Deer inside a U.S. Department of Agriculture Forest Service enclosure in northwestern Pennsylvania.

Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management

David S. deCalesta and Susan L. Stout

Relative deer density (RDD) provides managers with a way to broaden their approach to issues of deer overabundance from single-species management and carrying capacity to multiple-species management and ecosystems.

White-tailed deer (*Odocoileus virginianus*) populations and harvests of white-tailed deer have increased dramatically in the eastern United States on public and private lands during the 20th century (Porter 1992, Kroll 1994). Recognition of the impacts of deer on ecosystem components (deCalesta 1997) and controversy over management of deer populations (Porter 1992, Witmer and deCalesta 1992) have also increased. In the past, deer density was managed to provide an optimal and sustainable number of deer for harvest. However, with the advent of ecosystem management and its emphasis on management of all resources (Salwasser 1992, 1994; Christenson et al. 1996; Goodland and Daly 1996) we were required to abandon the single-species approach to deer management. We propose a framework for extending the single-species concept of carrying capacity to a more inclusive model for integrating management of deer with that of other ecosystem components.

Relative deer density

In 1984, McCullough published a deer recruitment curve for the George Reserve, Michigan. Net annual recruitment of deer was expressed as a function of the relationship between deer density and K, the eco-

Authors' address: Forestry Sciences Laboratory, PO Box 928, Warren, PA 16365, USA.

Key words: carrying capacity, *Odocoileus virginianus*, relative density, sustainablity, white-tailed deer

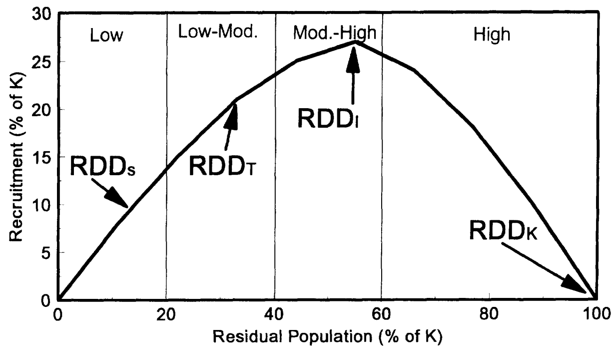


Fig. 1. Relative deer density (RDD) displayed on McCullough's (1984) graph. We show the approximate location of **RDD_S**, the level associated with sustaining biodiversity, **RDD_T**, the level at which timber productivity is sustained, and **RDD_I**, the level associated with maximum sustained yield of deer numbers for harvest.

logical carrying capacity of the George Reserve. We propose that this deer recruitment curve also can be used to provide a framework for predicting deer impacts on supporting resources (Fig. 1), and that similar resource impacts occur at similar relative deer densities on landscapes with widely varying carrying capacities. We suggest a framework for describing these impacts based on McCullough's (1984) definition of K carrying capacity, the population density at which mortality is balanced by recruitment, so that net recruitment is zero. The conceptual framework that we propose is relative deer density (RDD), or current deer density as a proportion of deer density (DD) at K carrying capacity: RDD = (DD/K) x 100. Further, we suggest using McCullough's (1979) deer population-recruitment curve (Fig. 1) as a backdrop for defining relative deer density as it relates to sustaining deer harvest or ecosystem components. Without explicitly using the concept of RDD, McCullough (1984) described the probability of seeing deer in the forest and the rate of recruitment as predictable functions of RDD. When interactions between deer and their environment are scaled to K, we have a standardized method for describing impacts of deer on ecosystem components and for making integrated predictions of the impacts of management choices. If we can estimate K and ambient deer density for a landscape, then we can derive RDD.

In many forest environments K is never reached. Losses to predation and extreme weather maintain deer populations below this deer density (Porter 1992). The definition is useful, however, as a way to characterize deer density and forage availability on specific landscapes and to predict the impact of deer on other resources. That is, any particular landscape has a maximum number of deer it can support on a sustained basis, based on forage and in the absence of predation, hunting, or extreme weather. If deer densities associated with sustainable deer harvest and impacts on various forest resources can be expressed relative to K, and if the relationship is consistent across differing landscapes, then managers will have a useful diagnostic tool with which to engage stakeholders in meaningful dialogue about the implications of different deer densities.

