

ECOLOGICAL IMPACTS OF DEER OVERABUNDANCE

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Key Words browsing, Cervidae, forest regeneration, herbivory, plant-herbivore interactions

■ **Abstract** Deer have expanded their range and increased dramatically in abundance worldwide in recent decades. They inflict major economic losses in forestry, agriculture, and transportation and contribute to the transmission of several animal and human diseases. Their impact on natural ecosystems is also dramatic but less quantified. By foraging selectively, deer affect the growth and survival of many herb, shrub, and tree species, modifying patterns of relative abundance and vegetation dynamics. Cascading effects on other species extend to insects, birds, and other mammals. In forests, sustained overbrowsing reduces plant cover and diversity, alters nutrient and carbon cycling, and redirects succession to shift future overstory composition. Many of these simplified alternative states appear to be stable and difficult to reverse. Given the influence of deer on other organisms and natural processes, ecologists should actively participate in efforts to understand, monitor, and reduce the impact of deer on ecosystems.

INTRODUCTION

Deer have excited the interest of ecologists since the birth of our discipline. Interest in managing game populations fostered the development of ecology, particularly the emergence of wildlife ecology (Leopold 1933). Deer management began with understanding which habitat conditions were most favorable for deer. Later, ecologists became interested in the effects of predators and hunters on deer and in the effects of deer on plant populations and habitat conditions. Ironically, within a century, deer management has reversed course from a preoccupation with augmenting population growth through habitat protection, hunting regulations, and predator control to serious concerns about how best to limit deer densities and the consequent impacts of these animals on other ecosystem constituents and functions (Garrott et al. 1993).

Overabundance is a value judgment that has a clear meaning only when placed in a specific context (McShea et al. 1997b). Caughley (1981) proposed a series of definitions to summarize the ecological and nonecological values upon which overabundance diagnostics have been based: Animals are overabundant when they (a) threaten human life or livelihood, (b) are too numerous for their “own good,” (c) depress the densities of economically or aesthetically important species, or (d) cause ecosystem dysfunction. Here, we follow this sequence and explore some of the human-deer conflicts implicit in points (a) and (c). We then emphasize point (d) throughout the review and show that negative effects of abundant deer occur at various densities in different habitats. The density-dependent effects on life-history traits implicit in point (b) are not addressed here, but see McCullough (1979, 1999) for more information.

We review some historic studies of the impact of overabundant deer and summarize how shifts in habitat conditions and levels of predation have boosted deer population growth in many temperate ecosystems. We explore how overabundant deer affect human health, forestry, and agriculture and describe the various methods used to evaluate how deer affect tree seedlings, shrubs, and herbaceous plants. We consider how deer alter interactions among competing plants; patterns of forest regeneration; succession; populations of insects, birds, and other mammals; ecosystem processes; and overall community structure. The number and significance of these effects make clear that deer can tip forest ecosystems toward alternative states by acting as “ecosystem engineers” or “keystone herbivores,” greatly affecting the structure and functioning of temperate and boreal forests (McShea & Rappole 1992, Stromayer & Warren 1997, Waller & Alverson 1997). These profound impacts lead us to ponder how ecology might inform approaches to mitigating the effects of overabundant deer. We discuss how ecological research might be extended and linked more tightly to deer management. Because space and our expertise are limited, we focus our attention on interactions between deer (family Cervidae) and temperate/boreal forests, primarily in Europe and North America.

HISTORICAL INTEREST IN DEER IMPACTS ON PLANT COMMUNITIES AND ECOSYSTEM STRUCTURE

By the nineteenth century, natural historians recognized that overabundant deer could exclude certain plants from the landscape (Watson 1983). Systematic studies of deer overabundance, however, did not occur until after the emergence of wildlife ecology, developed by Aldo Leopold. Based on his experiences with the dangers of deer overabundance, Leopold was the first to discuss threats posed by growing deer herds (Leopold 1933, Leopold et al. 1947). Leopold’s warnings sparked an initial period of concern in the 1940s and 1950s, mainly in the midwestern United States, which prompted the construction of exclosures to demonstrate the influence of native deer on forest regeneration (Beals et al. 1960, Pimlott 1963, Stoeckler

et al. 1957, Webb et al. 1956). Interest in deer impacts expanded in the 1970s, primarily in the Midwest and the Allegheny region of Pennsylvania (Anderson & Loucks 1979, Behrend et al. 1970, Harlow & Downing 1970), but with added attention to the introduced Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in the Queen Charlotte Islands of Canada (Pojar et al. 1980). Concerns about the impact of native deer populations in Europe (Dzieciolowski 1980) and introduced deer in New Zealand (Caughley 1983, Stewart & Burrows 1989) developed at the same time.

Seminal experiments on the population dynamics of white-tailed deer (*Odocoileus virginianus*) on the George Reserve in Michigan were conducted in the 1970s (McCullough 1979). The introduction of deer into a fenced area demonstrated that, because deer have such a high potential rate of increase, they can easily overwhelm the carrying capacity of their environment and consequently have strong and persistent negative impacts on vegetation (McCullough 1979, 1997).

In North America, the study of deer impacts soon broadened to include birds (Casey & Hein 1983), interactions with weeds (Horsley & Marquis 1983), and long-term effects on forest composition (Frelich & Lorimer 1985) and sapling-bank diversity (Whitney 1984). By the late 1980s and early 1990s, the impacts resulting from high densities of deer were being tallied in review articles (Alverson et al. 1988; Gill 1992a,b; McShea & Rappole 1992; Miller et al. 1992). Broad considerations of deer impacts also emerged in the 1994 conference hosted by the Smithsonian Institution (McShea et al. 1997b) and a 1997 special topics issue of the *Wildlife Society Bulletin* (Vol. 25, No. 2). Similar recent review issues of *Forestry* (2001, Vol. 74, No. 3) and *Forest Ecology and Management* (2003, Vol. 181, No. 2–3) focused mostly on how deer affect European forests.

CAUSES OF DEER OVERABUNDANCE

Overexploitation in the second half of the nineteenth century led to major declines in deer numbers and range. Subsequent protection of deer via restricted seasons and game laws then led to rapid population increases across Europe and North America over the past 75 to 150 years (Fuller & Gill 2001, Jedrzejska et al. 1997, Leopold et al. 1947, McShea et al. 1997b, Myrsterud et al. 2000). In Virginia, white-tailed deer increased from an estimated 25,000 animals in 1931 to 900,000 animals by the early 1990s (Knox 1997). Although whether North American deer are currently more abundant than before European colonization is not known, the evidence suggests that current deer numbers are unprecedented (McCabe & McCabe 1997).

Deer populations in North America have grown rapidly since the 1960s to 1970s in response to changes in their environment and reduction of hunting pressure (McShea et al. 1997b). The number of moose (*Alces alces*) in Scandinavia has similarly increased three to five times since the 1970s (Skolwing 1985, Solberg

et al. 1999). Deer densities above 10/km² are now common throughout temperate zones (Fuller & Gill 2001, Russell et al. 2001). In North America, deer have been reintroduced in many states (McShea et al. 1997b) and introduced to islands free of predators (e.g., Anticosti, PQ, Canada) (Côté et al. 2004). These introductions contributed to the recovery and subsequent overabundance of deer populations (Knox 1997).

