A research perspective on white-tailed deer overabundance in the northeastern United States

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Resolving issues of deer (*Odocoileus* spp.) overabundance will require gaining more reliable knowledge about their role in ecosystem dynamics. Science can contribute by advancing knowledge in 4 overlapping spheres of research: model development, measurement techniques, population management, and human behavior.

The concept of deer overabundance is best defined in terms of ecosystem management objectives (Underwood and Porter 1991). Overabundance has been defined in ecological terms (Warren 1991), but ultimately the determination is based on a value judgment. Deer are perceived as overabundant when they limit the abundance or occurrence of other resources or interfere with some valued ecosystem process or human activity. Examples include loss of plant diversity, damage to agriculture and forestry crops, loss of landscape plantings, deer-vehicle accidents, and changes in habitat for other species. Perceptions that deer are overabundant are likely to increase in the future.

Deer populations traditionally were viewed as outputs of plant communities, but recently deer have been recognized as important regulators of ecosystem processes (Hobbs 1996). This shift in perspective parallels the evolution of the concept of ecosystem management and the development of integrated-management goals that include maintaining ecosystem components and outputs of goods and services (Christensen et al. 1996).

There is a large body of literature describing effects of deer browsing on plant communities (e.g., Tilghman 1989) and some describing indirect effects of deer on associated animal communities (e.g., deCalesta 1994). We know that the impact of deer on ecosystem components is a joint function of deer density and forage availability (Redding 1995, deCalesta 1997). But most studies have been conducted at small scales (4-16 ha) and over short time periods (<10 years). What types of biological information will be needed as management horizons expand from stands to landscapes encompassing hundreds to thousands of hectares, and to time scales equal to multiple generation times of the dominant tree species?

Biologically sound and socially acceptable management will require greater knowledge of the human dimensions associated with deer and deer management. The primary method for managing deer abundance is deer harvest by hunters, which is manipulated by regulating season length and bag limit. Managing deer harvests will require maintaining adequate numbers of hunters and motivating them to participate in management programs. The numbers of deer hunters may be declining; in Pennsylvania the numbers of adult hunters and youth entering the hunting population have declined since mid-century (Witmer and deCalesta 1992). Our ability to recruit new hunters and motivate existing hunters to accept new management goals (e.g., lower populations) and regulations (e.g., proficiency tests) is questionable. Significant changes also are occurring in the demography and attitudes of the nonhunting population. Thus, the social context in which management decisions are made and the atti-

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tudes and values associated with perceptions that deer are overabundant will change in the future.

We think that the best approach to resolving specific issues of overabundance involves gaining a better understanding of the ecological connections between deer and other ecosystem components. Our perspective has been formed during research careers that together total about 55 years with the U.S. Forest Service, Northeastern Forest Experiment Station. Controversy about the abundance of deer has been the context for our studies on the effects of deer on various ecosystem components. Here, we look specifically at white-tailed deer (*Odocoileus virginianus*) in eastern forests, and focus on the information needs of resource managers. The need for brevity prohibits a review of the rich literature on deer ecology or a definition of all research needs associated with white-tailed deer. We outline promising opportunities for research directed at understanding the role of deer in ecosystem dynamics, and emphasize the importance of integrating knowledge across varying scales and disciplines.

Research approaches

Resolving specific issues of deer overabundance will require integrated research in 4 overlapping areas. First, we must provide improved methods for predicting responses of ecosystem components to deer density. This will involve a substantial synthesis and modeling effort. Second, research can develop more efficient methods for estimating deer population size and forage abundance at specific landscape scales, ranging from habitat patches to deer home ranges. Reliable data at these scales are essential for developing predictive models of deer impacts and monitoring progress toward management goals. Third, research can improve methods for regulating deer populations. Substantial opportunities exist for enhancing the effectiveness of public hunting and for developing alternatives to hunting, such as contraception. Finally, more information is needed on the human dimensions of resource management. Public involvement in management will increase; managers will need to understand human attitudes and motivations to gain support for and participation in deer management programs.

Modeling deer impacts on ecosystem components

The basic mechanisms by which deer modify ecosystems are known (nutrient cycling, net primary production, and disturbance regimes; Hobbs 1996), but our ability to predict deer and plant responses to management and resolve conflicts remains limited. Interactions between deer and their environment are complex, involving direct and indirect effects, feedback mechanisms, and time-lags (Pastor et al. 1988, Pastor and Naiman 1992, Ostfeld et al. 1996). Modeling these complex relationships should be a primary goal of future research motivated by issues of overabundance.

One class of simulation models (spatially explicit models) looks particularly promising for research and management (Moen et al. 1997). The forms and uses of spatially explicit population models and their linkages to vegetation models have been reviewed in a recent issue of *Ecological Applications* (Conroy et al. 1995, Dunning et al. 1995, Holt et al. 1995, Turner et al. 1995). We encourage this line of research, but note that developing spatially explicit models requires being able to measure deer and forage density at small spatial scales and over short time frames in real landscapes. These modeling efforts are also essential prior to large-scale manipulative experiments. Sensitivity analysis and hypothesis refinement through modeling are essential steps for optimizing the benefits of such research.