The relative deer density associated with a sustained yield of deer for harvest (RDD_I, where the subscript refers to McCullough's [1984] "I" carrying capacity, or maximum sustained yield of deer for harvest) is consistently higher than that associated with a sustained yield of timber (RDD_T, where the subscript refers to sustained yield of timber). The relative deer density associated with sustaining biological diversity (RDD_S, where the subscript refers to sustaining all resources) is yet lower. We offer these observations and this framework as management tools for integrating the important interactions among deer, plant communities, and other components of the ecosystem. Such a framework will not eliminate controversy among stakeholders in the deer management debate, but it will help participants understand trade-offs associated with different alternatives. Use of this tool will require techniques for estimating K and deer density at appropriate scales.

Some examples

Researchers have provided a few estimates of K. These have included an estimated 38 deer/km^2 at the George Reserve in central Michigan (McCullough 1979, 1984) and 55-60 deer/km^2 on Saratoga National Historical Park (SNHP) in northeastern New York (Underwood et al. 1994). Both sites included interspersion of old agricultural fields with forest land (old fields comprised 26% of the area at the George Reserve and 50% of SNHP). Porter and Underwood (1997) suggested that landscape carrying capacity (and thus K) for deer increased as the proportion of the landscape in old fields increased.

Healy (1997), working in a contiguous oak forest in central Massachusetts, observed deer densities approaching 20 deer/km^2 where hunting was prohibited. This provided another estimate of K in contiguous forest without the additional forage provided by old agricultural fields. Although oak mast production is highly variable from year to year (W. M. Healy, Northeast. For. Exp. Stn., U.S. For. Serv., Amherst, Mass., unpubl. data; Auchmoody et al. 1993), it is an important deer food, and effectively increases K in some years.

Healy's (1997) studies included 2 stands at 2 different ranges of deer density and RDD—a hunted area where deer densities ranged from 3 to 6 deer/km^2 (RDD 15-30) and a refuge where deer densities ranged from 10 to 17/km^2 (RDD 50-85). At RDD < 30, Healy (1997) found many small trees and seedlings well distributed throughout his study stands. At RDD > 33, he found fewer saplings and no oak seedlings >100 cm tall.

Based on a 10-year, deer-enclosure study (deCalesta 1994) we estimated K and RDD levels associated with deer impact on many forest resources. The study incorporated 4 65-ha study sites in northwestern Pennsylvania divided into 4 deer enclosures. We designed the study intending to maintain white-tailed deer densities of 4, 8, 16, and 32/km^2 within the enclosures for 10 years. As all sites were within large blocks of contiguous second-growth forest, we opened each enclosure by 10% clearcutting and 30% thinning for forage creation. We used only adult female deer, and we replaced losses due to escapes, predation, starvation, or poaching every spring to maintain desired densities.

Researchers were unable to maintain target deer densities of 32 deer/km^2 during the study (deCalesta 1994); starvation mortality resulted in actual densities of 25 deer/km^2, which we estimated as K for this artificial system. In this unfragmented forest, K was much lower than that estimated on the George Reserve or SNHP, but there were no interspersed old agricultural fields in the study landscape.

In the 10-year study in northwestern Pennsylvania, Tilghman (1989) and deCalesta (1992) determined that species richness and abundance of shrubs and herbaceous vegetation declined between 4 and 8 deer/km^2, (16<RDD<32, given K = 25 deer/km^2). This suggested an RDD ≤ 16 may be required to sustain this kind of vegetation. Similarly, outside the fences, white-tailed deer density in the region of the study has been >8 deer/km^2 (and thus above RDD = 16) for the last 70 years (Redding 1995). Hough (1965) and Whitney (1984) attribute the disappearance of common herb and shrub species to deer densities in this RDD range. Species richness and abundance of intermediate-canopy songbirds decreased, along with nesting and foraging habitat for these birds (deCalesta 1994) at these same RDD values (16<RDD<32). At RDD > 16 (4 deer/km^2), species richness of tree seedlings began to decline (deCalesta 1992). Relative deer density for sustaining species richness and abundance (RDD_S) of sensitive flora and fauna in this example was approximately 16.

