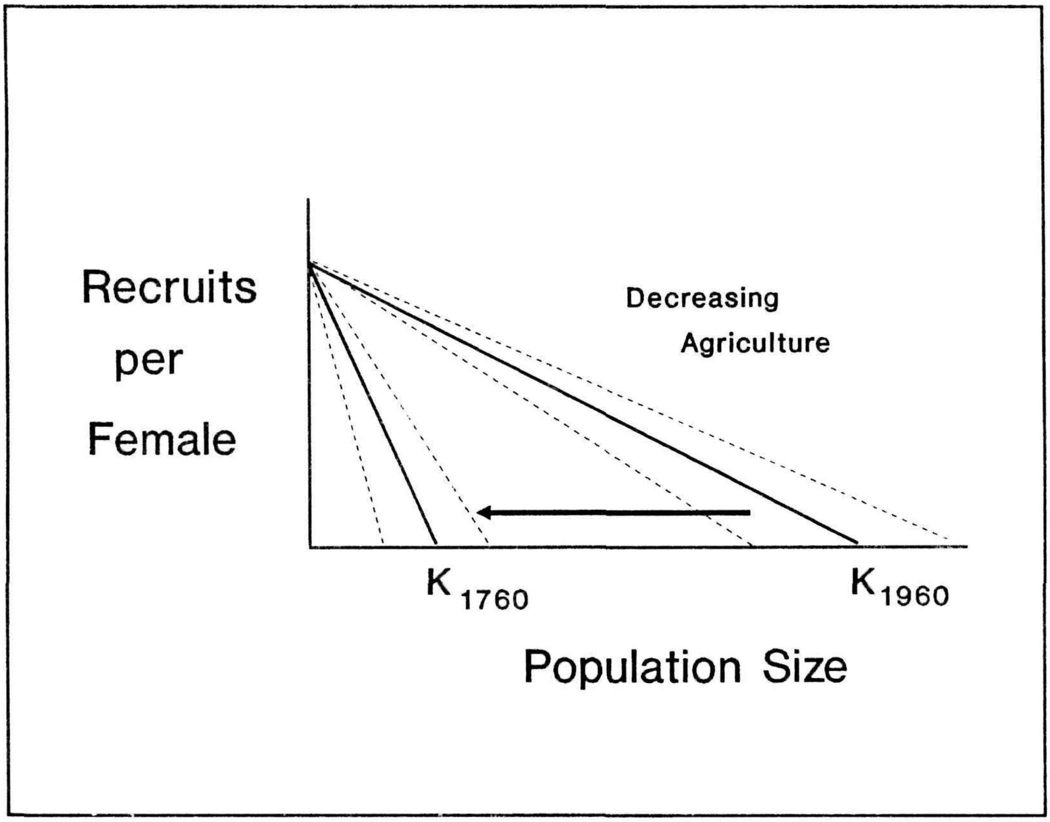


Figure 8. Ecological carrying capacity has increased dramatically in the past 200 years as a result of forest fragmentation and agriculture. K can be expected to decline as the amount of land in agriculture decreases in eastern North America.

***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 or stability are still inherent qualities of the system. Where forest/agricultural landscapes are constant, the system is centripetal. Centripetality is much stronger because the system is focused on a relatively stable, annual cycle. Deer populations will fluctuate with a smaller degree of variation, but with a much higher mean value than in the past.

Where agriculture is declining, the equilibrium will decline and centripetality will become weaker. Similarly, with decline in hunting, centripetality will become weaker. In these environments, fluctuation can be expected to be greater.

The greatest impacts of deer on vegetation will occur in the highly dynamic environments. Much of the impact will be manifest in changes to long term equitability of plant species. If species losses occur, they are most likely to occur in parks surrounded by rapidly changing agriculture and urban activities. 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.

Plant species loss is least likely where natural conditions prevail. Larger wilderness areas (e.g., Shennandoah) are responding to perturbations and equilibria points that are essentially unchanged in the past 200 years. In the absence of the dramatic increase in equilibrium, fluctuations in deer populations are likely to be within the historical ranges to which the plant community is adapted.