The most obvious factor contributing to the rapid growth of deer populations is increased forage. Widespread agricultural and silvicultural activities considerably improved deer habitat throughout the twentieth century (Alverson et al. 1988, Fuller & Gill 2001, Porter & Underwood 1999). Tree planting after logging and early successional forested landscapes provide abundant, high-quality food that increases deer habitat carrying capacity (Bobek et al. 1984, Fuller & Gill 2001, Sinclair 1997). Forest harvesting and the resulting interspersion of habitats provide good cover and abundant forage for deer (Diefenbach et al. 1997). Many openings are also intentionally managed to boost forage quality and population growth (Waller & Alverson 1997).

Reductions in hunting and natural predators across Europe and North America have also contributed to increasing deer populations. Since the 1920s, strict hunting regulations in North America have favored deer population increases, especially on some private lands and in parks where hunting was banned (Brown et al. 2000, Diefenbach et al. 1997, Porter & Underwood 1999). Even where hunting is allowed, game laws favor the killing of males, increasing female survival and, thus, population growth (Ozoga & Verme 1986, Solberg et al. 1999). In recent decades, the pressure has increased to reform game laws to allow hunting of more does and fawns in response to overabundant herds. Hunters, however, have been reluctant to embrace such reforms (Riley et al. 2003). The number of deer hunters has also stabilized or decreased with declines in the social acceptability of hunting (Brown et al. 2000, Enck et al. 2000, Riley et al. 2003). At the same time, land owners and municipalities increasingly prohibit hunting in response to safety concerns (Kilpatrick et al. 2002), which further diminishes hunting pressure (Brown et al. 2000).

By the middle of the twentieth century, wolves (*Canis lupus*) had disappeared from continental Europe and most areas south of the North American boreal forests (Boitani 1995, Paquet & Carbyn 2003). Mountain lions (*Puma concolor*) were also extirpated in eastern North America (McCullough 1997). Without predators, ungulate populations increase rapidly to (or beyond) the carrying capacity of available forage (McCullough 1997, Messier 1994, Potvin et al. 2003, Sæther et al. 1996). Their high intrinsic rate of population increase may also allow deer to escape predator control while making overshoot of habitat carrying capacity and fluctuations in population size more likely. Moderate climates as experienced recently may also contribute to deer overabundance (Forchhammer et al. 1998, Solberg et al. 1999). Mild winters increase deer body mass (Mysterud et al. 2001) and winter survival (Loison et al. 1999), which favor population growth.

SOCIAL AND ECONOMIC CONSEQUENCES OF DEER OVERABUNDANCE

Impacts on Human Activities

Deer generate both positive and negative economic values, and negative values increase as deer become overabundant (Conover 1997). Browsing of tree seedlings by deer reduces economic value, ecological stability, and species diversity of forests, in addition to reducing tree growth, which, in turn, diminishes protection from erosion and floods (Reimoser 2003). The total cost of deer damage to the forest industry is difficult to estimate. The loss of young trees, for example, results in long-term economic losses only if the composition and quality of the final stand are affected. Despite the apparent severity of deer damage to agriculture and forestry in Britain, the economic significance is considered negligible or small in many cases (Putman 1986, Putman & Moore 1998). In contrast, deer damage is considered a major problem in the United States and in Austria, where their annual impacts are estimated at more than \$750 million (Conover 1997) and more than €220 million (Reimoser 2003), respectively. In northern temperate forests, saplings 30 to 60 cm tall are most vulnerable to browsing (Andren & Angelstam 1993, Gill 1992a, Kay 1993, Welch et al. 1991). Browsing by deer can kill seedlings or reduce height growth, which results in lower-density stands and requires longer stand rotations (Kullberg & Bergström 2001). Stands subjected to heavy browsing of seedlings and saplings exhibit a size structure biased toward medium and large stems (Anderson & Loucks 1979, Potvin et al. 2003, Stromayer & Warren 1997, Tilghman 1989). When the terminal bud is browsed, the tree develops multiple leaders (Putman & Moore 1998), which decreases its commercial value. Lavsund (1987) indicated that the proportion of quality stems dropped from 63% to 18% in a stand subjected to heavy browsing by moose in Sweden. Bark stripping may kill trees but often decreases quality by girdling, growth reduction, and increased risk of fungal infections (Gill 1992b, Putman & Moore 1998).

Reimoser (2003) suggested that the severity of damage to trees depends more on forest attractiveness to deer than on deer abundance. Stands become more susceptible to deer damage with (a) a low density of alternate food plants (Gill 1992a, Partl et al. 2002, Welch et al. 1991), (b) a low density of seedlings (Andren & Angelstam 1993, Lyly & Saksa 1992, Reimoser & Gossow 1996), (c) abundant nitrogen in the foliage or soil (Gill 1992a), (d) hiding cover (Gill 1992a, Kay 1993, Partl et al. 2002), and (e) the presence of edges (Kay 1993, Lavsund 1987, Reimoser & Gossow 1996). On larger scales, deer impacts on vegetation are greater in fragmented landscapes (Hornberg 2001, Reimoser 2003) or low-productivity habitats (Danell et al. 1991).

White-tailed deer damage many agricultural crops in the United States (Conover 2001). In 1996, 14% of nursery owners in the northeastern United States reported damages exceeding \$10,000 (Lemieux et al. 2000). Deer damage to corn fields in the United States was estimated at 0.23% of the total production (\$26 million) in

1993 (Wywiałowski 1996). Abundant deer also damage gardens and ornamentals (McCullough et al. 1997, West & Parkhurst 2002). Deer damage to households and agriculture in the United States totaled \$351 million in 1991 (Conover 1997).

A primary cost to society of deer overabundance is increased vehicle accident rates, now a serious problem in Europe, the United States, and Japan. Deer-vehicle collisions increase as deer density and traffic volume increase (Groot Bruinderink & Hazebroek 1996). Groot Bruinderink & Hazebroek (1996) estimated that 507,000 collisions between vehicles and ungulates occur annually in Europe (excluding Russia) and result in 300 deaths, 30,000 injuries, and \$1 billion in material damage. In the United States, such accidents increased from 200,000 in 1980 to 500,000 in 1991 (Romin & Bissonette 1996) and cost more than \$1 billion in 1991 (Conover 1997). Many airports in Canada and the United States also experience deer-aircraft problems (Bashore & Bellis 1982, Fagerstone & Clay 1997).

Transmission of Wildlife Diseases and Zoonoses

In general, high population densities of deer favor the transmission of infectious agents (Davidson & Doster 1997). Increased deer densities appear to increase the transmission of tick-borne zoonoses directly by increasing tick (*Ixodes* spp.) abundance (Ostfeld et al. 1996, Wilson & Childs 1997). In North America, two tick-borne diseases threaten human health: Lyme disease and ehrlichiosis (<5% mortality in humans) (Telford III 2002). Lyme disease has quickly become the most common vector-borne disease in the United States (13,000 cases in 1994; Conover 1997) and is also found in Europe and Asia (Steere 1994). The incidence of Lyme disease appears to track deer density in the eastern United States (Telford III 2002; Wilson et al. 1988, 1990).

Deer transmit infectious agents directly to other deer, to livestock, and to humans, especially if deer density is high. Bovine tuberculosis (*Mycobacterium bovis*) causes mortality in deer, livestock, other wildlife species, and humans (Schmitt et al. 1997). *M. bovis* affects deer populations of New Zealand and Europe to various degrees (Clifton-Hadley & Wilesmith 1991). It has been rare in North America, but incidence could increase as deer densities increase (Schmitt et al. 1997). A recent outbreak in Michigan led to concern that it would spread to domestic cattle and to a ban on deer feeding (Miller et al. 2003).

