

## ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Year in Ecology and Conservation Biology***Ecology and management of white-tailed deer in a changing world**

William J. McShea

Center for Conservation Ecology, Smithsonian Conservation Biology Institute, Front Royal, Virginia

Address for correspondence: William J. McShea, Center for Conservation Ecology, Smithsonian Conservation Biology Institute, 1500 Remount Rd., Front Royal, VA 22630. mcsheaw@si.edu

Due to chronic high densities and preferential browsing, white-tailed deer have significant impacts on woody and herbaceous plants. These impacts have ramifications for animals that share resources and across trophic levels. High deer densities result from an absence of predators or high plant productivity, often due to human habitat modifications, and from the desires of stakeholders that set deer management goals based on cultural, rather than biological, carrying capacity. Success at maintaining forest ecosystems require regulating deer below biological carrying capacity, as measured by ecological impacts. Control methods limit reproduction through modifications in habitat productivity or increase mortality through increasing predators or hunting. Hunting is the primary deer management tool and relies on active participation of citizens. Hunters are capable of reducing deer densities but struggle with creating densities sufficiently low to ensure the persistence of rare species. Alternative management models may be necessary to achieve densities sufficiently below biological carrying capacity. Regardless of the population control adopted, success should be measured by ecological benchmarks and not solely by cultural acceptance.

**Keywords:** forest; *Odocoileus virginianus*; population control; hunting; carry capacity

**Introduction**

Large herbivores have a central role in the functioning of many terrestrial ecosystems.<sup>1–3</sup> Large carnivores are viewed as keystone species within terrestrial ecosystems primarily because of their role in regulating the numbers of herbivores, which convert plant material into energy and nutrients that are assessable to other animals.<sup>4–6</sup> By shaping plant communities and supporting apex predators, most forest ecosystems are structurally and compositionally different depending on whether or not large herbivores are present.<sup>7–9</sup> Whether ecosystems are regulated by top-down processes or bottom-up processes, significant energy and nutrients flow through the large herbivore community, and this feature makes understanding their ecology important for understanding ecosystem structure and functioning.<sup>2,10</sup>

White-tailed deer (*Odocoileus virginianus*) are the largest herbivore in many forested ecosystems in the

eastern United States. In many forests, deer densities are chronically above historical levels.<sup>11</sup> White-tailed deer are not the only ungulates in eastern North America, with the recolonization of moose (*Alces alces*) to many areas of the Northeast and the reintroduction of elk (*Cervus elaphus*) to reclaimed mining areas in the Appalachians.<sup>12,13</sup> The larger body size of these ungulates exacerbates animal-human conflicts such as damage from collisions with vehicles and crop loss, but their overall densities and distributions have yet to exceed historic levels. For moose and elk, the ecological principles and management options are generally the same as those outlined here, but I will not deal with them directly in this paper. I will also focus my review primarily on forests east of the Great Plains due to space limitations, depth of the literature, and commonality of habitat.

As opposed to most species in the eastern forests, expertise, manpower, and bureaucracy are in place to manage deer populations across its range. With

white-tailed deer, there is a dedicated management structure at all levels of government that can enact recommendations based on a public mandate. The critical junctures are often informing and engaging the public on the need for management, and managers and balancing the sometimes competing interests of stakeholders.<sup>14,15</sup> However, deer management is one of the few instances where citizens have an active and pivotal role. Whether the land is in public stewardship or is privately owned, governments rely primarily on citizens to enact deer management. This offers an opportunity to engage the public in ecosystem management, but it can also lead to conflicts between land manager and hunter goals and to uneven management across a landscape.<sup>16</sup>

The purpose of this paper is to review in brief the role of white-tailed deer (hereafter deer) in ecosystems in eastern North America and their impact on human communities, and then outline mechanisms and management strategies for controlling deer populations.

