The Science of Overabundance: The Ecology of Unmanaged Deer Populations

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Effect of Deer on the Regeneration of Eastern Hemlock (*Tsuga canadensis*) and White Cedar (*Thuja occidenta*) in Northern Forests

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Intentional habitat management, abundant summer forage, and mild winters have boosted densities of white-tailed deer to high levels in forests of the upper Midwest. To assess the extent and severity of browsing on sensitive conifers, we surveyed 235 forested sites in northern Wisconsin and the western Upper Peninsula of Michigan dominated by hemlock and/or white cedar. Our sites span a variety of land uses and deer densities and included managed forest stands, Native American reservations, the Superior Snow Belt, and the Apostle Islands. Data from our descriptive and experimental studies indicate that the density of 3-300 cm tall hemlock and white cedar seedlings varies considerably and appears correlated with scat-group counts and a browse index on sugar maple (*Acer saccharum*).

Surveys of Plants and Animals at High Versus Low Deer Density: A Class Project in Brown County State Park (BCSP) and Yellowwood State Forest (YSF), Indiana

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Consistent with policy, Brown County State Park's 25,000 acres are not normally hunted. As a consequence, the white-tailed deer (*Odocoileus virginianus*) population in the park is estimated to be five times that of hunted properties, such as the adjacent Yellowwood State Forest. To reconfirm the density estimates, we conducted line-intercept pellet counts on transects of about 10 kilometers in each park. Our counts supported the previous estimates, so we continued with comparative surveys of understory vegetation cover and plant species composition. We also made early morning song counts of two ground nesting neotropical migrant birds, and counts of chipmunks seen and heard in similar physical sites in the two forest properties. Understory vegetation was significantly less abundant and diverse, and lower in seedling abundance in BCSP than in YSF. Ovenbird (*Seiurus aurocapillus*) numbers did not differ between the two sites, while worm-eating warblers (*Helmitheros vermivorous*) were less abundant in the state park than the state forest property. Eastern chipmunk (*Eutamias minimus*) counts were extremely variable within both sites, providing a weak trend suggestive of lower numbers were deer density was higher.

Influence of Deer and Other Factors on an Old-Field Plant Community: An Eight Year Exclosure Study

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Spatial and temporal patterns of variation in plant community composition of a Virginia old-field were studied over eight years following a widespread disturbance. In this paper, I focus on patterns of woody plant establishment in the presence and absence of white-tailed deer (*Odocoileus virginianus*) using fenced exclosures. Results showed that woody plant species richness was significantly higher: 1) where deer were excluded compared to where they were present; 2) nearer-to than far-from an adjacent oak-hickory-elm (*Quercus-Carya-Ulmus*) woodlot; and 3) near exclosure fences than away. The total number of woody stems did not vary with accessibility to deer or with distance from the woodlot. Of 19 woody plant species present in the field, only black walnut (*Juglans nigra*) showed a significant exclosure effect--it was found more often where deer were present than absent. By contrast, the presence of four species was correlated with distance from the woodlot, three species with soil moisture, three species with exclosure fences, and five species with the abundance and diversity of herbaceous vegetation during the first four years of succession. These results suggest that the impact of deer, even though they are locally abundant, is relatively minor when compared to other environmental effects. The deer impact might have been stronger if the field had not been adjacent to an agricultural field, or if the experiment focused on a later rather than an earlier stage of plant succession.

Comparison of Adjacent Hunted and Unhunted Systems Within a Landscape

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Problem deer populations are those that interfere with planned landscape uses, but who are not subject to easy management solutions. Developing and adopting management tactics that minimize the complex interaction of social, legal, biological, and physical constraints are often frustrated by a lack of site-specific experience that can be used to predict treatment results. One way of overcoming a lack of data is by simulating management using models that allow landscape constraints to produce the logistical behavior of populations. This study compares the results of desert mule deer hunting on Terlingua Ranch and Black Gap Wildlife Management Area in west Texas, to changes in the deer population on an adjacent preserve (Big Bend National Park). I used an individual-based, spatially-explicit model of desert mule deer movements to predict how the landscape may have shaped the histories of these three sites. I claim that the Chihuahuan desert is self-fragmenting at the scale that desert mule deer use it. The self-fragmenting nature of this desert may have created unique dispersion patterns of deer across this landscape that substantially contributed to the ultimate management result.