In the same study, regeneration of commercial hardwood species began to fail at RDD > 32 (8 deer/km^2; Tilghman 1989). Thus RDD for sustained yield of timber (RDD_T) in our example was about 32.

The estimates of K and RDD derived from the 10-year study have limited application because of the restrictive nature of the study. However, we feel that the basic relationships of K to RDD values extracted from the study will apply to other landscapes, providing a useful starting point for integrating management of deer and other forest resources based on deer density and forage availability. Absolute deer densities at each of the RDD values may differ among landscapes with different quality and quantity of deer forage, but we hypothesize that the ratios of RDD to K will be consistent.

We summarized the interactions of deer with plant communities as a function of RDD and integrated results of deer impact studies with McCullough's (1984) observations about deer population dynamics and visibility (Table 1). McCullough's (1984) recruitment curve provided a powerful framework for integrating information on deer population dynamics with information on deer impacts on ecosystems (Fig. 1).

However, there is more to this emerging paradigm for deer management than simply including multiple resources. The impact of a given deer density on resources depends on the surrounding landscape. Results of the northwestern Pennsylvania enclosure study (Tilghman 1989, deCalesta 1992) suggested that the impact of deer on ecosystem components was a function not only of deer density but also of forage availability (Fig. 2, from Marquis et al. 1992). Other scientists (Palmer et al. 1997) linked deer condition and recruitment to deer density and forage availability. These studies suggest the need to express impacts of deer on ecosystem components *relative* to forage availability and scaled to the landscape where they occur.

By linking deer-ecosystem interactions to RDDs of specific landscapes, we account for the dramatic differences in carrying capacity and resulting ecosystem effects that have been discussed by many researchers (Porter et al. 1994, Stout and Lawrence 1996, Porter and Underwood 1997). RDD also provides a framework for understanding why deer impacts change even as deer density remains the same, e.g., as a forested landscape develops from one dominated by seedling-sapling stage stands with abundant deer food to one dominated by poletimber stands with little deer food. Before the RDD model can be used with confidence, we must define the scale required

Table 1. Interactions of deer with plant communities as a function of RDD, Relative Deer Density. This table shows integrated results of deer impact studies (Tilghman 1989, deCalesta 1994, Healy 1997) with McCullough's (1984) observations about deer population dynamics and visibility. We show RDD_S, the level associated with sustaining biodiversity, RDD_T, the level at which timber productivity is sustained, and RDD_I, the level associated with maximum sustained yield of deer numbers for harvest.

RDD	Effects on flora and fauna	Effects on deer dynamics	Implications for hunting
Low <20% RDD_S	Some browsing of preferred plant species, standing crop and productivity controlled by ecosystem.	Reproduction and recruitment at biological potential. Deer seldom seen.	Hunting yields low, but sustainable. Trophy deer available.
Low-moderate 20–39% RDD_T	Moderate change in relative abundance of plants. Herbs and shrubs especially vulnerable. Production and standing crop declines visibly for preferred species, but total crop unchanged. Wildlife species susceptible to changes in habitat may decline.	Rate of reproduction declines, but recruitment is still high.	Harvest yield high, trophy deer abundant.
Moderate-high 40–59% RDD_I	Impacts are obvious: structure and species composition change, total standing crop and productivity are decreased. Susceptible woody and herb species eliminated locally, habitat structure much reduced.	Reproduction and recruitment decline at upper end of this range. Deer are frequently seen.	Maximum sustained yield of deer for harvest. Few trophy animals.
High ≥60% K	Great impacts: changes in structure and species composition; reduced productivity, standing crop; reduced species richness of flora and fauna.	Recruitment nears zero as K is approached. Large numbers of deer are seen.	Animal condition poor, neither quality nor quantity of harvest is maximized.

for evaluating deer impacts on ecosystem components within landscapes and improve our ability to estimate K in real landscapes. Recent work, such as that on the Huntington Forest (Matthews 1996) and on the Allegheny Plateau (Brenneman 1987) is beginning to provide answers for the first question; the second represents an important area of needed research.