### Ecological impacts

For most of eastern North America, the climax terrestrial community is forest.<sup>17,18</sup> In the most southeastern and northern climes, forests are primarily coniferous, but deer primarily exist within forests composed of diverse deciduous tree species that occur along a gradient of moisture and soil nutrients. Rare herbaceous plants or trees are impacted by deer in northern coniferous forests,<sup>19–23</sup> but it is primarily within deciduous forests that deer reach their highest densities and have been documented to have profound and consequential impacts on plant species.<sup>24–27</sup>

Deer are primarily browsers.<sup>28</sup> Their diet consists of buds and young leaves and branches, as well as forbs that occur within forests.<sup>29</sup> These forage items are not generally abundant in mature forests, except in temporary canopy gaps or along natural edges.<sup>30,31</sup> In human-modified forests, deer can increase their access to forage by moving between forested and human landscapes.<sup>32–34</sup> Agricultural crop damage is highest along the forest boundary, and these crops enhance the productivity of the landscape.<sup>35,36</sup> Forestry practices create large patches of early successional trees that are readily fed upon by deer.<sup>37,38</sup> Mature forest productivity alone likely would not support high deer densities, but sea-

sonal access to human-added productivity results in seasonal bouts of heavy browsing pressure on natural systems.<sup>19</sup> No high-density populations have been reported outside of this human–natural system dynamic, with the exception of deer isolated from predators due to natural or human-made barriers.<sup>27</sup>

As its primary forage item, the abundance and distribution of woody seedlings and saplings can be significantly impacted by deer.<sup>21,39–41</sup> Studies of canopy gaps, logging operations, and mature forest find that deer browsing can shift woody plant composition toward unpalatable species or toward low species richness or density.<sup>21,39,42</sup> Shifts in plant composition toward unpalatable invasive species can alter forest succession by reducing light levels on forest floor, and deer herbivory after canopy tree defoliation can change successional patterns.<sup>43–45</sup> At the highest deer densities, forest succession is halted, and natural disturbance or timber harvest transitions the forest into an alternative stable or climax community of open woodland with a grass, fern, or exotic forb ground cover.<sup>46–49</sup>

Herbaceous plants are a rich species component of eastern deciduous forests.<sup>17</sup> Species extirpation has been postulated for midwestern forest patches, and overall diversity and density measures for forbs are generally lower when deer densities are high.<sup>19,24,25,50,51</sup> Plant competitive interactions are altered by preferential browsing by deer, with nonpalatable species (including exotic species) becoming dominant.<sup>26,52</sup> The spread of invasive plants into a forest understory also can be facilitated by deer, both through transport of seeds and through altering forest floor conditions.<sup>52,53</sup> Deer browsing may not cause plant mortality, as many perennial forest forbs store significant resources in belowground roots, but does decrease plant growth during that year and lowers rates of flowering and fruit production.<sup>54,55</sup> Deer do have preferred browse species, but even unpalatable species can be impacted at high deer densities through changes in soil compaction and possibly nutrients.<sup>56</sup>

If deer can shape the diversity and structure of plant communities, then possibly this foraging will impact other species within the ecosystem.<sup>26,27,57</sup> These impacts fall into two categories: food web impacts for species that consume the same food resources or trophic level effects where shifts in resources at one trophic level have significant impacts at multiple levels. Consumption of key resources,

such as acorns for small mammals and plant biomass for insect densities, leads to lower densities of these animals and are indications of direct impacts on food webs.<sup>58–60</sup> As with other large herbivore systems, these direct impacts have consequences at multiple trophic levels within forest systems, with changes in bird communities and both insect and disease outbreaks.<sup>61–64</sup> Most trophic level and food web interactions are only obvious with the addition or removal of apex predators or the exclusion of deer from small areas.<sup>5,6,62</sup>

An important consideration is that deer impacts on vegetation are not proportional to their density. For most large herbivores, the shape of the functional response curve to plant biomass depends on relative forage preference, the animal's nutritional state, and predation risks.<sup>6,65,66</sup> Augustine *et al.* demonstrated a Hollings Type II functional response curve for a forest herb, *Laportea canadensis*, in Wisconsin forests.<sup>67</sup> Elk browsing in riparian areas of Yellowstone ecosystem shifted in response to the arrival of wolves (*Canis lupus*), in the absence of significant changes in elk density aspen regeneration increased.<sup>68</sup> In addition to lower herbivore densities, this spatial and temporal variability results in a heterogeneous distribution of plants.<sup>66</sup> As examples of this effect, Royo *et al.* found that the low levels of deer browsing increased forest forb diversity, and Parker *et al.* reported that intermediate deer browsing on a herbaceous plant (*Oenothera biennis*) increased the genetic diversity within the population and thereby reduced overall damage by the main herbivore, *Microtus pennsylvanicus*.<sup>31,69</sup> Although these considerations are important at low or intermediate deer densities, high deer densities (i.e., approaching carrying capacity) result in homogenization of forest understory communities through chronic heavy browsing.<sup>70</sup>