Health Characteristics of Overpopulated White-tailed Deer Herds in the Southeastern United States

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Significant disease-related morbidity and mortality among white-tailed deer (*Odocoileus virginianus*) in the southeastern United States is due to two major problems. One is a syndrome of malnutrition and parasitism with the principal parasitic agents being the large lungworm (*Dictyocaulus viviparus*) and the large stomach worm (*Haemonchus contortus*). The second is hemorrhagic disease which is caused by either epizootic hemorrhagic disease (EHD) or bluetongue (BT) viruses, both of which are transmitted by biting midges (*Culicoides* spp.). Other infectious and parasitic agents may be important on a local scale or may serve as stressors compounding the syndrome of malnutrition and parasitism. Based on their epidemiologic features, these two disease problems were evaluated for compliance with the conceptual model of changes in herd health attributable to increasing population density as presented by Eve (1981). The syndrome of malnutrition and parasitism is a density dependent phenomenon across the region, although the inherent nutritional quality of habitats and the identity of parasitic agents vary among geographic areas. Hemorrhagic disease activity is less clearly related to deer density because of its epidemiologic complexity (i.e., multiple virus serotypes, regulation of susceptibility by existing herd immunity, involvement of domestic ruminant hosts, multiple species of *Culicoides* vectors, and distinct geographic patterns of occurrence). Eve's conceptual model, Shea and Osborne's (1994) delineation of nutritionally low quality habitats, and the geographic distributions of important deer pathogens were used to construct elementary predictions of probable health problems among unmanaged white-tailed deer populations in different portions of the southeastern United States.

Deer Density and Ecosystems Management

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Ecosystems management is comprised of a number of components (biodiversity, ecological processes, communities, identified consumable and non-consumable products, forest condition) and contexts (landscapes of space and time, forest health, climate, sustainability, and human and deer impacts). All the components and some of the contexts are impacted by deer, generally as a function of deer density. Management of these components and contexts by humans is influenced by deer density. Management of deer has resulted in densities ranging from almost 0 to more than 25 deer/km^2 over the last century with associated impacts on components and contexts of ecosystem management. Within the forested landscape of western Pennsylvania, these impacts become discernable once deer density exceeds 4 deer/km^2.

Seasonal Home Range and Habitat Selection by White-tailed Deer in Northwestern Virginia

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I studied home range size and composition, habitat selection, and habitat factors that determine such selection of white-tailed deer (*Odocoileus virginianus*) in Posey Hollow, near Front Royal, Virginia. At least 10 radio-tagged adult females were located three times each week for 14 months in 1989-1990 to determine home range sizes during each season. McPaal personal computer software was used to determine home range sizes by convex polygon model. GIS was used to estimate the proportions of each habitat type within home ranges to determine the influence of habitat types on size of home ranges. Seasonal habitat selection was determined by two methods: first, from the number of deer locations on habitat types compared to their availability, and second, habitat factors, determined by sampling 180 random points in all habitat types, were compared to factors at 720 deer locations as determined by radio-telemetry.

Two-way ANOVA showed that home range sizes differed by season. Seasonal home ranges were largest in autumn. Linear regression showed that home range areas were most influenced by their proportions of oak, hardwoods, and black locust habitat types. Chi-square goodness-of-fit determined that deer were selective in habitat use during all seasons. Black locust habitat type was most preferred during spring and summer, and was second to grassland in autumn and winter. Discriminant function analysis showed that deer were selective during all seasons. Deer selected locations with higher forb cover and higher coralberry (*Symphoricarpos orbiculatus*) cover during spring, higher grass and coralberry cover during summer, and with higher grass cover during autumn and winter. The high productivity of black locust habitat type was due to the openings in its forest canopy, resulting in more grasses and forbs than other wooded habitats. Signs of habitat overuse call for population reduction.