Chronic wasting disease (CWD) is a transmissible spongiform encephalopathy similar to "mad cow" disease (Williams et al. 2002). The disease was first noticed in 1967 in mule deer (*Odocoileus hemionus*) and has now spread to elk (*Cervus elaphus*), white-tailed deer, and black-tailed deer across a broad region (Figure 1) (Williams et al. 2002). The pattern of spread suggests that the disease may be transmitted from farm-raised herds (25 identified with CWD by 2002) to wild animals (Williams et al. 2002). Although it can be transmitted within and among cervid species (Gross & Miller 2001), transmission to humans or noncervid species appears unlikely (Raymond et al. 2000). Because it develops slowly, it would not appear to limit population growth greatly, but some experts express concern that it could cause population extinctions (Williams et al. 2002). Concerns over potential

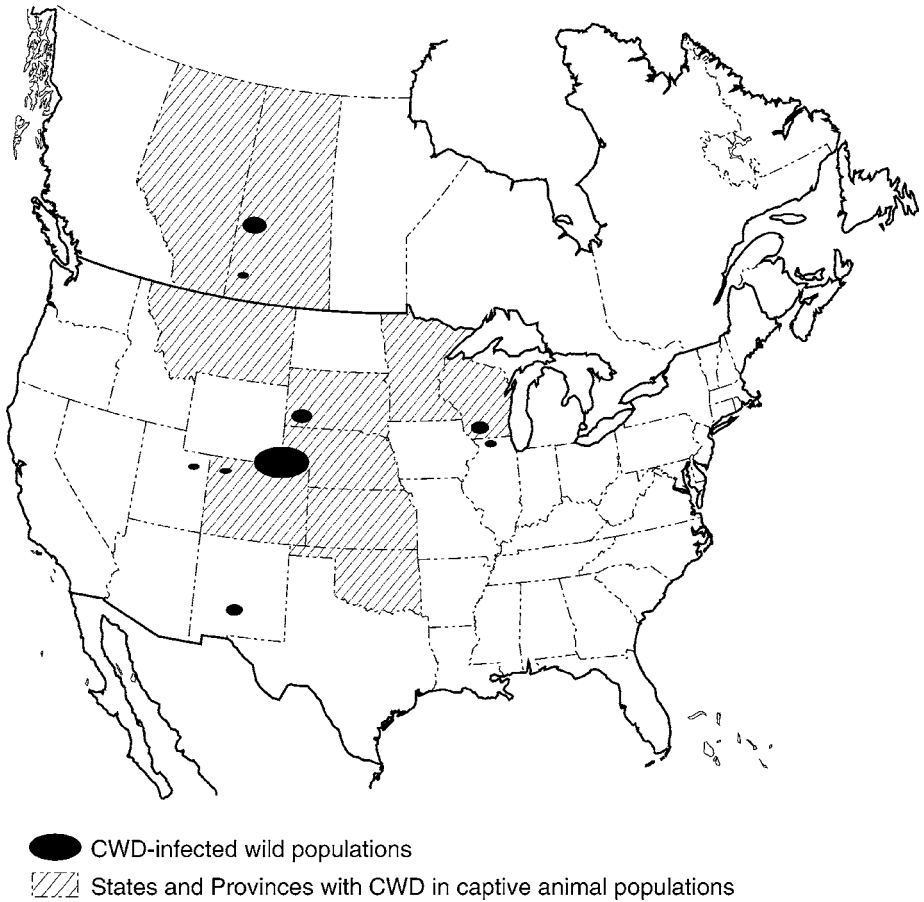


Figure 1 Map showing states and provinces where chronic wasting disease (CWD) has been found in wild deer or elk populations or in captive herds across North America. Note the association between captive animals with CWD and escape into the wild.

human health risks from CWD could also substantially reduce hunter efforts, which already appear too low to control deer populations effectively (see the Management Issues section).

ASSESSING ECOLOGICAL EFFECTS OF DEER OVERABUNDANCE

Through most of the twentieth century, research focused on how deer affected particular species of interest (often trees) or specific areas of concern. Because site-specific management concerns drove research programs, pseudoreplication was a common feature of early research (Hurlbert 1984). There has been a gradual

shift toward understanding overabundance within a stronger scientific framework. Despite this shift, the most common approaches for assessing deer impacts have not changed. Following Diamond (1983), we distinguish among natural, field, and laboratory experimental approaches.

In natural experiments, researchers select sites and collect data where spatial variation in deer abundance can be exploited. Spatial variation in deer densities allows the creation of discrete or continuous independent variables. Discrete variation arises in island-mainland systems. Deer may be absent on some islands but overabundant on others; both states offer a contrast to populations on the mainland (Balgooyen & Waller 1995, Beals et al. 1960, Côté et al. 2004, Vourc'h et al. 2001). Discrete variation may also appear in mainland systems if management varies starkly across ownership boundaries. Hunting bans on private lands and, particularly, on public lands can cause population densities to exceed those in the surrounding landscape (Nixon et al. 1991, Porter & Underwood 1999). The presence of ungulate predators can have the opposite effect; that is, reducing deer densities and impacts (Ripple & Beschta 2003, White et al. 2003). Within habitats, cliffs, boulder tops, and other physical features of the environment can create ungulate-free refuges for plants (Long et al. 1998, Rooney 1997). Such variation creates opportunities to study deer impacts by using discrete variation. Deer abundance also varies across landscapes in response to predation pressure (Lewis & Murray 1993, Martin & Baltzinger 2002) and habitat quality (Alverson et al. 1988, Reimoser & Gossow 1996), and this variation can be used to analyze ecosystem responses across gradients in deer density (Alverson & Waller 1997; Didier & Porter 2003; Rooney et al. 2000, 2002; Takada et al. 2001; Waller et al. 1996). The drawbacks of this approach are the difficulty in establishing replicates and the problem of confounding site factors (such as productivity) that themselves affect deer densities or responses to herbivory (Bergström & Edenius 2003).

The effects of overabundant deer on plants can also be studied across time. Vila et al. (2001, 2003), for example, tied browsing scars and historical variation in growth rates to fluctuating deer densities on the Queen Charlotte Islands, Canada. Before-and-after or snapshot-type studies have also been used to infer how species respond to fluctuating browsing pressure when baseline data exist (Husheer et al. 2003, Rooney & Dress 1997, Sage et al. 2003, Whitney 1984). Many such studies reflect conspicuous "signatures" of deer browsing as community composition shifts toward browse-tolerant or unpalatable species (Husheer et al. 2003). Long-term monitoring can, thus, provide powerful insights into how deer drive changes in plant communities, particularly when combined with exclosures or direct observations of which plants deer preferentially consume.

In field experiments, researchers manipulate deer densities or vegetation to study deer impacts. The use of fencing (exclosures) to exclude deer from study plots is a venerable experimental approach (Daubenmire 1940). Despite all the insights that exclosure studies bring to our understanding of deer-forest interactions, they are limited to binary treatments: They allow researchers to infer what alternate trajectory a site would take in the absence of deer. Controlled grazing experiments

that utilize known deer density in enclosures appear more realistic and can be used to infer whole-community responses to manipulated deer densities (Côté et al. 2004, deCalesta 1994, Hester et al. 2000, Horsley et al. 2003, McShea & Rappole 2000, Tilghman 1989). Deer densities can also be manipulated through culling. Researchers can take advantage of culling efforts in parks and natural areas by monitoring vegetation or other response variables (Cooke & Farrell 2001). Direct manipulations of density through localized management can also be conducted under scientific objectives (Côté et al. 2004). Alternatively, vegetation can be subjected to experimental treatment. Simulated browsing treatments reveal how plants respond to defoliation in natural environments (Bergström & Danell 1995, Rooney & Waller 2001). Experimental plantings in conjunction with enclosures more accurately compare the effects of deer browsing on plant growth and mortality (Alverson & Waller 1997, Fletcher et al. 2001b, Ruhren & Handel 2003).