## Human impacts

In addition to the significant ecological impact of deer, it would be remiss to review the species without detailing the economic benefits, and both economic and health risks, which are also a product of their abundance on the landscape. Approximately 12.5 million Americans hunt and 25 billion dollars are spent each year on hunting activities in the United States, with deer hunting being the dominant activity.<sup>71</sup> This revenue comes through three main avenues: sale of licenses to

hunters, leasing of land by landowners, and purchase of hunting gear and logistics around the actual hunt (e.g., hotel, travel, guides). License sales are directly related to deer management; for example, Virginia sells over 250,000 hunting licenses annually, which are the primary means of supporting their wildlife department.<sup>72</sup> In addition, the federal tax on hunting gear annually returns 265 million dollars (2007 estimates) to states for wildlife conservation through the Pittman–Robertson Federal Aid in Wildlife Restoration Program.<sup>71</sup> Maintaining these revenue sources is critical for many states.

The economic benefits of deer are countered by costs incurred by multiple segments of the community. In 2009, the insurance industry estimated that 2.4 million deer–vehicle collisions had occurred over the previous 24 months, with an estimated cost of over 7 billion dollars and 300 human fatalities.<sup>73</sup> These collisions increased 18% over the previous five years, although an unknown portion of this increase is due to better record keeping.<sup>73</sup> These numbers are alarmingly high from an economic standpoint, but removing 1.2 million deer per year from a national population that exceeds 25 million is well below the annual recruitment rate. For example, the legal harvest and vehicle collisions of deer was followed for two years within a rural county in Virginia, and the combined annual mortality did not exceed 20% of the estimated population.<sup>74</sup> Deer are estimated to cause more damage to agricultural crops than any other wildlife species.<sup>75</sup> Drake *et al.* estimated 94 million dollars in annual vegetable crop damage and 74 million dollars in grain crop damage for 13 northeastern states.<sup>76</sup> The same study estimated annual residential and commercial ornamental damage at 49 million dollars.<sup>76</sup> These large losses have consequences on landowner attitudes toward deer. For Virginia farmers, the percentage desiring lower deer numbers across the landscape increased from 50% to 93% if they had experienced crop damage in the last year.<sup>77</sup> The industrial forest community has long advocated lower deer densities due to the ability of deer to halt regeneration of valuable timber species.<sup>78,79</sup> Direct estimates of forestry losses due to deer browsing are difficult to determine, but a small subset of forest practices (nurseries) estimated their annual stock damage at 27 million dollars for 13 northeastern states.<sup>76</sup>

Disease transmission between deer and livestock is a consideration for both deer population

regulation and economic costs incurred by high deer densities. Bovine tuberculosis (*Mycobacterium bovis*) and brucellosis (*Brucella abortus*) are bacterial diseases capable of moving between livestock and deer, and, where the disease is present in wild deer, deer likely are a reservoir for diseases they contracted from livestock.<sup>80</sup> Bovine tuberculosis has been found in deer in Michigan and, although no transmission to livestock has been documented, control measures do cost state agencies.<sup>80</sup> Chronic wasting disease is a transportable spongiform encephalopathy, or a prion disease, that is specific to deer and is not a concern from transmission to livestock, except farmed deer, but is a concern if transmitted to the wild deer population.<sup>80</sup>

One cost of having wildlife on the landscape is the transmission of zoonoses, and deer are not different from other abundant wildlife. Deer serve as an intermediate host for several diseases that are transmitted to humans through ticks (*Ixodes* sp.), such as Rocky Mountain spotted fever (*Rickettsia rickettsii*) and Lyme disease (*Borrelia burgdorferi*). Lyme disease is found in 12 eastern states and was found to affect over 38,000 people in 2009.<sup>81</sup> Deer are the primary host for adult ticks, but risk factors for the disease are better predicted by knowing small mammal abundance (the host for intermediate stages) than the abundance of deer.<sup>82</sup> The primary role of deer in tick-borne diseases is transporting ticks across the landscape, through their propensity to move in response to variable mast production and other shifting food resources.<sup>83</sup> Whether deer herds can be reduced sufficiently to reduce transmission rates is unclear and doubtful. Application of an acaricide to deer can reduce the prevalence of tick-borne diseases.<sup>84</sup> However, logistical concerns, which include baiting deer, limit its applicability.