Estimating deer impact at the stand level

Understanding ecosystem function at large scales will require developing better techniques for measuring events at small scales. In particular, more efficient methods of measuring deer abundance are essential for understanding interactions between deer and vegetation. Gill (1992) reviewed deer damage to temperate forests and noted that a failure to define a relationship between deer density and damage and the inability to predict damage were the results of crude or unreliable methods of estimating deer density. Among many studies of the effects of deer on vegetation few have accurately measured or controlled deer density. Macnab (1985) noted that manipulations of deer density for management purposes could not be accomplished until managers developed reliable methods for estimating deer density.

The scales at which deer and vegetation are monitored and managed are often incompatible. Estimates of deer density are conducted over landscapes much larger than individual stands, which are the basic units of forest-vegetation management. Habitat selectivity by deer results in unequal use of habitat patches within landscapes. For example, in Pennsylvania and Massachusetts we routinely observe a 10-fold variation in pellet-group counts (and thus in derived estimates of deer density) among stands within management units. Scientists and managers often need to know how many deer used an individual stand or patch during a specific time period (i.e., growing or dormant seasons) to evaluate management practices or experimental treatments.

Lack of efficient techniques for estimating deer abundance locally has been a vexing problem in our work, and unreliable density estimates confound the interpretation of much work done in the past. Some form of pellet-group count or vegetation-use survey may provide an appropriate technique, but we are unaware of efforts to develop new or enhance existing techniques. The ideal abundance estimator could be applied quickly, by 1 person with minimal equipment.

There are reliable methods for estimating forage abundance, but all are labor intensive. Yield tables depicting forage production by habitat type (combinations of cover type, stand age, and stocking level) would be useful for research and management. Measures of forage availability for deer have not usually included tree seeds, but Rogers et al. (1990) provide a notable exception. Future estimates of forage production should include seeds, particularly oaks. Deer select acorns over most other foods; acorn abundance influences the consumption of other vegetation by deer, the distribution of deer within the landscape, and the physical condition of the deer. All of these interactions affect ecosystem-level response of deer and vegetation to management.

Regulating deer populations

The application of ecosystem management and resolution of conflicts surrounding overabundance will require sophisticated control of deer populations. Public hunting is the primary tool for managing deer populations, yet little research is directed at improving its effectiveness or acceptability. More effective public-hunting strategies would maintain the value of deer as a resource and minimize public expenditures to resolve issues of overabundance. There are important opportunities for developing new norms of hunter behavior and approaches to hunting. We have been encouraged by the effectiveness of controlled hunts that involved minimal investments in hunter training (Deblinger et al. 1993, Winchombe 1993). The spread of the concept of quality deer management is also encouraging. The quality-deer-management approach seems to hold opportunities for involving hunters in management and for integrating deer population management with ecosystem management (Woods et al. 1996).

Research also should be directed at developing alternatives to hunting. Controversies over deer abundance often involve suburban or protected populations that cannot be hunted effectively because of limitations on hunter access or safety concerns. Contraceptive techniques offer a promising alternative for controlling deer populations (Warren 1995), and we encourage research to refine and develop contraceptive technologies and other alternatives to public hunting.

Human-dimensions research

Successful deer management, including the resolution of problems caused by deer overabundance, will routinely incorporate the results of human-dimensions research. Knowledge of human attitudes and values will be needed in all phases of management from establishing goals to gaining support for the methods used to meet those goals. Human-dimensions research should be an integral part of improving methods for population control of deer. Research is essential for identifying factors that will stimulate hunters to participate in management programs. Human-dimensions research will also be a part of improving hunter skills and knowledge, and in gaining the support of hunters and nonhunters for deer population regulation by hunting or other means.

Fitting the pieces together

The most direct approach to understanding how deer regulate ecosystem processes would be to manipulate deer populations experimentally while measuring appropriate effects on selected ecosystem components. The experimental approach has contributed greatly to our knowledge of ecosystem function (Tilghman 1989; deCalesta 1994; Hobbs et al. 1996 *a,b*). Future use of experiments with large herbivores may be limited by declining research budgets and the logistical constraints of controlling animal density over large areas for long time periods.

In the absence of experimental control, the best opportunities for observing ecosystem response to deer may be provided by the application of ecosystem management to land management and quality deer management to herd regulation. Ecosystem management is being applied to some national forest lands at an operational scale, resulting in changes in vegetation structure and composition and the abundance of forage for deer (Bukenhofer and Hendrick 1997). New approaches to deer management are also being applied at a landscape scale. For example, large timber companies in Pennsylvania (Tom Eubanks, Int. Paper Co., Coudersport, Pa., pers. commun.) are experimenting with hunting leases and harvest strategies to achieve management goals. The

Department of Natural Resources has been testing a quality-deer-management program in Dooley County, Georgia, since 1993 (Kile 1996). Many of these large-scale management experiments are based on the concept of adaptive management, and include monitoring and spatially explicit data bases. These new management efforts offer opportunities for the development of conceptual models, new techniques, and approaches to resolving issues of overabundance.