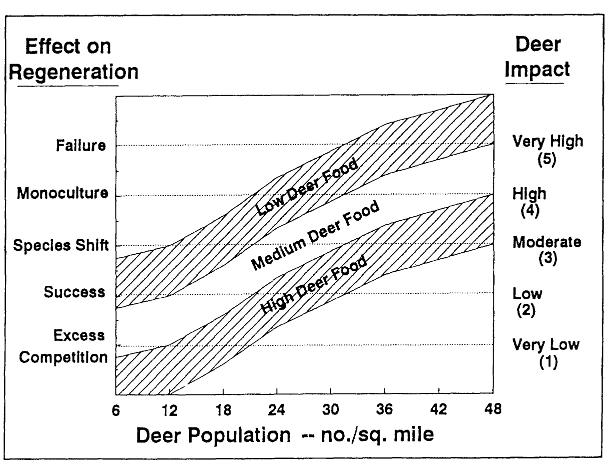


Fig. 2. Deer Impact Index (from Marquis et al. 1992). The authors developed this index to help managers predict whether deer impact would limit regeneration success. At any given deer density, the actual impact of deer on forest regeneration is determined by the amount of forage produced on the surrounding landscape; thus managers must assess not only deer density, but alternate forage when they plan regeneration cuts.

Using RDD to set goals for sustaining forest resources

Although RDD provides a useful tool for describing the interactions between deer and their ecosystems, and for projecting the impacts of management actions, it is a neutral tool. Describing deer densities in a different way does not resolve management controversies. We propose that deer density be managed to match RDD to management goals for sustaining forest resources affected by deer. Levels of RDD could be matched to selected, ecosystem-management goals. An additional benefit of managing for RDD is that it would provide an objective standard by which the status of resources affected by deer could be contrasted at different levels of deer density and across landscapes with different carrying capacities.

Where the goal is sustaining biodiversity, we suggest managing for RDD_S. This RDD would be appropriate for public and private forests where ecosystem management is emphasized. If sustained output of commercial wood products is the primary goal, such as on private forest industry lands or on public lands

Hobblebush in bloom. Hough (1965) documented the dramatic reduction in abundance of hobblebush in the Allegheny Plateau region of northwestern Pennsylvania as the relative deer density (RDD) of deer passed RDD_S (relative deer density associated with sustaining biodiversity) in the 1930s and 1940s.

zoned for a focus on timber production, then we suggest managing for RDD_T. If sustained yield of deer numbers or biomass (MSY) is the goal, such as on land managed for a hunting club, then we suggest managing for RDD_I.

Managing deer density to achieve RDD_S (sustain biodiversity) should also result in sustained timber and deer harvests, but numbers of deer and biomass of deer harvested may be lower than that at RDD_I. Managing RDD for $<RDD_I$ will result in fewer but larger deer and more bucks with trophy racks, which is a tenet of quality deer management (Brothers and Ray 1975, Miller and Marchinton 1995). As deer densities exceed RDD_S, fewer resources will be sustained. When RDD_I is exceeded, the only beneficiaries will be hunters who want to see as many deer as possible in the forest; remaining herbs, shrubs, woody regeneration, and wildlife habitat will be increasingly impacted as RDD approaches K.