I have listed some direct economic costs and benefits of deer, but most estimates are rough approximations. Estimating economic costs for items with known value (e.g., automobiles, crops) is relatively easy compared to estimating ecological costs, which I have not attempted. The key point is to view each cost and benefit as representing a strong stakeholder group that has a voice in deer management.

### Carrying capacity

The impacts of deer may be significant, but they are not an invasive or exotic species; their removal from

an ecosystem does not “restore” natural conditions. Part of the management conflict with deer is that many present-day forests were initiated after logging activities in the first half of 20th century, when deer were absent or at much lower densities on the landscape, and these forests are currently difficult to restore after harvest.<sup>85,86</sup> For example, oak forest reestablishment after harvest depends on relatively low deer densities, but is only successful in conjunction with other factors, such as fire.<sup>87,88</sup> Reducing deer numbers does not always achieve objectives, as herbaceous plant recovery depends partially on soil and seed bank conditions that may no longer support rich communities.<sup>89</sup> Deer are an adaptive, prolific species, whose selective browsing has ramifications that are important for forest managers, not because they are exotic, but because of their sheer numbers. The question is when managers should regulate deer.

How and when to regulate deer herds is tied to the concept of carrying capacity. Carrying capacity is the sustainable biological limit of a population with its environment; a sum total of mortality and reproduction rates that will fluctuate over time as the environment changes.<sup>90,91</sup> As a population approaches carrying capacity, recruitment is limited and adult mortality increases.<sup>92</sup> For deer managers, there are two important population levels: when numbers equal those that can be supported by the plant productivity (i.e., carrying capacity), and the point where the annual mortality of deer (both harvest and natural) equals the annual recruitment of deer, which is referred to as maximum sustainable yield (MSY). Agencies and landowners interested in maximizing hunting opportunities manage for populations approaching MSY.<sup>91–93</sup> Carrying capacity is one of the oldest concepts in wildlife management.<sup>94–96</sup> It is a wonderful theory for explaining the limit of environments, but it is nearly impossible to calculate for a specific area without extensive data.<sup>92</sup> With regard to MSY, deer harvest and other sources of mortality that do not exceed annual fawn production will not reduce deer populations over the long term. Many control efforts remove animals from the population, but few reduce numbers sufficiently to counter annual recruitment of this fecund animal.

For managed wildlife populations such as deer, the concept of a biological carrying capacity is often replaced by the concept of a cultural carrying

capacity.<sup>16,91</sup> The cultural carry capacity is based on a political process among community stakeholders.<sup>14,15</sup> Cultural carrying capacity is usually below biological carrying capacity, but depends less on the attributes of the habitat and more on the views of the stakeholders. Many states have adopted a stakeholder approach to managing deer to a cultural carrying capacity for each specific community.<sup>14,72</sup>

Ecological carrying capacity is the primary concept for protected areas that have management goals based on biodiversity or on endangered species that are impacted by deer browsing.<sup>26,97</sup> The functional foraging response of deer means they will not select forage randomly, but will preferentially browse on specific plant species.<sup>65,98</sup> These preferred species will decline or disappear long before the deer population is limited by plant productivity and probably before the limits imposed by cultural carrying capacity. This functional response is exacerbated by productivity inputs from humans that increase biological carrying capacity but do not change the browsing preferences of the deer. Some preferred browse species can be impacted at densities of 3 deer/km<sup>2</sup>.<sup>21</sup> Deer densities that are well below both cultural carry capacity and achievable goals for state management agencies.<sup>99</sup> Therefore, it is hard to manage for rare species on private or public lands while staying within the strictures of public hunting.<sup>100</sup>

These differing concepts of carrying capacity do not impact how the deer are managed but do impact how management success is measured. Biological carrying capacity is a quantifiable measure based on deer population metrics. Ecological carrying capacity is based on deer impacts to a single species or guild of species that can be measured directly on the landscape. Cultural carrying capacity is derived from stakeholder meetings and is measured through feedback from the constituent groups involved. A deer management program adopts one of these measures and proceeds to limit the deer population according to the metrics adopted.