Role of Refuges in Regional Deer Population Dynamics in the Midwest

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Deer refuges in the midwest may have contrasting functions and effects. In some parts of the midwest, refuges were designated to serve as protected areas within larger heavily hunted tracts. These core areas were designed to act as refugia in which deer could escape from hunters and as sources of immigrants to repopulate surrounding hunted areas. In contrast, some areas closed to hunting develop extreme deer densities and may contribute to human/deer conflicts and reduce the ability to manage deer numbers.

To determine the impact of refuges on regional deer populations in the midwest, from 1980 to 1993, we examined the demography of deer on 4 study areas in Illinois and Missouri. Dispersal/migration rates varied among sites and averaged highest for male fawns (65%), followed by female fawns (34%), adult males (23%), and adult females (16%). Most movements were dispersals (60% and 96% of doe and buck movements, respectively) and occurred during spring (84%). On refuge portions of the study areas, annual survival and reproductive rates were generally high. Modeling the impacts of these refuges on outlying populations revealed significant contributions that enhance or deter management efforts depending on land use, hunting intensity, and population goals.

Evidence for External Regulation in an Unmanaged Deer Population

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White-tailed deer lack intrinsic mechanisms to regulate populations below K carrying capacity. Thus, deer on a large island where large predators have been extirpated, and where hunting is prohibited would be at high risk of over-exploiting vegetation. We evaluated changes in browse availability and use for deer in Acadia National Park (ANP), Mount Desert Island, Maine, from 1980 to 1989, winter nutritional status of deer, predation by a recently established population of coyotes, and cause-specific mortality rates of fawns and adult does. From 1980 to 1989, availability of preferred browse species was relatively unchanged, utilization of highly preferred browse species increased, and utilization of species of low to intermediate preference declined. Spatial differences in fecal crude protein levels were positively correlated with both utilization and availability of preferred species. Reproductive data and body weights of captured animals further indicated that the population was well below K carrying capacity. Recently established coyotes utilized deer extensively during spring, early summer, and winter. Six family groups occupied the island and densities of resident coyotes exceeded densities on the adjacent mainland. Fawn recruitment was low and resulted from mortalities caused by vehicles, coyotes, dogs, and drowning. The resulting age structure for adult deer was skewed towards older individuals; however, adult does were also susceptible to occasional mortality caused by vehicles, dogs, and coyotes. We conclude that the combined influences of vehicles, coyote predation, and dog predation initiated a decline in the deer population, and we speculate that these influences may exert a regulatory effect on future populations.

Influence of Deer on the Development of Forest Structure and Composition in Central Massachusetts

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Throughout eastern North America, oak (*Quercus*) forests do not appear to be replacing themselves, particularly on mesic sites. Most of these forests originated when white-tailed deer (*Odocoileus virginianus*) populations were at low levels. Deer can cause regeneration failures, but the role of deer in altering successional pathways in these forests is not clear. I examined even-aged oak forests in Massachusetts that originated between 1882 and 1935. Eight stands occurred where deer were hunted, and 8 occurred where hunting had been prohibited since 1938. Half the stands in each areas had been thinned, and half never received any silvicultural treatment. Estimates of deer density made each fall from 1983 through 1992 ranged from 10 to 17/km^2 for the protected area (high deer density) and from 1-3/km^2 for the hunted (low deer density) area.

There were fewer small trees (2.5-10.0 cm diameter) in the high than low deer density area. This change in overstory structure occurred after stand establishment. Tree seedlings of all species were most abundant where deer density was low; thinning increased seeding density regardless of deer density. Tree seedlings were abundant and well distributed in low deer density stands that had been thinned. Oak seedlings, however, were well distributed in only 2 of 4 of these stands. Seedling density increased where deer were excluded for 6 growing seasons (1984-1991), but oaks were not well represented. However, no tall oak seedlings (>100 cm) were observed in high deer density stands and only 2 of these stands had oak seedlings 30-99 cm tall. These observations suggest that there is little probability of replacing oak in the high deer density stands, and that replacement stands will not be fully occupied by trees. Excluded deer for 6 years did not reverse these conditions. Stands where deer were less abundant will replace themselves, although some future stands may have less oak than the present ones.