Comparison of RDD_S with traditional deer management

Our analysis suggests that RDD_S falls far below traditional management goals for deer density. Pre-European-settlement deer densities may have approximated RDD_S rather than RDD_I or K. Deer density in northern hardwood forests prior to European settlement was estimated at 4 deer/km^2 for the eastern United States (Dahlberg and Guettinger 1956, McCabe and McCabe 1984, Alverson et al. 1988). This density was lower than I or K levels identified by McCullough (1979). It is not surprising that management for white-tailed deer based on I (for sustained harvest) or K (for parks and refuges without hunting; MacNab 1985) brought about negative effects on understory plants and associated wildlife communities that co-evolved with deer at densities below I and K. This historical evidence, combined with the limited data available from Tilghman (1989), deCalesta (1994), Healy (1997), and others suggests that when the management objective is sustaining biodiversity, the target should be ≤16 RDD, or 1/3 of I.

When landowners and managers choose to achieve and maintain deer populations at RDD_S, they need to make a long-term commitment to annual herd reduction. In some places, such as the relatively small Gettysburg National Military Park, in Gettysburg, Pennsylvania, government sharpshooters are reducing deer density to levels below RDD_S (B. Frost, Natl. Geol. Surv., Gettysburg, Pa., pers. commun.). On larger landscapes however, the use of government sharpshooters may be impractical. On these larger landscapes, managers may require other means to achieve RDDs, where that is the management goal. One option is to raise K by increasing the amount of forage available to deer while keeping deer density constant. Preliminary results from an adaptive management study underway on the Allegheny National Forest (ANF) in northwestern Pennsylvania (Stout et al. 1993, 1996) indicated that maximizing forage production by clearcutting 14% and thinning 33% of a 4.4-km^2 forested landscape resulted in successful stocking of a diverse mix of tree seedlings.

The actual deer density associated with RDD will vary within landscapes, depending on the amount of forage available for deer and associated K. The ANF serves as an example. Much (65%) of the forest is managed for benefits including timber production, using clearcutting and thinning (Allegheny Natl. For. 1986). These areas produce more deer forage and higher K values than on areas managed for wilderness or recreation, where no cutting is allowed. The deer density associated with any particular RDD—RDD_S for sustaining biological diversity, for example—is higher on areas where managers use timber harvesting than on other areas because K is higher in landscapes featuring timber harvests. Thus, management areas allowing timber harvest can support higher deer densities while sustaining biological diversity, and might be favored by hunters who like to see many deer during hunting season. Management areas with less forage production will support lower deer densities, and may be favored by hunters who enjoy a wilderness experience in less accessible areas (i.e., without logging roads).

Validation and data needs

Adoption of this conceptual framework will require research that provides managers with better tools than are currently available to assess the carrying capacity of specific landscapes. Better understanding of the effective scale at which deer interact with habitats is needed, such as research underway at Huntington Forest (Matthews 1996). We also need straightforward ways to estimate the K carrying capacity of these habitats. Similarly, more effective tools for the estimation of deer density itself are also required (Healy et al. 1997). In particular, research should be designed to test systems in which K changes (or is changed by human uses, such as agricultural) on short time scales (B. P. Shissler, Nat. Resour. Consultants, Inc., Fort Hill, Pa., pers. commun.).

The George Reserve study (McCullough 1979, 1984) may provide information that would validate the RDD concept; vegetation data were collected regularly during the experimental manipulations of deer density within the reserve. Analysis of those data would provide an excellent test of the RDD concept for linking deer population dynamics to plant community dynamics.

Summary

Controversy surrounding the management of white-tailed deer populations in the United States has grown nearly as rapidly as deer populations themselves. Management paradigms based on the jumble of ecological and political definitions of carrying capacity have failed to resolve these conflicts, while obscuring important relationships among ecosystem elements. Sustaining the forests on which deer depend requires a new conceptual framework for management. We propose managing deer for sustainability of ecosystems, using RDD, or relative deer density (deer density as a percent of K), as the framework.

This framework replaces the variety of old carrying capacity concepts: sustained yield of maximum numbers of deer for harvest and sustained yield of timber. All of these can be expressed in the common currency of RDD, which would help clarify apparent differences when data are collected on landscapes with differing carrying capacities. Instead of a management target based on an often value-and-conflict-ridden assessment of deer impacts and deer population dynamics, the RDD framework focuses attention on the interactions of deer and other ecosystem elements. Stakeholders can focus on what information is needed to define relationships locally and plan management to sustain critical elements—for wildlife habitat conservation, plant community conservation, or the conservation of deer habitat over the long term. However, these concepts offer no panacea for conflict-weary managers because they demonstrate clearly that RDD_S is <1/3 the RDD associated with maximum sustained yield of deer for hunter harvest.