### **Managing deer densities that exceed carry capacity**

Deer population size is determined by reproduction and mortality, and control is focused on impacting at least one of those demographic traits.

### **Reproduction**

In the absence of major predators, the case for much of the eastern United States, the primary limit to deer numbers is access to plant productivity.<sup>27,92,101</sup> White-tailed deer are one of the most fecund deer species in the world, with females in un hunted populations capable of producing 30 offsprings in their lifetime.<sup>28,102</sup> High lifetime fecundity means deer numbers can change quickly to fluctuations in forage availability or predation. Island populations of deer are good examples of the potential for rapid increases.<sup>63,103</sup> Forestry practices in Pennsylvania during the early 20th century shifted forests dramatically to younger age classes, which coincided with rapid increases in deer numbers.<sup>79,97</sup>

As discussed throughout this review, landscape productivity is the key to deer population growth and reduced productivity, or access to productivity, will lower deer densities. Reduced productivity occurs as human landscapes transition from rural to suburban to urban. Reduced access to productivity can occur as major roads bisect deer ranges or fences restrict movement of deer across landscapes. Agricultural shifts from edible crops to bio-fuel have the potential to lower landscape productivity.<sup>104</sup> Lower palatability of invasive plants may initially shift browsing to native species,<sup>105</sup> but ultimately these exotics will lower habitat productivity for deer. These are all unintentional consequences of human development that might ultimately reduce deer densities in many regions where densities are currently high. Intentional reductions in habitat productivity usually entail limiting access through repellents, fences, or dogs.<sup>16</sup> These remedies may work for individual landowners or small landholdings, but are not effective across landscapes or away from human habitation. A subset of this approach is to shift productivity in an effort to shift the browsing pressure of deer. Foresters have had success shifting deer through placement of food plots or precuts away from valuable timber stands before harvest.<sup>38</sup> This short-term relief from browsing pressure will be counter-productive over the long term, as it raises overall landscape productivity, but it can achieve immediate goals.

Rather than reducing productivity, it might be possible to reduce the ability of deer to utilize plant energy by limiting their reproduction. Extensive research has gone into developing contraceptives that limit reproduction in female deer and, if applied

properly, could limit deer population growth.<sup>106–109</sup> GonaCon™ (U.S. Dept. of Agriculture, Animal and Plant Health Inspection Service, Fort Collins, CO, USA) is currently the sole contraception approved by USDA for commercial use, and an intramuscular application results in female deer producing GnRH antibodies, which prevent development of a corpus luteum in the ovaries and thereby eliminates mating behavior and ovulation.<sup>108,110</sup> A present limitation is that the contraceptive must be hand-injected, entailing capture of individuals. Development of an oral or remote-delivered contraceptive will remove this limitation, but contraception does not directly reduce the population number, only the recruitment rate. Used in conjunction with increased mortality, it has potential for limiting populations around human development if sufficient females can be maintained in a contraceptive state.<sup>111</sup>

### Mortality

Limiting habitat productivity will not only limit reproduction, but also can increase mortality, as food restrictions can increase overwinter mortality and disease susceptibility.<sup>92,112</sup> Most overwinter mortality is confined to fawns of the year, although severe winter weather can impact adults.<sup>92</sup> Malnourished deer do suffer higher parasite rates that may increase their mortality rate.<sup>112</sup> Viral diseases, such as bluetongue and various hemorrhagic diseases, are episodic, but more prevalent in high-density populations of deer, and might reduce populations by 15% in a single year.<sup>112</sup> Neither these diseases nor hunger, however, will regulate deer numbers at densities well below biological carrying capacity. Both bovine tuberculosis and chronic wasting disease are transmitted by contact with infected individuals or materials, and transmission should increase with density.<sup>80</sup> Theoretically, chronic wasting disease is more likely to persist in deer populations where the carrying capacity has been increased through human modification of habitat.<sup>113</sup> However, there is yet no empirical evidence that either of these diseases limit deer populations.<sup>80</sup>