Changes in the Distribution of Deer Within Virginia

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Historical changes in deer distribution patterns and population trends in Virginia are similar to many southeastern states. Virginia's deer population at the time of European colonization may have range from 120,000-800,000. Following colonization, Virginia's deer herd exhibited a long-term and significant population decline. This decrease was caused by over-harvest, habitat loss to agriculture and deforestation, and ineffective enforcement of game laws and regulations. In 1931, the Virginia deer population was estimated to be only 25,000 animals. A restoration program initiated in 1926 resulted in the release of more than 4,200 deer. Ensuing hunter harvests have risen from an estimated 793 deer in 1923 to a known minimum of 201,122 in 1993. Current population estimates indicate a stable statewide population of approximately 900,000. Human population growth, urban development, and accelerated habitat loss will have profound impacts on Virginia's deer herd and management philosophy in the future. Management and research efforts to address deer-ecosystem impacts, crop depredation, vehicle collisions, and urban deer management problems are expected to increase significantly.

Effects of Social Structure on the Genetic Structure of White-tailed Deer: A Summary of Protein and DNA-microsatellite Data

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We investigated the association between social structure and genetic structure of white-tailed deer in an unharvested population in the Adirondack Mountains. Social groups, defined by intensive radio telemetry, are groups of female deer displaying a high degree of philopatry to geographic areas during both winter and summer. Allozymic characteristics show genetic structure at the resolution of a social group despite the high probability that males interbreed among groups. As a result of relatively low levels of genetic variation, allozymic data do not allow an evaluation of the relatedness of the individuals within the social group. In a related study (J. A. DeWoody, unpub. thesis, Texas A&M University), PCR was used to amplify white-tailed deer DNA microsatellites from a pedigreed herd. Five markers were highly polymorphic, showed codominant inheritance, and can reliably identify genetic variability. We anticipate that with a minimum of 10 markers, we will be able to identify related individuals within the social group and confirm genetic structure. This approach, based on the powerful technique of PCR, will provide a more thorough understanding of deer dispersal and philopatry and their influence on the genetic structure of white-tailed deer. Ultimately, these types of data will provide the basis for effective management of problems herds with minimal negative impact on genetic structure.

Historical Review of White-tailed Deer Populations in the United States

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Despite evidence to the contrary, the notion persists that white-tailed deer are more abundant now than they were ever before. In any case, the question of relative abundance of white-tails in an historic context appears to have only limited direct biological or ecological significance. However, it can imply or impose public value judgements about deer or wildlife generally that may significantly influence the nature of wildlife management and the capacity of wildlife managers. Equally value-laden is the term "overabundance" when used in regard to a species of major economic, aesthetic, biologic and recreational importance, yet which has the audacity to thrive in the face of unregulated human population growth and sprawl. For at least the United States, history reveals that managed wildlife invariably now is considered to be a resource, whereas unmanaged wildlife tends to be characterized as a source of conflict, real, potential, or imagined. Any wildlife population that exceeds its recognized actual utility, amenity value or exploitability, in time or space, is likely to be viewed as an imposition. Synonymous with imposition in this context is overabundance, regardless of the population size.

Studies of Irruptive Behavior in Deer

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I review three studies of irruptive behavior of deer, the George Reserve, Michigan, and North Manitou Island, Michigan, with white-tailed deer (*Odocoileus virginianus*), and Angel Island, California, with black-tailed deer (*Q. hemionus columbianus*), as well as review the literature. Irruptive behavior traces to time lags between vegetation-herbivore responses that do not achieve equilibrium in these systems. Populations crashes occur in seasons with most limited resources: winter in Michigan and late summer in coastal California. Irruptive behavior is amplified by containment by fence, or water for islands, so that dispersal and source-sink dynamics are restricted. Time interval between irruptions depends on recovery time of vegetation, which is most rapid for the herbaceous layer. The three cases reported are driven largely by herbaceous vegetation, show little time lag for recovery, and peak numbers of deer do not decline in successive oscillations. Thus, habitat damage and lowered carrying capacity predicted by most traditional irruptive models do not apply. These deer populations show irruptive behavior more like those of Soay sheep on St. Kilda Island. In the absence of natural predators, these periodic irruptions will continue if not controlled by humans.