**SUMMARY: While landscapes in eastern North America have been dramatically altered by forest fragmentation and agriculture, centripetality still functions. *K* has increased by at least 10x between 1760 and 1960. Loss of agriculture will result in a long term decline in *K*. In the short term, deer populations are likely to increase because hunting is projected to decline. If losses of plant species occur, they are most likely to occur in parks surrounded by agricultural and urbanizing areas because deer population fluctuations are greatest in these environments.**

# CHAPTER 3.

## MANAGEMENT APPLICATION

The analysis in Chapter 2 suggests that deer populations of today probably do not pose a serious threat to the long term integrity of the eastern ecosystems. 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 judgement and therefore belongs in the realm of management.

This section describes how the background material presented above might be applied to management of deer and vegetation in a specific park. I first discuss the importance of setting clear objectives. Then I outline the specific information that a park must obtain prior to considering management action.

### Formulating Goals and Objectives for Management

The first requisite for management is a set of clearly articulated objectives. This 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 interpretability. 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.

***Formulating 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 outside groups. 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 come to quick agreement 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.

NPS sustained its management policy, in part because it was securely anchored politically and in part because it 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 NPS. There was broad understanding and "ownership" of the policy. Scientifically, NPS 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.

***Setting Objectives for Deer and Vegetation Management.*** -- A comparison of three NPS units, Saratoga, Gettysburg and Fire Island, provides an interesting illustration of the difficulties in formulating objectives. The common denominator is that deer are perceived to be a problem in all three parks. At Saratoga, a five year study concluded 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.

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, respectively. Both studies showed that deer are having a significant impact on 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 complete. Agricultural crops were part of the historic scene and it is clear that deer on the southern units of the park are precluding any 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 position to formulate policy that can be anchored to science.

One of the goals of Fire Island is preserving coastal forest ecosystems. Interest groups outside of NPS suggest that the goals and objectives should be to cast in terms of ecological balance as measured by the health of the deer herd, or some index of damage to the flora caused by deer. Such an approach is ultimately illogical.

Ecological balance is technically defined as a system at its equilibrium point. As discussed above, eastern systems are rarely at equilibrium under natural conditions. Perturbation by hurricanes and continual recovery <u>is</u> the norm. Health of the deer herd is more readily cast into objectives (minimum body weight or antler size on yearling males) but is not a logical extension of the broader goal of preserving ecosystem function. Periodic malnutrition and death is a normal ecological condition for deer.

Finally, damage implies the system is in a condition that is outside of the normal cycle of change, and from which it will have difficulty recovering. How do we translate this into a statement of objective? Some fluctuation in deer populations, including periodic crashes, may be essential to maintaining the system. To evaluate a condition, we must know the full range of change from which a system can recover. Logically, we can never be certain we have defined the full range of normal variation.

The practical solution is to identify and control any influence of man on the deer/vegetation interaction. We know that deer affect vegetation, and that this is part of the natural process in eastern forests. We must establish that man is altering the natural process, such as feeding deer through the winter, and thereby increasing survival and reproductive performance.

Thus, undertaking management of deer and vegetation requires two essential steps. First, we must formulate clear objectives that are consistent with the goals of the park. Second, we must be able to show that deer are causing management failure, or that the actions of man are creating an undesirable condition in the deer population.

**SUMMARY: Management is inherently value-driven. It is when we cast objectives that we reap the most criticism. 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 source of conflict with management objectives. Given that deer and vegetation in eastern landscapes are highly dynamic, concepts such as *ecological balance* and *deer health*, probably do not constitute reasonable approaches for NPS management.**

**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, and an understanding of how these resources interact with one another. To manipulate one resource will affect many others. The interactions are complicated because resources are constantly changing. These changes occur on time scales varying from months to decades, and different resources change on different time scales. We can cope with this complexity only if we can predict 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. Done well, monitoring provides long term data sets that enable us to see subtle, as well as bold, patterns of change (e.g., Magnuson 1990, Swanson and Sparks 1990). Doing monitoring well requires careful attention to decisions about what variables are important to measure and to measuring them consistently.

For our purposes, the intent of monitoring is to predict how various resources will change when deer populations change. There are four variables of primary importance to monitoring deer and vegetation interaction: 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 is important because it allows us to begin to understand the forces that cause change and to predict how the population will change in the future.

Effectively monitoring abundance of deer requires a sound statistical design but does not need to be expensive. Our intent is to compare population size from one time to the next. We do not need an absolute estimate of deer populations (although they 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 the function between the number of deer seen and true abundance is constant. In practical terms, this function expresses our ability to detect deer. It doesn't matter whether our survey technique is able to detect 10% of 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.