Laboratory experiments give researchers a high degree of control over experimental systems. Defoliation experiments can be conducted under a range of controlled environmental conditions in greenhouses or growth chambers to investigate the mechanisms of plant responses (Canham et al. 1994). Simulation models also allow researchers to forecast how deer might affect ecosystems under a broad range of deer-population and forest-management scenarios (Tremblay et al. 2004).

Each of these approaches has its strengths and weaknesses. Stronger inferences can be drawn when they are combined. Waller & Alverson (1997), for example, combined experimental plantings, enclosures, and geographic variation in deer densities to examine the effects of deer browsing on *Tsuga canadensis* growth and survival rates across a broad region. Augustine et al. (1998) combined enclosures, geographic variation in deer densities, and a simple plant-herbivore functional response model to predict time-to-extinction of forest herb populations as a function of initial abundance. Balgooyen & Waller (1995) and Martin & Balzinger (2002) compared plant responses across islands that varied in deer abundance because of hunting and introductions, both currently and historically. Meta-analysis can similarly strengthen our inferences. Gill & Beardall (2001) combined data from 13 studies to examine the effects of ungulate browsing on richness and diversity of tree species in British woodlands.

ECOLOGICAL CONSEQUENCES OF DEER OVERABUNDANCE

Plant Tolerance and Resistance to Herbivory

Deer directly affect the growth, reproduction, and survival of plants by consuming leaves, stems, flowers, and fruits. Plants defend themselves against herbivores in various ways that affect which plants are attacked, how they respond to those attacks, how herbivore individuals and populations respond to those defenses, and, ultimately, how herbivores affect ecosystem productivity and rates of nutrient

cycling. Plants are often classified according to the degree to which they either resist herbivory or tolerate it. Resistant plants have traits that reduce plant selection (such as chemical defenses or low digestible content) or traits that reduce intake rates (such as leaf toughness or morphological defenses). Tolerant species can endure some defoliation with little change in growth, survival, or reproduction, whereas intolerant species are more sensitive to defoliation. In addition, woody plants often reduce their chemical and physical defenses as they grow beyond the range of mammal browsing (Bryant & Raffa 1995).

In environments with herbivores, natural selection should favor enhanced morphological and chemical defenses in plants with low tolerance. Takada et al. (2001) examined populations of the shrub *Damnacanthus indicus* (Rubiaceae) in areas with and without deer. Individual plants in areas with deer increased allocation to thorns: Both spine thickness and density were greater where deer were present. Induced and constitutive chemical defenses can make plants less palatable to deer. Red deer (*Cervus elaphus*) tend to avoid *Picea sitchensis* saplings that have higher concentrations of monoterpenes in their foliage (Duncan et al. 2001). Vourc'h et al. (2001) demonstrated that *Thuja plicata* saplings growing on islands without deer had evolved lower concentrations of foliar monoterpenes than mainland saplings growing in areas with deer. The rapid evolution of reduced defenses in cases like these strongly implies that anti-herbivore defenses are costly in terms of energy (or fitness) in situations where herbivores are scarce or absent. In environments without herbivores, undefended plants outperform defended plants (Gomez & Zamora 2002). However, selection will rarely occur quickly enough to rescue palatable populations faced with sustained overabundant deer, especially in trees where reproducing individuals are not subjected to browsing.

Tolerance to herbivory differs among species and among individuals within species. It depends on the timing and intensity of herbivory (Doak 1992, Saunders & Puettmann 1999), individual plant genotype (Hochwender et al. 2000), specific growth strategies (Canham et al. 1994, Danell et al. 1994), history of past defoliation or other stress (Cronin & Hay 1996, Gill 1992b), the density of competitors, and the degree to which the plant is under nutrient or moisture stress (Canham et al. 1994, Maschinski & Whitham 1989). Plants that lose only a small fraction of their leaves or flowers, store resources underground, hide their meristems (as in grasses), or regrow quickly via indeterminate growth tolerate deer herbivory better (Augustine & McNaughton 1998). Such species include many annuals, graminoids, deciduous trees, and shrubs and many herbs and forbs that mature in late summer. Some of the browse-tolerant species even appear to gain more biomass (or more flowers and seeds) over the course of a season than undefoliated control plants (Hobbs 1996, McNaughton 1979, Paige & Whitham 1987). Increases in final biomass yield could reflect shifts in either allocation and growth form, increased photosynthetic rates, or both. Browsing alters plant growth forms when a single terminal leader is removed, apical dominance is broken, and axillary buds give rise to a profusion of branches. Photosynthetic rates rise when changes in the water balance of residual leaves lead to an increase in stomatal conductance and foliar concentrations

of carboxylating enzymes (McNaughton 1983). Although such overcompensation might be temporary, plants such as graminoids no doubt thrive under repeated grazing. Other plants can compensate at low to moderate levels of defoliation but decline once herbivore densities are high (Bergelson & Crawley 1992). Plants may also reallocate resources to grow taller or shorter when browsed (Bergström & Danell 1995, Canham et al. 1994, Edenius et al. 1993, Saunders & Puettmann 1999). Compensatory growth, however, can limit radial growth and rarely appears under repeated and heavy browsing pressure. Trees with a history of browsing also appear more susceptible to new browsing, reflecting reduced reserves, changes in tree morphology, or both (Bergqvist et al. 2003, Danell et al. 1994, Palmer & Truscott 2003, Welch et al. 1992). Deer, however, often avoid previously browsed twigs, perhaps because of induced defenses (Duncan et al. 1998).

In general, slow-growing plants will tolerate browsing less, particularly if such browsing is repeated. Shady forest understory plants, including shade-tolerant shrubs and tree seedlings, may thus be particularly vulnerable to deer browsing. Small spring ephemeral and early summer forest herbs that lose all their leaves or flowers in a single bite and cannot regrow also tolerate herbivory poorly (Augustine & McNaughton 1998, Augustine & DeCalesta 2003). Browse-intolerant species such as *Trillium* regularly suffer low or negative growth after defoliation (Rooney & Waller 2001).

Browsing directly affects reproduction in many plants, particularly if deer preferentially forage on reproductive plants or consume flowers (Augustine & Frelich 1998). Individuals of some species may not flower again for several seasons after defoliation (Whigham 1990). Where deer are abundant, browse-intolerant herbs tend to be smaller, less likely to flower, and less likely to survive relative to plants in exclosures (Anderson 1994; Augustine & Frelich 1998; Fletcher et al. 2001a; Ruhren & Handel 2000, 2003). Over time, the density of such intolerant plants tends to decline, and populations may be extirpated (Rooney & Dress 1997). Palatable herbs and shrubs such as *Taxus canadensis* remain susceptible to deer browsing throughout their lives and usually become more vulnerable to browsing as they grow larger. Deer forage selectively on the larger *Trillium grandiflorum* plants (Anderson 1994, Knight 2003). This foraging does not kill these plants because they have large, below-ground storage organs. However, defoliation often takes tall flowering stems and may cause the plants to regress in size (Knight 2003, Rooney & Waller 2001). Thus, populations subjected to abundant deer become both scarcer and dominated by small, often nonreproductive plants (Anderson 1994, Knight 2003).