Forest Understory, White-tailed Deer and Understory Dependent Species

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Forest understory characteristics may be shaped by large ungulates, such as white-tailed deer when these species are at high densities. Many other vertebrate species may be dependent on the composition and density of the forest understory plant community. We have established 12 4-ha sites within mature deciduous forests in the ridge-and-valley region of Virginia to examine the influence of white-tailed deer on select vertebrate species. Ten migratory bird species captured at these sites either nest or forage within the strata browsed by deer. We have recorded the density of these species and the characteristics of the vegetation for 4 years following exclosure of deer from 6 of these sites. Several species, such as the American redstart (*Setophaga ruticilla*) and hooded warbler (*Wilsonia citrina*), have shown significant increases in number after exclusion of deer, but other target species, such as wood thrush (*Hylocichla mustelina*) and ovenbird (*Seiurus aurocapillus*), have shown no response. Small mammal densities have also increased within exclosures, and these potential nest predators may differentially impact understory bird species. The removal of deer may start a cascade of effects that do not result in direct correlations between vegetation and migratory bird densities.

Density Impacts on Deer Sociobiology

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Escalating deer numbers, fewer natural predators, human encroachment into natural environments, along with ill-conceived deer harvest and forest management strategies based on emotional demands and economies, have contributed to many deer populations that are now socially as well as nutritionally out-of-balance. Such socially abnormal herds can result from direct human actions such as harvest strategies designed to maintain abnormally high populations for recreational hunting. They also can result from indirect actions such as eliminating natural mortality patterns around which the animal evolved. Regardless of the initiating cause, this abnormal social behavior may become self-perpetuating. We discuss the social consequences of white-tailed deer overpopulation in comparison to what we believe to be "natural" social conditions. We argue for management strategies that are based on a scientific understanding of deer behavior and natural mortality patterns, not on political, emotional, or economic considerations.

Demographics and Management of an Insular White-tailed Deer Population Exposed to Different Land-Use Practices

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We examined the demographics of a white-tailed deer (*Odocoileus virginianus*) population between 1983 and 1991 on Fire Island, an Atlantic barrier island located south of Long Island, New York, characterized by a variety of land-use and management strategies. Reproduction, physiological indices, and food habits along the entire island, especially for fawns, were indicative of a high density population experiencing physiological stress. Trends in population growth suggested that among residential communities, deer numbers increased rapidly over the study period, whereas deer on park lands were at or near ecological carrying capacity and population size remained relatively constant. Differences in diet ($p = 0.007$), movements and home ranges, and selected fat indices and blood chemistry parameters between park lands and residential communities were evident and may be attributed to primary land-use and local deer densities. Fire Island is endemic for Lyme disease and most deer (70%) were exposed to the Lyme disease spirochete (*Borrelia burgdorferi*). Increasing deer numbers generated concern among government and community officials. In 1989, a controlled sport hunt was used by the National Park Service to collect additional biological information from deer within Fire Island National Seashore and to evaluate the efficiency of hunting as a management tool. Intense public opposition toward hunting in a suburban landscape and on National Park Service lands resulted in additional expenses to insure employee and public safety and compliance with federal and state regulations. Thus, it is not likely that hunting is a viable alternative for deer management on Fire Island.

Demographic Profiles of Deer under Different Management Strategies in Pennsylvania

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Information on demographic and health profiles is essential to understand population dynamics of white-tailed deer (*Odocoileus virginianus*) and to minimize conflicts between deer and other natural resources. In this report we present data on abundance, herd composition, reproduction, mortality, survival, and health parameters associated with deer populations under 3 management strategies in south-central Pennsylvania: an unhunted population in the historic areas at Gettysburg (GETT), a fenced and hunted population within the Letterkenny Army Depot (LEAD), and hunted populations in surrounding Adams and Franklin counties. The abundance of deer at GETT (>90 per 2.59 km^2) was over 5 times the abundance in surrounding Adams County. The abundance of deer at LEAD (>160 per 2.59 km_2) was over 7 times the abundance in Franklin County. Differences among populations at GETT, LEAD, and surrounding counties were evident in the age composition, sex ratios, productivity, and health parameters. We have no evidence of self-regulation, irruptions, or drastic declines in the deer population at GETT despite high deer density and low quality habitat during winter. However, reductions in body weight, kidney fat, and productivity in young females (< 1 yr.) coupled with high deer density and poor habitat in LEAD suggest a potential for significant changes in the structure and function of the fenced population.