Unfortunately, several factors influence detection. Most of these are related to behavior of deer. For instance, deer are more active in late fall than in mid-summer and thus more likely to be seen. 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 be examined using multiple regression. We can statistically 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 et al. (1990) illustrate the application of this technique.

***Recruitment of Deer.*** -- Recruitment is an important variable because it is probably the most sensitive to competition for resources, and thus helps us make judgements 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 thus deer are most visible.

The intent 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 necessary because each count is a sample of the population, and mean and variance are needed for comparative purposes. Interpretation is relatively straightforward if adult mortality is reasonable 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. The objective of monitoring is to characterize species richness and document the continuing presence of plant species. This aspect of a monitoring program should include two components.

First, a park should establish a reference collection of plants found on the park. This collection is essential to scientifically document those species that are present on 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 of particular importance to management. These other species may be designated because they are sensitive to deer browsing, considered important to the ecosystem or interpretation at the park, or are of value to some particular management objective.

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

***Plant Species Equitability.*** -- This variable measures the proportional distribution of the species in the plant community. 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 degree of 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.

The sample points should be referenced on maps and marked with permanent stakes in the field. At each sample point a series of plots are established. The size and location of plots vary with the growth form of the plant species. Ideally, these should be remeasured annually at the same time of year. Plant communities are frequently impacted by short term phenomena, such as human activities, drought or the eruption of a particular insect. This adds variation to our analysis of deer and vegetation interaction. Annual remeasurement allows greater ability to account for and control this variation.

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 used has a long archival life.

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**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. Vegetation monitoring requires annual measurement of species at permanent sample points to account for changes in species richness and equitability. Pictures at sample points can be invaluable.**

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# CHAPTER 4

## FUTURE RESEARCH ON DEER AND VEGETATION IN NATIONAL PARKS

If park management is going to have a solid anchor in science, NPS must adopt a different 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. Specifically, five qualities should be considered in the formulation of future research programming: a commitment to building long term databases, an integrative approach to investigation, an orchestration of comparative studies, development of modeling, and experimentation.

### Long Term Databases

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

The major studies of herbivore/vegetation interaction on Isle Royale, the Serengeti, Yellowstone and Australia all show the same basic pattern. Herbivores and vegetation are definitely linked through a feedback loop, but the relationship is complex because they 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 20 year data sets within the NPS framework seems superficially unrealistic. Certainly, maintaining a funding commitment to intensive, long term research is very difficult. However, continual intensive research is not necessary. The ideal approach may actually be one which weds long term monitoring with periodic intensive research.

Monitoring provides long time perspective on key variables that is lacking in current 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 different from those being monitored.

NPS may be in a better position than any other land-management agency to utilize this approach. National parks are among the few places where continuity of management allows examination of natural processes. Parks are protected from capricious change and thus can allow long term dynamics to occur. Many parks now have solid historical databases on deer and vegetation. Finally, monitoring fits well within the structure of the park system because Resource Management Specialists are present in most parks and can 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 will not provide the answers.

Again, the classic studies of Isle Royale, Serengeti, Yellowstone and Australia provide important models. These investigations were built on intensive study of each of several trophic levels. They incorporated multiple studies, each focusing on individual components of the system, but conducted in close collaboration. Their power arises from this orchestration of these individual efforts to yield a synthesis.

NPS Science offices can provide the leadership in formulating and integrated study design. It can orchestrate the various projects. Close collaborative relations with outside scientists appears to offers a strong approach to constructing the synthesis from a multifaceted 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 was the approach employed by the International Biological Program (IBP) and no other program has ever stimulated as much conceptual development in the realm of ecosystems.

One of the most important contributors to good scientists' 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 brought to bear on the analysis of the problem in a particular park.

NPS is in 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 NPS technically owns the data, access to combined databases by various users can be assured.

**Modeling**

Recent advances in modeling provide techniques essential to understanding deer and 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 ready 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 thus provide direction for research.

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., Starfield and Bleloch 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 a range of natural conditions and are generally less impacted by man in comparison to other lands. This allows testing of models across broad gradients, under conditions where the role of man is tightly controlled.

**Experimentation**

The key to understanding herbivore/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.

The most effective way to achieve this rigor is to conduct the research in an experimental mode. Most often this takes the form of a 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.