Trees are obviously most vulnerable to herbivory as seeds (e.g., *Quercus* acorns), seedlings, or small saplings (Potvin et al. 2003). *Tsuga canadensis* seedlings and saplings have become scarce across much of their range in the upper Midwest in apparent response to deer browsing (Alverson & Waller 1997, Anderson & Katz 1993, Frelich & Lorimer 1985, Rooney et al. 2000, Waller et al. 1996). *Thuja occidentalis* is also disappearing from most sites in this region because deer have eliminated nearly every sapling taller than 30 cm (Rooney et al. 2002). Persistent

mature trees could repopulate sites with new seedlings and saplings if browsing declined for some window of time, but this window may be as long as 70 years for slow-growing understory species such as *Tsuga* (Anderson & Katz 1993). Evergreen conifers may be particularly intolerant of browsing because they invest heavily in leaves, retain them, and do not retranslocate nutrients to stems and roots as much as deciduous species do (Ammer 1996). In addition, deer focus their browsing on evergreens in winter as other food becomes scarce.

Effects on Plant Community Structure and Interspecific Competition

Because deer forage selectively, they strongly affect competitive relationships among plant species. These shifts, in turn, may either increase or decrease overall cover and diversity. The result depends on whether or not deer primarily consume dominant species. Selective foraging on tall dominant plants in an alpine meadow favored short-statured plants, which caused species richness to increase (Schütz et al. 2003). On Isle Royale, Risenhoover & Maass (1987) attributed the higher diversity of woody vegetation in moose-browsed areas to increased light in the understory. Deer play a similar keystone role on other Lake Superior islands, where they can either enhance herbaceous plant cover and diversity (by removing *Taxus canadensis* cover) or reduce this cover and diversity as they become overabundant (Judziewicz & Koch 1993). Declines in plant cover and species richness usually occur once resistant or browse-tolerant species become dominant. Overabundant deer also commonly cause tree diversity to decline (Gill & Beardall 2001, Horsley et al. 2003, Kuiters & Slim 2002). We summarize contemporary browse-related compositional shifts in boreal and temperate forests in Table 1.

TABLE 1 Compositional shifts in dominant tree species induced by deer browsing in boreal and temperate forests

Former dominant	New dominant	Source
Balsam fir (<i>Abies balsamea</i>)	White spruce (<i>Picea glauca</i>)	Brandner et al. 1990, McInnes et al. 1992, Potvin et al. 2003
Birch (<i>Betula</i> spp.)	Norway spruce (<i>Picea abies</i>)	Engelmark et al. 1998
Eastern hemlock (<i>Tsuga canadensis</i>)	Sugar maple (<i>Acer saccharum</i>)	Alverson & Waller 1997, Anderson & Loucks 1979, Frelich & Lorimer 1985, Rooney et al. 2000
Mixed hardwoods	Black cherry (<i>Prunus serotina</i>)	Horsley et al. 2003, Tilghman 1989
Oak (<i>Quercus</i> spp.)	Savanna type system	Healy et al. 1997
Scots pine (<i>Pinus sylvestris</i>)	Hardwoods and Norway spruce	Gill 1992b

Although deer browsing can enhance ground cover and diversity, research in Pennsylvania demonstrates that indirect effects of browsing can also act against tree seedlings and herb cover. In that study, openings were often invaded by the thorny shrub *Rubus allegheniensis*, which promotes the establishment of tree seedlings (Horsley & Marquis 1983). However, deer prefer this species and, thus, reduce its abundance. This circumstance favors a competitor, the hay-scented fern *Dennstaedia punctilobula*, which deer avoid. As this species becomes more abundant, it inhibits the establishment of tree seedlings (George & Bazzaz 1999, Horsley & Marquis 1983) and excludes smaller-stature herbs (Rooney & Dress 1997). Once *Dennstaedia* is established, cessation of browsing rarely results in a recovery by *Rubus* or other species. Thus, browsing by deer shifts the forest understory to an alternate stable state that is resistant to invasion by originally dominant species (Stromayer & Warren 1997).

The extent to which deer deplete a plant population often depends on plant as well as deer abundance. Augustine et al. (1998) documented that deer have a Holling type II functional response to variable densities of the herb *Laportea canadensis*. This response results in alternative states: only moderate impacts of deer when *Laportea* is common at a site but extirpation when *Laportea* is rare. Thus, we should not assume that deer impacts are simply proportional to deer density across sites and should expect extirpations to accelerate once plant populations grow sparse. These effects likely accentuate the complex deer-plant dynamics we describe below (see Dynamics and Reversibility of Deer Impacts).

Effects on Forest Succession

Contemporary models of succession include multiple directional pathways and alternative stable states that are dependent on the local abundance and colonization potential of species, competitive interactions, and disturbance regimes (Connell & Slatyer 1977, Glenn-Lewin & van der Maarel 1992). Sustained selective browsing can sway these factors enough to affect forest succession dramatically (Engelmark et al. 1998, Frelich & Lorimer 1985, Hobbs 1996, Huntly 1991). Succession accelerates if deer break up the vegetation matrix enough to favor the establishment of later successional plants (Crawley 1997, Hobbs 1996) or if deer prefer species from early seral stages (Seagle & Liang 2001). Alternatively, succession may be stalled if browsing reduces colonization, growth, or survival in later successional species (Hobbs 1996, Ritchie et al. 1998).

Effects on Ecosystem Properties

By affecting competitive interactions among plants with varying levels of chemical defenses and by altering successional trajectories, deer alter ecosystem processes that include energy transfer, soil development, and nutrient and water cycles (Hobbs 1996, Paine 2000). When deer consume an amount of biomass that is small relative to the standing crop, as it is in grassland systems, effects on net primary productivity may be negligible or positive (Hobbs 1996). Thus, in open and productive grassland systems, grazing can increase primary production if grazing induces

overcompensation in individual plants, favors more productive species, and accelerates soil processes (McNaughton 1979, 1983; Ritchie et al. 1998). Browsers accelerate nitrogen and carbon cycling if they increase the quantity and the quality of litter returned to the soil (Wardle et al. 2002). This phenomenon is more prevalent in nutrient-rich systems (Bardgett & Wardle 2003) or when deer browsing shifts the canopy composition from conifers to deciduous hardwoods (Frelich & Lorimer 1985). Browsing in early successional communities can also facilitate successional transitions toward nitrogen-fixing species such as *Alnus* sp. (Kielland & Bryant 1998). Animal excretion also increases nitrogen cycling and modifies its distribution across the landscape, which locally enhances availability (Bardgett & Wardle 2003, Singer & Schoenecker 2003). In some cases, the relative contribution of this source of nitrogen may be small compared with the adverse effects of browsing (Pastor & Naiman 1992, Pastor et al. 1993).

With an overabundant deer population, the biomass deer consume becomes large relative to standing crops, particularly in low-productivity environments such as forest understories (Brathen & Oksanen 2001). Thus, we generally expect deer to reduce productivity and decelerate nutrient cycling in forest ecosystems. Here, compensation is uncommon, growth rates are low, and deer browsing decreases the quality and quantity of litter inputs (e.g., Ritchie et al. 1998). Browsed forest plots generally show reductions in understory and woody biomass accumulation (Ammer 1996, Riggs et al. 2000). Similarly, if nitrogen limits productivity, converting plant communities from palatable, deciduous, nitrogen-rich species to species with low tissue nitrogen and more chemical defenses (e.g., conifers) will decelerate nutrient cycling as the quantity and quality of litter available to decomposers decline (Bardgett & Wardle 2003, Pastor & Naiman 1992, Pastor et al. 1993, Ritchie et al. 1998). Browsing has also been shown to reduce ectomycorrhizal infections, which amplifies reductions in nutrient intake (Rossow et al. 1997).