The research community needs to form partnerships with management to turn these new forest and deer management programs into opportunities to understand system behavior in response to herbivory by deer. Wildlife and land management agencies, and timber, agriculture, and hunting interests are obvious partners; all are interested in large-scale, long-term responses, and some already monitor key components of the system. Scientists can help managers design and justify experimental management plans. Scientists should provide the theoretical background for selecting alternative management hypotheses and predicting the possible outcomes of alternative management actions. They can also ensure adequate spatial replication and control. Large management experiments will serve as templates for numerous small and precise experiments. Walters and Holling (1990) provide a thorough discussion of designing experimental management programs and their value for understanding ecosystem behavior. The concept is straightforward. The challenge to research is to provide the enthusiasm and imagination needed to form working partnerships among those interested in sustaining forest ecosystems that include deer.

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Literature cited

Bukenhofer, G. A., and L. D. Hendrick. 1997. Shortleaf Pine/Bluestem Grass ecosystem renewal in the Ouachita Mountains. Trans. North Am. Wildl. and Nat. Resour. Conf. 62:In Press.

Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, C. H. Peterson, M. G. Turner, and R. G. Woodmansee. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecol. Appl. 6:665-691.

Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecol. Appl. 5:17-19.

Deblinger, R. D., D. W. Rimmer, J. J. Vaske, G. M. Vecellio, and M. P. Donnelly. 1993. Ecological benefits and hunter acceptance of a controlled deer hunt in coastal Massachusetts. Northeast Wildl. 50:11-21.

deCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manage. 58:711-718.

deCalesta, D. S. 1997. Deer and ecosystem management. Pages 267-279 *in* W. J. McShea, H. B. Underwood, and J. H. Rappole, eds. The science of overabundance: deer ecology and population management. Smithsonian Inst. Press, Washington, D.C.

Dunning, J. B. Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecol. Appl. 5:3-11.

Gill, R. M. A. 1992. A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65:145-169.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60:695-713.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996*a*. Ungulate grazing in sagebrush grassland: mechanisms of resource competition. Ecol. Appl. 6:200-217.

Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996*b*. Ungulate grazing in sagebrush grassland: effects of resource competition on secondary production. Ecol. Appl. 6:218-227.

Holt, R. D., S. W. Pacala, T. W. Smith, and J. Lin. 1995. Linking contemporary vegetation models with spatially explicit animal population models. Ecol. Appl. 5:20-27.

Kile, T. 1996. Dooly County, Georgia has Wisconsin on its mind. Sand County Found. Newsl. (Madison, Wis.) Summer:1-2.

Macnab, J. 1985. Carrying capacity and related slippery shibboleths. Wildl. Soc. Bull. 13:403-410.

Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. Ecology 78:505-521.

Ostfeld, R. S., C. G. Jones, and J. O. Wolff. 1996. Of mice and mast, ecological connections in eastern deciduous forests. Bioscience 46:323-330.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. Am. Nat. 139:690-705.

Pastor, J., R. J. Naiman, B. Dewey, and P. McInnes. 1988. Moose, microbes, and the boreal forest. Bioscience 38:770-777.

Redding, J. A. 1995. History of deer population trends and forest cutting on the Allegheny National Forest. Pages 214-224 *in* Proc. tenth central hardwood forest conference. U.S. Dep. Agric., For. Serv., Gen. Tech. Rep. NE-197.

Rogers, M. J., L. K. Halls, and J. G. Dickson. 1990. Deer habitat in Ozark forests of Arkansas. U.S. Dep. Agric., For. Serv., South. For. Exp. Stn., Res. Pap. SO-259. 17pp.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53:524-532.

Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. Ecol. Appl. 5:12-16.

Underwood, H. B., and W. F. Porter. 1991. Values and science: white-tailed deer management in eastern national parks. Trans. North Am. Wildl. and Nat. Resour. Conf. 56:67-73.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060-2068.

Warren, R. J. 1991. Ecological justification for controlling deer populations in eastern national parks. Trans. North Am. Wildl. and Nat. Resour. Conf. 56:56-66.

Warren, R. J. 1995. Should wildlife biologists be involved in wildlife contraception research and management? Wildl. Soc. Bull. 23:441-444.

WINCHCOMBE, R. J. 1993. Controlled access hunting for deer population management: a case study. Northeast Wildl. 50:1-9.

WITMER, G. W., AND D. S. DECALESTA. 1992. The need and difficulty of bringing the Pennsylvania deer herd under control. Proc. East. Wildl. Damage Control Conf. 5:130-137.

WOODS, G. R., D. C. GUYNN, W. E. HAMMITT, AND M. E. PATTERSON. 1996. Determinants of participant satisfaction with quality deer management. Wildl. Soc. Bull. 24:318-324.

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