Case History: Deer Populations are Saratoga National Historical Park

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Recognizing that management of large herbivores in National Parks is surrounded by controversy, the National Park Service initiated a series of research projects at Saratoga National Historical Park (SARA) with a goal of providing a scientific basis for policy. To document current conditions of the deer population, we captured and tagged animals, conducted population surveys and examined animals found dead or harvested. During the mid-1980's, a large portion of these animals were seasonally migratory and spent summers outside the Park. The population declined in 1986 following a severe winter, but recovered. Physical condition of deer showed adults in similar condition to deer in eastern New York, but fawns and yearlings are smaller. Adult and yearling females are reproducing at rates comparable to hunted populations, but fawns are generally not reproducing. Survival of adult females is relatively high and automobiles are the greatest source of mortality. Survival of young (0-11 mo.) is low (50 fawns/100 adult females). These conditions are indicative of a population nearing ecological carrying capacity. Predictions of future trends suggest a slow increase in the deer population. Because of high chronic mortality and frequent severe winters, a classic population eruption which overshoots carrying capacity is unlikely. We project a maximum average population of 500 animals. Amplitude of fluctuation around this average is expected to be about 35%.

A Spatially-explicit Modelling Environment for Evaluating Deer Management Strategies in Unhunted Systems

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Over-abundant white-tailed deer populations can adversely impact features of landscapes being managed for aesthetic or historical values. Under such circumstances, active intervention may be required to preserve these unique attributes and to adhere to existing policies governing Park management. However, success at managing deer populations is likely to vary among parks depending upon their size, position in the landscape matrix, and their attractiveness to deer occurring in neighboring areas. Given the significance of these variables, it is difficult to predict which of the potential treatment options (i.e., harvest, habitat modification, fencing, sterilization, etc.) is most likely to accomplish management objectives (i.e., reduce deer densities) for individual parks. Justification of deer population control programs is especially important in National Parks due to the controversial nature of the problem, and the increased attention afforded them by the public and special interest groups. We present a simulation environment which combines spatially-explicit habitat features from a Park's existing geographic information system (GIS) with an individual-based deer population model to evaluate *a priori* the likelihood that alternative management strategies will achieve park management goals. The system imposes user-defined treatments on the deer population and/or the habitat/landscape matrix, and monitors individual deer movements and spatial responses of the population on a daily time step over a five-year period. Multiple iterations of each treatment scenario are conducted to evaluate the relative probabilities of potential outcomes. Deer responses to treatment scenarios can be viewed numerically, as changes in population size and composition over time, or visually, by contrasting changes in deer spatial distribution using spectral maps generated by the simulation. Additional features include identifying travel corridors and areas of high seasonal use by deer. Treatments can be customized and applied to entire populations, specific sex-age classes, or to specific areas delineated by the user. Results of treatment scenarios can be contrasted by users to provide strategic input which can be incorporated into park management and planning activities.

Multiple Ecosystem States: Rethinking the Role of Deer in Forest Ecosystem Dynamics