Cascading Effects on Animal Species

Deer exert cascading effects on animals both by competing directly for resources with other herbivores and by indirectly modifying the composition and physical structure of habitats (Fuller 2001, Stewart 2001, van Wieren 1998). For example, browsing by deer affects the population and community composition of many invertebrates, birds, and small mammals (Table 2). Maximum diversity within a stand often appears to occur at moderate browsing levels (deCalesta & Stout 1997, Fuller 2001, Rooney & Waller 2003, Suominen et al. 2003, van Wieren 1998). Heavier browsing reduces vegetative cover and complexity in the understory, which often leads to reduced habitat availability for animals. Invertebrate and bird communities are sensitive to changes in forest understory, especially foliage density (McShea & Rappole 1997, Miyashita et al. 2004). Ungulates also disrupt associations of plants and pollinators by shifting patterns of relative flower abundance (Vázquez & Simberloff 2003). Few studies have experimentally manipulated deer densities,

TABLE 2 Summary of studies addressing the effects of deer browsing on community structure of invertebrates, birds, and small mammals, using either experimental manipulation of deer browsing pressure (including enclosure studies) or field experiments with adequate replications

Taxon/source	Forest type and site	Cervid species	Results	Comments
Invertebrates				
Bailey & Whitham 2002	<i>Populus tremuloides</i> grasslands (Arizona, US)	<i>Cervus elaphus</i>	Increase by 30% in arthropod species richness and 40% increase in abundance after intermediate-severity fire and browsing exclusion; 69% and 72% declines in richness and abundance, respectively, after high-severity fire and heavy browsing (n = 3)	
Baines et al. 1994	<i>Pinus sylvestris</i> coniferous forest (Scotland, UK)	<i>Cervus elaphus</i>	Higher abundance of most taxa in ungrazed sites (n = 8); 83% of variation in number of lepidopterous larvae explained by two indices of grazing intensity, mean annual rainfall, altitude, and tree density	
Danell & Huss-Danell 1985	<i>Betula pendula</i> , <i>Betula pubescens</i> boreal forest (Sweden)	<i>Alces alces</i>	Higher abundance of leaf-eating insects on moderately browsed birches	
Suominen et al. 1999a	<i>Pinus sylvestris</i> coniferous forest (Sweden)	<i>Alces alces</i> , <i>Capreolus capreolus</i>	Lower abundance and higher diversity of ground-dwelling insects in grazed sites in a productive location (n = 5); no consistent differences in abundance, species richness, and diversity between grazed and ungrazed sites (n = 4) in an unproductive location	High moose density; effect of browsing on plant community composition

(Continued)

TABLE 2 (Continued)

Taxon/source	Forest type and site	Cervid species	Results	Comments
Suominen et al. 1999b	<i>Salix</i> sp.— <i>Populus balsamifera</i> early successional boreal forest (Alaska, US)	<i>Alces alces</i>	Trends toward higher abundance and species richness of ground-dwelling insects in browsed sites (n = 7), except for specialized herbivores (Cureulionidae)	Moderate moose density
Suominen et al. 2003	<i>Pinus sylvestris</i> or <i>Betula pubescens</i> or <i>Picea abies</i> boreal forest (Finland)	<i>Rangifer tarandus</i>	Higher abundance, species richness, and diversity of ground-dwelling beetles in grazed sites (n = 15 in four locations), except for unproductive sites where diversity was lower than in grazed sites	
Wardle et al. 2001	Southern temperate forest (New Zealand)		Lower abundance of microarthropods and macrofaunal groups in grazed sites (n = 30)	Large geographical extent
Birds				
deCalesta 1994	<i>Prunus serotina</i> , <i>Acer rubrum</i> , <i>A. saccharum</i> , <i>Fagus grandifolia</i> northern hardwoods (Pennsylvania, US)	<i>Odocoileus virginianus</i>	Declines of 27% and 37% in species richness and abundance of intermediate canopy nesters between lowest and highest deer densities; no effect on ground and canopy nesters; density threshold between 7.9 and 14.9 deer/km ²	Controlled grazing experiment with four simulated densities

DeGraaf et al. 1991	<i>Quercus</i> sp. dominated northern hardwoods (Massachusetts, US)	<i>Odocoileus virginianus</i>	Lower species richness and abundance of canopy feeders at higher deer density; lower migratory species richness and higher resident species richness in thinned stands with high browsing; no difference in omnivorous, insectivorous, and ground-feeding species richness and abundance (n = 12)	
McShea & Rappole 2000	<i>Quercus</i> sp. dominated mixed hardwoods (Virginia, US)	<i>Odocoileus virginianus</i>	Increased abundance of ground nesters and intermediate canopy nesters as understory vegetation resumed growth in exclosures (n = 4), but no increase in diversity because of species replacement	Exclosures of 20 to 40 ha
Moser & Witmer 2000	<i>Pinus ponderosa</i> coniferous forest (Oregon, US)	<i>Cervus elaphus</i>	No difference in abundance, species richness and diversity between ungrazed (n = 3) and grazed (n = 3) sites	
Small mammals McShea 2000	<i>Quercus</i> sp. dominated mixed hardwoods (Virginia, US)	<i>Odocoileus virginianus</i>	Interaction between deer browsing and previous year acorn crop: higher <i>Tamias striatus</i> and <i>Peromyscus leucopus</i> abundance in exclosures (n = 4) after low-mast years, but no difference after good-mast years	
Moser & Witmer 2000	<i>Pinus ponderosa</i> coniferous forest (Oregon, US)	<i>Cervus elaphus</i>	Higher abundance, species richness, and diversity in ungrazed (n = 3) than in grazed (n = 3) sites	Exclosures of 20 to 40 ha

which makes drawing strong inferences about the relationship between animal diversity and deer density difficult. A notable exception is the study by deCalesta (1994) of songbirds, in which a controlled grazing experiment (Horsley et al. 2003) was used to demonstrate negative and nonlinear relationships between bird diversity and deer abundance.

By modifying species abundance and diversity, deer can modify trophic interactions among species. For example, deer potentially change the interactions between mast availability, small mammals, birds, and insects (McShea 2000, McShea & Schwede 1993, Ostfeld et al. 1996). Effects on interactions within the food web may be particularly important in ecosystems where several species of large herbivores coexist, such as in western North America, Spain, or the United Kingdom.

Dynamics and Reversibility of Deer Impacts

Large herbivores have the ability to act as “biological switches” that move forest communities toward alternative successional pathways and distinct stable states (Hobbs 1996, Laycock 1991, Schmitz & Sinclair 1997). Models of forest dynamics also demonstrate how browsing by deer can alter the rate of succession (Seagle & Liang 2001), forest structure and composition (Kienast et al. 1999), successional pathways (Jorritsma et al. 1999, Tester et al. 1997), and ultimate stable states (Kramer et al. 2003). In classical succession models, the relation between deer browsing and plant abundance is gradual (Figure 2a) or sudden (Figure 2b) but in both cases, reversible. Unlike succession, however, alternative stable states are not readily reversible when the browsing pressure is reduced (Scheffer et al. 2001, Westoby et al. 1989). In Figure 2c, the system may not appear to change much as deer densities gradually increase. Then, a sudden transition may occur that sharply reduces plant population levels (or overall system diversity or productivity). Even dramatic declines in deer density at this point have little effect; recovery only occurs if deer densities remain low through some extended period of time and interventions favoring vegetation recovery are applied (May 1977, Scheffer et al. 2001, Schmitz & Sinclair 1997). By analogy with physical systems, such lags and history dependence are termed “ecological hysteresis.” Such nonlinear dynamics have been described in rangeland pastures (May 1977, Laycock 1991, Lockwood & Lockwood 1993), savanna-woodland systems (Dublin 1995, Scheffer et al. 2001), and temperate and boreal forests (Augustine et al. 1998, Pastor et al. 1993).