Acknowledgments. We were greatly aided in preparation of this paper by reviews and discussions with many colleagues. In particular, W. M. Healy provided invaluable input. Other colleagues who have helped us include B. Shissler, R. Lawrence, W. Porter, B. Underwood, C. Nowak, and S. Horsley.

Literature cited

Allegheny National Forest. 1986. Land and resource management plan. U.S. Dep. Agric. For. Serv., Reg. 9, Milwaukee, Wis. 346pp.

Alverson, W. S., D. M. Waller, and S. L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. Conserv. Biol. 2:348-358.

Auchmoody, L. R., H. C. Smith, and R. S. Walters. 1993. Acorn production in northern red oak stands in northwestern Pennsylvania. U.S. Dep. Agric. For. Serv., Northeast. For. Exp. Stn. Res. Pap. NE-680. 5pp.

Brothers, A., and M. E. Ray, Jr. 1975. Producing quality whitetails. Fiesta Publ. Co., Laredo, Tex. 244pp.

Brenneman, R. 1987. Movements of deer into hardwood clearcuts in Pennsylvania. Abstr. Page 87 *in* R. Labar, ed. Proc.: Deer, forestry, and agriculture: interactions and strategies for management. Soc. Am. For., Warren, Pa. 183pp.

Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. McMahon, 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.

Dahlberg, B. L., and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin. Tech. Wildl. Bull. No. 14, Wisconsin Conserv. Dep., Madison. 282pp.

deCalesta, D. S. 1992. Impact of deer on species diversity of Allegheny hardwood stands. Proc. Northeast. Weed Sci. Soc. 46:135 (Abstr.).

deCalesta, D. S. 1994. Impact 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.

Goodland, R., and H. Daly. 1996. Environmental sustainability: universal and non-negotiable. Ecol. Appl. 6:1002-1017.

Healy, W. M. 1997. Influence of deer on the development of forest structure and composition in central Massachusetts. Pages 249-266 *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.

Healy, W. M., D. S. deCalesta, and S. L. Stout. 1997. A research perspective on white-tailed deer overabundance in the northeastern United States. Wildl. Soc. Bull. 25:259-264.

Hough, A. F. 1965. A twenty-year record of understory vegetation change in a virgin Pennsylvania forest. Ecology 46:370-373.

Kroll, J. C. 1994. These were the good old days: a new paradigm for white-tailed deer management. Proc. Annu. Southeast Deer Study Group 17:20-21.

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

Marquis, D. A., R. L. Ernst, and S. L. Stout. 1992. Prescribing silvicultural treatments in hardwood stands of the Alleghenies (revised). U.S. Dep. Agric. For. Serv. Northeast. For. Exp. Stn. Gen. Tech. Rep. NE-96. 101pp.

Matthews, N. 1996. Localized management of deer: a new paradigm for managers. The Sand County Found. Newsl. Summer 1996:4.

McCabe, R. E., and T. R. McCabe. 1984. Of slings and arrows: an historical perspective. Pages 19-72 *in* L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

McCullough, D. R. 1979. The George Reserve deer herd: population ecology of a K-selected species. Univ. Mich. Press, Ann Arbor. 271pp.

McCullough, D. R. 1984. Lessons from the George Reserve, Michigan. Pages 211-242 *in* L. K. Halls, ed. White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pa.

Miller, K. V., and L. Marchinton. 1995. Quality whitetails: the why and how of quality deer management. Stackpole Books, Mechanicsburg, Pa. 322pp.

Palmer, W. L., G. L. Storm, W. M. Tzilkowski, and M. J. Lovallo. 1997. Demographic profiles of deer under different management strategies in Pennsylvania. Pages 151-163 *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.