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A large amount of research has demonstrated that white-tailed deer can have dramatic effects on both the abundance and biological diversity of woody plant species in forest ecosystems. This evidence is derived largely from experiments in which deer are excluded from certain areas and allowed to exist in others. These exclosure experiments have led to the perception that deer are the major "controlling" influence in forest ecosystem dynamics. Consequently, management plans directed at restoring woody species production and diversity typically focus on lowering deer numbers as a major part of management. We caution that the practice of lowering deer numbers to enhance plant productivity and diversity may be based on incomplete information; hence management may fail to reach its goal in many cases. A survey of studies examining the impacts of large ungulates in natural, unmanaged forest ecosystems shows that there are often threshold levels of impact depending on herbivore density and woody plant abundance. These thresholds are reminiscent of alternative ecosystem states predicted by conventional predator-prey and grazing system theory and observed in other plant-herbivore systems, including African savanna. In a multiple states system, ungulates regulate or "control" woody plant production over certain densities of woody biomass, in which case excluding them is warranted. However, at alternative states of the same ecosystem, ungulates only limit plant production, in which case management that enhances tree growth rates, rather than lowering deer numbers, is more appropriate. We argue that conclusive evidence for multiple states is largely nonexistent because the proper field experiments needed to detect this dynamical property have yet to be conducted. Simple exclosure experiments do not give sufficient insight into dynamics. We show how the theory can guide thinking about the kind of information needed to understand the role of deer in forest ecosystem dynamics. Finally, we discuss the application of multiple states theory to experimental management of forest ecosystem dynamics. We show that when experimental management is conducted in ways that can test the theory, empirical evidence indicates that the existence of multiple states cannot be ruled out in deer-hardwood forest systems.

Deer Browsing Effects on Ecosystem Processes

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In theory, vertebrates can have both direct and indirect impacts on ecosystem processes, such as energy flow, nutrient cycling, and succession. Previous studies of forest ecosystem energy budgets suggest that deer have little direct impact on energy flow. In addition, relatively few studies document direct impacts of browsing animals on forest nutrient cycling. Numerous studies, however, have found direct impacts of white-tailed deer browsing on forest regeneration. We feel that this impact on regeneration needs further evaluation in an ecosystem context with concurrent consideration of tree species life-history characteristics, community composition, and exogenous ecosystem disturbance. Using vegetation and deer browsing data from an ongoing bottomland hardwood study, we simulate long-term browsing to look for patterns of indirect impact on forest stand dynamics.

Regional Variation in the Impacts of Browsing by White-tailed Deer on the Regeneration of Eastern Hemlock (*Tsuga canadensis*) and Northern White Cedar (*Thuja occidentali*)

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Although once dominant in the upper Midwest, old-growth Hemlock-Hardwoods became rare through logging and are now experiencing regeneration failure in many areas. White cedar forests, habitat for many rare herbaceous species, have also declined and contain few seedlings. To assess the severity and regional extent of these failures, we surveyed 235 hemlock- and cedar-dominated sites across northern Wisconsin and the western Upper Peninsula of Michigan. We found widespread variation among these sites in densities of large seedlings and small saplings. Seedlings of both species are found most abundantly on logs or other coarse woody debris, but subsequent survival seems to be limited by other factors. Similarly, local light levels, measured as % open sky via a fish-eye photo technique, enhance establishment and growth, but account for only a small proportion of regional variance in regeneration success. Thus, although site factors influence local patterns of hemlock and white cedar seedling establishment, other factors acting primarily on larger seedlings appear critical to limit successful regeneration in these important forest types. We have initiated further studies to determine how landscape-level effects of intensive management for game and forestry inadvertently threaten populations of herbaceous and woody plant specimens sensitive to this keystone herbivore.

The Significance of Large Mammals to Protected Area Conservation

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Mega-vertebrates are highly visible, often lucrative, and tangible components of ecological communities. As such, they receive a disproportionate share of attention from wildlife agencies, non-governmental conservation organizations, the media, and the public. Mammals, and ungulates in particular, figure largely in this group of charismatic mega-vertebrates. In spite of their visibility, large mammals present as many challenges to conservation as more elusive and less-known species.

Their significance is related to several characteristics: 1) many are keystone species whose removal can have major impacts on communities; 2) they often encompass the ideal features of "flagship species," and lend themselves well to conservation organizations to bait members for contribution to urgent causes; 3) they are often destructive to croplands, and dangerous to man, and as such inspire strong sentiments and drastic actions by the victims; and 4) populations of large mammals are as difficult to measure as those of smaller and seemingly more elusive vertebrates, and this has led to many misconceptions by the media, the public, and decision makers about their conservation and management.

Calls for the conservation action of large mammals, and deer in particular, are almost always based on inadequate ecological information. In general, prescriptions for conservation of large mammals emphasize mitigation of often unverified threats, bypass investigation of ecology, lean heavily on expatriate and foreign expertise, and overlook the importance of developing local institutional capacity. A tactical approach to conservation being developed by the IUCN Deer Specialist Group is described which addresses these deficiencies.