Interactions with Predators

The role of predators in controlling ungulate populations remains uncertain, at least in some systems. Particular examples exist where the introduction of a predator did not, by itself, control ungulate populations. Wolves moving onto Isle Royale did not prevent moose overpopulation, food depletion, and a subsequent crash caused by starvation (Peterson 1999).

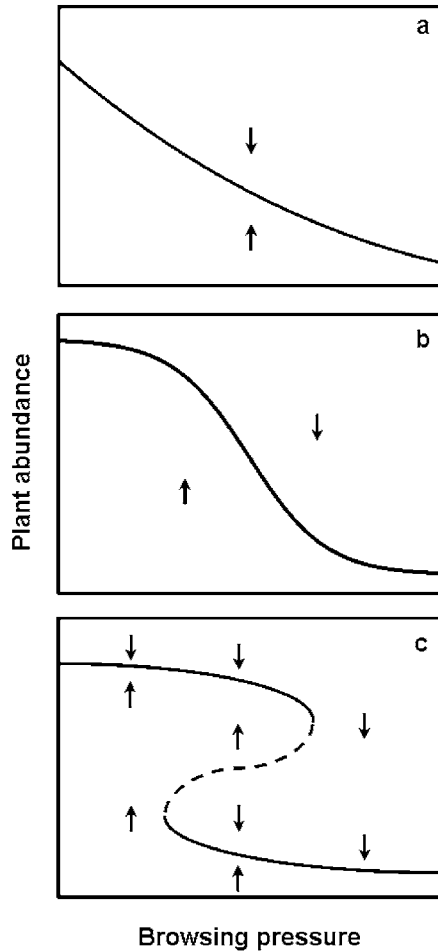


Figure 2 Three hypothetical relationships between the abundance of a forage plant and deer browsing pressure. (a) Deer have only modest and monotonic effects on the population. (b) A reversible threshold exists beyond which plant abundance drops precipitously. (c) Browsing beyond a certain threshold point causes a nonlinear decline that is not simply reversible. The plant population requires a large (or prolonged) reduction in browsing as well as a disturbance factor that promotes an increase of its abundance to recover. This requirement indicates an “alternate stable state.” Arrows indicate dynamic changes at various points. Modified from Scheffer et al. (2001).

Recent research suggests, however, that large predators play important ecological roles. They appear to control the abundance of the “mesopredators” [e.g., raccoon (*Procyon lotor*), skunk (*Mephitis mephitis*), etc.] that prey on birds and small mammals (Crooks & Soulé 1999, Terborgh 1988). The presence of two or more predator species in the same region could work synergistically to exert significantly more population control on ungulates than either alone could exert (e.g., Gasaway et al. 1992). In the Glacier National Park area, a study by Kunkel & Pletscher (1999) concluded that combined predation from cougar and wolves is the primary factor that limits deer and elk populations. Analyzing results from 27 studies across North America, Messier (1994) used functional and numerical responses of wolves to moose to conclude that equilibrium moose densities would decline (from 2.0/km² to 1.3/km²) in the presence of wolves. Furthermore, if habitat quality deteriorates or mortality from another predator increases, wolves are predicted to hold moose to a much lower equilibrium (0.2 to 0.4 moose/km²). Predation effects are often nonlinear (Noy-Meir 1975) and involve lags in the manner illustrated in Figure 2*b* and 2*c* (substitute deer for plant abundance on the *y*-axis and predation for browsing pressure on the *x*-axis). Indeed, under a combined scenario, a functional guild of large predators might keep deer populations down to densities compatible with the upper curve of plant abundance in Figure 2*c*. Loss of predators could then flip the system to the alternate state represented by the bottom curve.

RESEARCH NEEDS

Whereas some species benefit from overabundant deer populations (Fuller & Gill 2001, Russell et al. 2001), overabundant deer annihilate many taxa, which disrupts community composition and ecosystem properties (Table 2) (deCalesta & Stout 1997, McShea & Rappole 1997). Between these extremes, we face much uncertainty. Ecologists should now work to identify threshold densities at which substantial impacts occur and devise effective strategies to limit deer impacts and sustain ecosystem integrity, i.e., the capacity of an ecosystem to preserve all its components and the functional relationships among those components following an external perturbation (*sensu* De Leo & Levin 1997; see also Hester et al. 2000, Scheffer & Carpenter 2003). Which species are affected by deer and at what densities? How fast do impacts occur? How quickly do plant populations, forest structure, and ecosystem processes recover? To what extent are deer populations and impacts constrained by food resources, predators, diseases, or hunting, and how do these limiting factors interact? This uncertainty places ecologists in an awkward position when they try to make deer management recommendations (see final section, (How) Can We Limit Deer Impacts?). Because forest communities can suffer long-term effects that are difficult to reverse, ecologists should make precautionary recommendations.

Given potential threshold effects and alternative stable states, how should we design our research? We need more controlled experiments that directly manipulate

deer densities and other factors known to influence forest dynamics (e.g., logging) (Bergström & Edenius 2003, Fuller 2001, Healy et al. 1997, Hester et al. 2000, Hobbs 1996, Rooney & Waller 2003). Such experiments should span different forest types, which would allow us to predict how forest types will respond to variable deer densities (Hjalten et al. 1993, Riggs et al. 2000). We should also monitor both immediate and delayed effects and track dynamic responses to both increases and decreases in deer density. Results from such manipulations would allow us to identify what windows of low deer density are needed across space and time to allow deer-sensitive plants to persist or recover in the landscape (Sage et al. 2003, Westoby et al. 1989). Eventually, results from such experiments will allow ecologists to make specific recommendations at the right scales, such as 10 years of fewer than 7 deer/km² over areas of at least 60 km² (Hobbs 2003, Weisberg et al. 2004).

Deer management must move beyond a population-based approach to an approach that considers whole-ecosystem effects (McShea et al. 1997b). Fuller & Gill (2001) suggest that we quantify the relationships between community composition across taxa and deer at various abundances to understand the full range of deer impacts on biodiversity. Knowing how deer affect the moss layer, herbs, shrubs, saplings, trees, invertebrates, small mammals, and birds at low, intermediate, and high grazing intensities would be a major step forward. In the absence of fenced-in areas with known numbers of deer, such approaches will require that we improve our ability to estimate local deer abundances. Indicators based on vegetation measurements increase our capacity to implement localized management programs and to monitor progress toward specific management goals (Augustine & DeCalesta 2003, Augustine & Jordan 1998, Balgooyen & Waller 1995, McShea & Rappole 2000). Applied research extends to include the selection of species, varieties, and genotypes more resistant to browsing (Gill 1992b) and evaluating the risks of epidemics associated with high deer densities.

We must also learn more about how forage conditions, predator populations, and human hunting interact to affect deer population dynamics. We should seek to understand the potentially complex dynamics of tritrophic-level interactions. We need more data from a variety of systems on when predators can, alone or in combination with other factors, control deer densities. Likewise, we need to learn more about the “ecology of fear” (Brown et al. 1999), that is, how predators might influence browsing behavior even before they are numerous enough to reduce population growth appreciably (Ripple & Beschta 2003). We also have more to learn about sport hunting. We cannot yet predict, for example, how local hunting of philopatric females influences subsequent local deer densities (Côté et al. 2004, McNulty et al. 1997, but see Oyer & Porter 2004).