NPS is one of the few agencies that can conduct the experimental work necessary. 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 to time because management programs are more consistent than those on other government lands, or private lands. Finally, NPS 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 development of long term databases. The focus of research needs to be on the process more than the components. Understanding process will require comparative studies and modeling. Controlled experimentation, involving manipulation, will be essential to applying science to management problems. NPS, perhaps more than any land-management agency, is in position to apply the power of this approach.**

**Recommendations for Research Programming**

***Recommendation #1: Monitoring Should Be Expanded.*** -- To obtain the long term perspectives necessary, NPS should develop a strong monitoring system in most of its eastern parks. Resource managers and scientists should meet to decide on the variables to be monitored and the protocol to be followed for measurement and data entry. The variables listed above provide a starting point for discussion. The National Science Foundation, through its Long Term Ecological Monitoring program (LTER) provides a example of more comprehensive monitoring (e.g., Michener 1986, Franklin et al. 1990)

NPS should negotiate with principal investigators to 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 one of the regional offices in the East. With improving communication capabilities through national computer networks, access should be relatively easy. Once this is in place, workshops should be held for NPS scientists, resource managers and university cooperators to teach all participants measurement procedures and data management protocol.

***Recommendation #2: A Coordinated, Inter-regional Research Program Should Be Initiated.*** -- To maximize the potential for addressing ecosystem level questions, studies should be conducted in a few parks that offer comparative value. Two environmental gradients should be considered in selection of study locations, a north-south latitudinal gradient and a forest fragmentation gradient. Additional criteria for selecting study sites should be a strong historical database 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 NPS 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 ongoing NPS symposium series to broaden communication.

***Recommendation #3: Studies Should Be Multi-Disciplinary, 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 vegetation/large herbivore interaction. 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. NPS should play a role in assisting scientists to maintain currency with state-of-the-art technique. 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.*** -- NPS should look carefully at the needs for immediate management action to relieve problems. These present excellent opportunities for experimental research and consideration should be given to conducting the manipulations within the context of science. However, experimentation should not be limited to immediate management problems. NPS should undertake experimentation in tests of specific hypotheses that contribute to a fundamental understanding of the system. The experimentation should be designed with consideration to the importance of long time perspectives, opportunities for comparative analysis, and values of a multi-disciplinary 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 proved difficult because of a lack of information in the fundamental ecology.

As NPS moves forward it should consider funding projects that meet immediate management needs, and 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 the specific, but unpredictable problems of the future is pursuit of basic research.

***Recommendation #7: NPS Should Initiate Research in Two Areas.*** -- First, NPS needs to begin examining the influence of the surrounding landscape on deer/vegetation interactions. Much what happens in parks is a result of the conditions surrounding the park. Comparative studies across both the fragmentation and the urbanization gradients would be especially appropriate. Modeling efforts that link population dynamics and movement behavior of deer with spatial pattern are important. Advances in population modeling and geographic information systems make such an effort tractable.

Second, NPS should undertake direct experimentation of several management alternatives that have been proposed. Of particular importance is the hypothesis that localized management of deer populations can be achieved via removal of discrete family units (Figure 10). Each experiment should be replicated on at least two parks across the forest fragmentation gradient. The strong needs identified across the eastern regions make this effort politically feasible.