Porter, W. F. 1992. Burgeoning ungulate populations in national parks: Is intervention warranted? Pages 304-312 *in* D.R. McCullough, and R.H. Barrett, eds. Wildlife 2001: populations. Elsevier Sci. Publ., New York, N.Y.

Porter, W. F., M. A. Coffey, and J. Hadidian. 1994. In search of a litmus test: wildlife management in U.S. national parks. Wildl. Soc. Bull. 22:301-306.

Porter, W. F., and H. B. Underwood. 1997. Case history: deer populations are [*sic*] Saratoga National Historical Park. Pages 185-200 *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.

Redding, J. A. 1995. History of deer population trends and forest cutting on the Allegheny National Forest. Pages 214-224 *in* K. Gottschalk and S. L. Fosbroke, eds. Proc. Tenth Central Hardwood Forest Conference. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-197.

Salwasser, H. 1992. From new perspectives to ecosystem management: response to Frissell et al. and Lawrence and Murphy. Conserv. Biol. 6:469-472.

Salwasser, H. 1994. Ecosystem management: can it sustain diversity and productivity? J. For. 92:6-10.

Stout, S. L., J. A. Redding, and L. DeMarco. 1993. Technology transfer at the heart of a research/management partnership. Pages 188-193 *in* L. H. Foley, comp. Silviculture: from the cradle of forestry to ecosystem management: Proc. National Silviculture Workshop. U. S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-88.

Stout, S. L., and R. Lawrence. 1996. Deer in Allegheny Plateau forests: learning the lessons of scale. Pages 92-98 *in* Proc. 1995 Society of American Foresters Convention, Portland, Me., 28 October-1 November 1995. Soc. Am. For., Bethesda, Md.

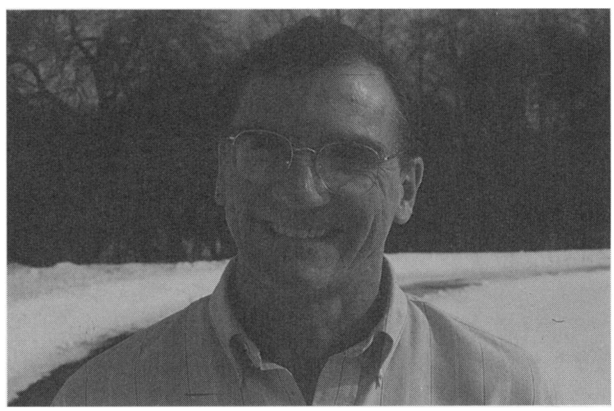
Stout, S. L., D. S. deCalesta, and L. DeMarco. 1996. Can silviculture change deer impact? Pages 437-438 *in* Proc. 1995 Society of American Foresters Convention, Portland, Me., 28 October-1 November 1995. Soc. Am. For., Bethesda, Md.

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

Underwood, B. H., K. A. Austin, W. F. Porter, R. L. Burgess, and R. W. Sage, Jr. 1994. Interactions of white-tailed deer and vegetation at Saratoga National Historical Park. Coll. Environ. Sci. and For., State Univ. New York, Syracuse. 33pp.

Whitney, G. C. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, and old-growth hemlock-white pine-northern hardwood stand. Ecology 65:403-408.

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.



David S. [Deke] deCalesta (photo) is a research wildlife biologist with the U.S. Department of Agriculture Forest Service Northeastern Forest Experiment Station in Warren, Pennsylvania. His research there includes studies of deer impact on forest ecosystems and studies of wildlife community-habitat relationships. He received his Ph.D. from Colorado State University, and he has worked at Oregon State University. ***Susan L. Stout*** is a research silviculturist and project leader with the U.S. Department of Agriculture Forest Service Northeastern Forest Experiment Station in Warren, Pennsylvania. Her research includes the relationship of silvicultural practices to deer impact, uneven-age silvicultural systems, and measures of relative density. She holds a master's degree from the State University of New York and a D.F. from Yale University.