Finally, ecologists should work to integrate the results of individual studies into models capable of forecasting deer populations and impacts accurately enough to provide managers with sound guidance when they make decisions. Such models should integrate deer population dynamics with forest dynamics and deer hunter impacts (Tester et al. 1997). They should also incorporate the uncertainty that underpins interactions between management and science (Bergström & Edenius

2003, Bugmann & Weisberg 2003, Tremblay et al. 2004). Such models, and the research previously mentioned, have a logical place in hunter education programs and revised programs of deer management.

MANAGEMENT ISSUES

Historically, game managers strove to augment and protect deer populations, and hunters learned to limit takes and favor bucks. Today, such precepts are outmoded, but unlearning old lessons and reversing this cultural momentum has proved difficult.

The management of deer and the management of vegetation remains divorced, and this situation hampers our ability to manage them jointly (Healy et al. 1997). Their management commonly occurs in different agencies with contrasting goals and paradigms. Even the scales are different; deer density is usually estimated regionally, whereas forest managers operate on individual stands. In contrast, adaptive management seeks to merge research with management by using management prescriptions as experimental manipulations, with appropriate control areas, and by regularly incorporating research results into revised management practices (Holling 1978, Walters 1986). Ecosystem management is a further extension of conventional management that emphasizes historical patterns of abundance and disturbance and ecosystem dynamics at various scales (Christensen et al. 1996). Such approaches emphasize the importance of managing deer as part of a complex system. That promise has yet to be fully realized. Nevertheless, ecologists and wildlife managers are beginning to integrate biodiversity concerns into deer management (deCalesta & Stout 1997, Rooney 2001).

(How) Can We Limit Deer Impacts?

Foresters exploit a variety of techniques to control deer impacts locally. Keeping sapling stem density high through thinning or planting and increasing hunting pressure, for example, can allow a greater proportion of stems to escape browsing (Lyly & Saksala 1992, Martin & Baltzinger 2002, Welch et al. 1991, Reimoser 2003). Evidence indicates that within species, individual seedlings differ genetically in their susceptibility to browsing (Gill 1992b, Roche & Fritz 1997, Rousi et al. 1997, Vourc'h et al. 2002), which suggests that selection for more resistant saplings might be possible. Individual plastic tubes and wire fencing efficiently exclude deer but are costly, which limits their use to valuable seedlings or stands (Côté et al. 2004, Lavsund 1987). Electric fences are less effective but are also less expensive (Hygnstrom & Craven 1988). Repellents are also available. The most efficient repellents create fear (e.g., predator urine) (Nolte 1998, Nolte et al. 1994, Swihart et al. 1991, Wagner & Nolte 2001). The effectiveness of repellents increases with their concentration (Andelt et al. 1992, Baker et al. 1999) but decreases with (a) time since application (Andelt et al. 1992, Nolte 1998), (b) attractiveness of the food (Nolte 1998, Swihart et al. 1991, Wagner & Nolte 2001), (c) deer hunger

(Andelt et al. 1992), and (d) rainfall (Sayre & Richmond 1992). Similar methods are often employed to prevent accidents near airfields and highways (Groot Bruinderink & Hazebroek 1996, Putman 1997). Reflectors (Groot Bruinderink & Hazebroek 1996) and sound devices (Bomford & O'Brien 1990), such as gas exploders, appear ineffective in deterring deer for long periods unless the devices are activated by motion sensors (Belant et al. 1996).

Sport hunting and relocation are two methods available for controlling deer populations. Most wildlife managers consider sport hunting to be the most efficient and cost-effective method of controlling deer over large areas (Brown et al. 2000). Relocation is expensive, and relocated deer do not remain in the area of release. They also suffer high mortality (Beringer et al. 2002, McCullough et al. 1997). Sport hunting is often limited, however. For example, sport hunting cannot take place on private lands posted against hunting, in remote locations, or in urban and suburban areas. The number of hunters is also declining (Enck et al. 2000). Hunters rarely focus on young animals or hunt throughout the year as other predators do. Thus, the effectiveness of hunters is reduced. These trends, combined with growing deer populations, suggest that deer may have surpassed the point where sport hunting can reliably control their numbers (Brown et al. 2000, Giles & Findlay 2004). "Quality deer management" programs constitute an important countertrend. These programs emphasize killing doe and young animals to reduce densities, which favors the growth of large trophy bucks (Miller & Marchinton 1995).

The need for intentional culling will continue for the foreseeable future as deer populations continue to increase worldwide (McIntosh et al. 1995, McLean 1999). Hunting antlerless deer generally reduces abundance on a local scale because social groups of females usually remain in the same area from year to year (Kilpatrick et al. 2001, McNulty et al. 1997, Sage et al. 2003). This behavior prevents a rapid recolonization of the hunted area (Oyer & Porter 2004). Some affluent suburban neighborhoods employ sharpshooters working at night with low-light optics and silencers to control deer. Others have begun to experiment with birth control methods. Various fertility control and immunoconceptive techniques can limit reproduction in deer (McShea et al. 1997a, Turner et al. 1992, Waddell et al. 2001). However, these methods are labor intensive and disrupt normal reproductive behavior (Nettles 1997); thus, their application is expensive and difficult to scale up (McCullough et al. 1997, McShea et al. 1997a, Turner et al. 1992).

Deer control efforts to date have focused on redirecting sport hunting, applying hunts specifically to reduce deer numbers, and a few high-cost techniques aimed at protecting small areas that are typically of high value. All these methods have proved inadequate thus far in preventing deer from overpopulating broad areas. Some hunters and deer managers dispute that we have any problem associated with high deer density. Still others argue that such problems are temporary or local. Even where we have agreement on the need to control deer, we see little consensus on how to achieve it. No new hunter ethos emphasizing the ecological role of hunters in limiting deer numbers and impacts has yet emerged.

Experimental hunting sites with longer seasons, liberalization of bag limits (especially for antlerless deer), and increased hunter participation could help reduce local deer density (Brown et al. 2000, Côté et al. 2004, Martin & Baltzinger 2002). Because hunters rarely fully understand deer effects on ecosystems (Diefenbach et al. 1997), scientists should provide them and society with specific goals, strategies, and actions to conserve ecosystems better.

Given divergent opinions and uncertainty, what should ecologists recommend to wildlife and land managers? The answer clearly depends on local situations and what is known about them. We urge ecologists to promote a precautionary approach. Because overabundant deer can cause severe, long-term impacts that are difficult to reverse, ecologists should persuade managers to reduce deer numbers before and not after such impacts become evident. Although research results and active involvement by ecologists may not change attitudes quickly, they play crucial long-term roles in redirecting people's attitudes and patterns of management.

ACKNOWLEDGMENTS

We thank D. Simberloff for the invitation to write this review and S. de Bellefeuille for precious help with the literature review. Research by S.D.C. and J.P.T. on deer-forest ecology is supported by the Natural Sciences and Engineering Research Council of Canada, Produits forestiers Anticosti Inc., the Fonds québécois de la recherche sur la nature et les technologies, Laval University, the Centre d'études nordiques, and the Ministère des Ressources Naturelles, de la Faune et des Parcs du Québec. Research by D.M.W. and T.P.R. is supported by the National Science Foundation Ecology Program (DEB-023633) and the United States Department of Agriculture (NRI-CRIS-2003-02472).

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