Detection of Density Dependence in a Colorado Mule Deer Population

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Density dependence in a population requires a relationship between one of the basic parameters of population growth, birth or mortality rate, and the size of the population. Compensatory mortality further requires that a change in one source of mortality results in a compensating change in a second source of mortality. We have documented these relationships with 2 independent experiments on the Piceance mule deer (*Odocoileus hemionus*) population in northwest Colorado. In a study involving 3 pastures (31-83 ha) stocked at densities of 33, 89, and 133 deer/km^2, over-winter survival of fawns was directly related to stocking rates of pastures, with approximately a 2 times increase in survival at one-half the density. In a predator control study, we demonstrated an increase in mortality rates of over-wintering fawns from malnutrition when the mortality rate from coyote (*Canis latrans*) predation was decreased, with no overall change in survival rate.

Temporal variation in over-winter fawn survival was estimated to be 0.017 with mean survival of 0.248. The value of 0.017 suggests that for over-winter survival rates modeled with a normal distribution, 95% of the winters would be within ±0.26 of the mean. Because of this large temporal variation in over-winter fawn survival rates, detection of density-dependent and compensatory mortality effects with reasonable (>0.80) power requires one, or more likely, all of the following conditions: 1) large sample sizes to decrease sampling variation, 2) large treatment effects to be able to separate the treatment effect from sampling and temporal/spatial variation, and 3) large numbers of years and/or study areas to separate treatment effects from temporal and/or spatial variation.

Effect of Coyote Predation on Population Dynamics of Sympatric Deer Species

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We studied the population dynamics of sympatric mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) on Rocky Mountain Arsenal, northeast of Denver, Colorado. Although both species increased during the 4-year period, mule deer increased at about twice the rate of the white-tails. Adult survival and natality were similar for the two species, but early survival of fawns was greater for mule deer. Principle cause of death in fawns (<30 days) of both species was coyote predation. The less abundant white-tail fawns were born significantly earlier than mule deer fawns and experienced proportionately greater coyote predation. Difference in population growth of these ecologically similar, sympatric deer species appeared largely explained by predator swamping, enhancing survival of mule deer fawns. Predation will continue to influence the balance of mule deer and white-tailed deer population on Rocky Mountain Arsenal.

Deer and the Epidemiology of Lyme Disease

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During the past two decades, Lyme disease has emerged to become the most frequently diagnosed arthropod-borne illness in North America. The causative agent is a bacterial spirochete (*Borrelia burgdorferi*) transmitted by the tick *Ixodes scapularis* (= *I. dammini*). Natural enzootic maintenance of *B. burgdorferi* transmission in the eastern and north-central U.S., where most Lyme disease occurs, involves larval and nymphal ticks that feed on small mammals, principally white-footed mice (*Peromyscus leucopus*). While white-tailed deer play no role in this enzootic cycle, extensive evidence demonstrates that deer are the single most important vertebrate host for feeding by adult ticks, thereby strongly influencing the tick's reproduction, abundance, and distribution. Interactions among deer density, *I. scapularis* abundance and Lyme disease risk will be reviewed. Efforts to reduce risk by manipulating deer density or distribution will be examined.

Assessing, Interpreting, and Modelling Long-term (>10 year) Fluctuations in Deer Population Abundance Within Refuges and Parks

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The assessment of long-term fluctuations in abundance has practical significance to the understanding and management of deer populations on parks and refuges. Even simple analyses of time trends in abundance can reveal a population's growth rate and its associated variability. As datasets from routine monitoring activities grow, so has interest in utilizing time-series methods for extracting the most information possible about the process of interest. For wildlife populations, temporal dynamics are generated through a birth-death process, which is determined by the prevailing schedules of fecundity and survival. Because the population's growth rate integrates survival and fecundity into a single value, specific time-series models can be identified that reveal more about a population than just how fast it is growing. In this paper, I will present some useful time-series methods, from simple to complex, for extracting the greatest amount of information about deer population trends and fluctuations. Using both simulated and real data, I will detail a step-by-step process for determining important elements of deer populations necessary for informed and guided management.