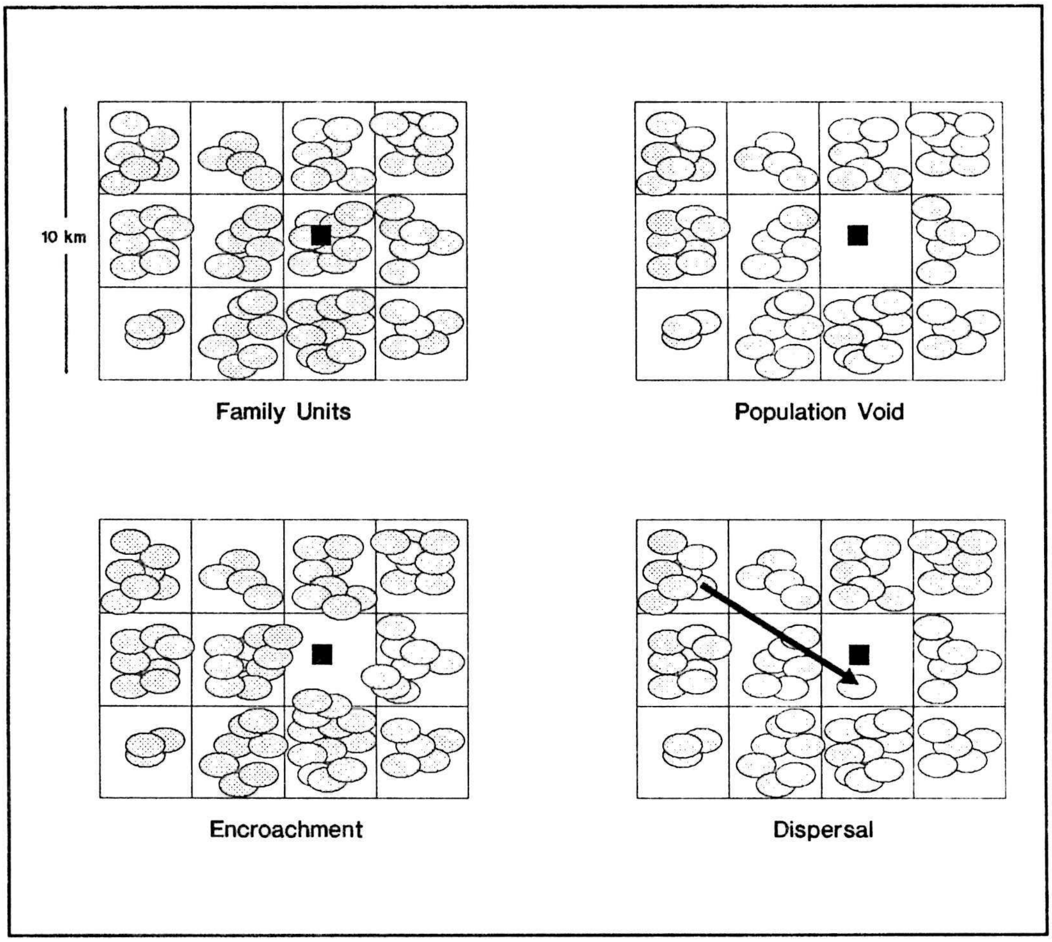


Figure 9. Model of localized reduction of a deer population through elimination of the family unit surrounding a cultural resource (black square). The family unit is removed and the area remains void of deer until encroachment or dispersal causes new growth in that area (from Porter et al. 1990).

## Selected Research Questions

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

***Are eastern deer/vegetation systems centripetal, given the dynamic landscape?*** This question is of obvious importance in the context of NPS responsibilities to preserving process. Specific hypotheses were advanced above for different environments, but no work has been done in eastern landscapes. This question would be amenable to modeling.

***Will introduction of predators affect the population dynamics of deer and the centripetality of the deer/vegetation interaction?*** This is a commonly proposed solution to deer problems and is readily addressed using modeling. Coyotes are thought to be increasing in eastern parks. What affect will they have on the period and amplitude of fluctuation. The recent work modeling the impacts of wolves on large herbivores in Yellowstone would serve as a place to begin such an effort.

***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 presence of a common species that is also highly preferred as a food item. Other levels of browse intensity may reduce equitability be nearly eliminating some species. The approach used by Underwood et al. (1990) which characterized a gradient of browsing impact could be easily adapted to addressing 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. A specific hypothesis was described above, but no rigorous science 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 process is the goal?*** We tend to think about management in terms of identifying and maintaining a static condition. Is this ecologically sound? How will plant communities differ if deer populations are allowed to fluctuate widely? 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?*** The hypothesis that can be derived from above is that hunting of the periphery would remove migrants, but would have little long term impact on the population. A first test of this hypothesis could be achieved via modeling.

***Can we control deer using surgical removal of family units?*** 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 will 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 the parks have significant impact on deer that use the park. These surrounding lands are dynamic but we can predict their character over the next 20 years. The impacts of these changes on deer could be modeled readily.

***How will changes in park boundaries influence harvest of deer and, consequently, behavior and population dynamics?*** This question is corollary to hunting on the periphery because changing park boundaries influences the portion of the population that is vulnerable to this mortality factor. It's also corollary to the question of surrounding landscapes because as parks get larger, surrounding landscape becomes less important. 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 boundary changes can be anticipated.

***How will changes in the vegetation within parks influence deer population dynamics?*** 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 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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