Predation has been shown to significantly reduce deer populations. The reintroduction of wolves into both western ecosystems have changed both the behavior and the number of large herbivores.<sup>5,114</sup> Large predators accomplish many of the goals of

ecological carrying capacity by both reducing overall numbers and increasing the perceived predation risk of deer.<sup>114</sup> In the case of the Yellowstone system, the reintroduction of wolves caused elk and bison to spend less time in open riparian areas and less time feeding overall, which resulted in increased stem density of aspen within riparian areas.<sup>5</sup> Increased predation risks also lowered reproduction in elk through increased glucocorticoid stress hormones, reducing fawn production.<sup>115,116</sup> In northern Minnesota, wolves were the main source of mortality for female deer within five years of their arrival.<sup>117</sup> Wolves were historically part of eastern forests, but the politics of their return in significant numbers is problematic.

Besides wolves, there is evidence that cougars (*Puma concolor*) limit deer populations in western states, but eastern cougar populations only occur in Florida.<sup>118</sup> Coyotes (*Canis latrans*) do reduce deer numbers in eastern Canada and are postulated to be able to reduce southern deer populations.<sup>119,120</sup> There is, however, limited evidence that deer densities are lower throughout the expanding range of coyotes. Introduction of bobcats to a South Carolina island did reduce deer numbers, whereas other forest carnivores seem to be incidental predators on fawns.<sup>16</sup>

Extirpated predators should be reintroduced where possible to both reduce numbers and change the functional foraging of deer, but this option will not be always be viable. Hunting is currently the primary tool for deer management in the United States. Nationwide in 2006 (the most current year with summary statistics), 10.7 million hunters harvested 6.2 million deer.<sup>121</sup> Deer herds can be reduced when exposed to hunters, and indexes show lower deer damage when herds are newly harvested.<sup>122–124</sup> Hunters do not mimic predators, as they only impact the number of deer and not their preferential browsing.<sup>125</sup> It has not been demonstrated that hunters with restricted seasons, locations, and hours can duplicate the presence of apex predators on the landscape. Hunting, however, is the sole tool currently available that can significantly reduce deer numbers at limited cost and has the potential to achieve management goals.

### Managing hunters in North America

It is difficult to generalize the current densities of deer in eastern United States and their impact on

forest resources. Unhunted population in moderate or highly productive landscapes are found in densities of 30–50 deer/km<sup>2</sup>, with isolated examples of >100 deer/km<sup>2</sup>.<sup>24,26,27,32,35,62</sup> Hunted populations generally are in a range of 15–30 deer/km<sup>2</sup>, and preferred browse species have been demonstrated to be impacted at 3–10 deer km<sup>2</sup>.<sup>21,24,26,32,40</sup> Without affecting functional foraging responses, it will be difficult to maintain preferred browse species through use of hunters unless deer densities are reduced to numbers significantly below biological carrying capacity. Achieving these low densities through hunting is a matter of managing hunters and their behavior.<sup>126</sup>

Hunting policy in the United States is unlike hunting in most of the world. In most developing countries, hunting is banned because of inadequate enforcement and low wildlife densities. In Europe, wildlife belongs to the landowner.<sup>127,128</sup> A landowner can manage their wildlife as they would their livestock, setting their own limits and rules, and meat and wildlife products can be sold to restaurants and shops.<sup>129</sup> Government funds are limited for wildlife management and focused on conservation of rare species, as most management is under private control.<sup>128</sup> In the United States, wildlife does not belong to the landowner, but the citizen, and in most states the landowner cannot restrict the movement of wildlife across their land.<sup>130</sup> Landowners may try to entice wildlife by planting food plots or bait piles, but they can only harvest the animals at the discretion of the state. Any game, or its product, killed by the landowner cannot be sold; meat not used for personal consumption can be donated to public food banks or institutions. Management of deer herds is a state function and deer managers set permit levels at a county or regional scale with limited attention to the local property.<sup>72,99</sup> An exception is the issuance of damage control permits for landowners that can demonstrate economic losses due to deer, and these allow for harvest outside of standard regulations.<sup>72</sup> Public lands that wish to engage in hunting must conduct lengthy sessions with public stakeholders and state agencies, and national lands must allow input from citizens and organizations throughout the country.<sup>14</sup> As mentioned earlier, revenues generated from sale of licenses and taxes placed on hunting equipment are used to manage the wildlife and in some states are the sole source of wildlife agency funds.<sup>71</sup>

The reliance on citizen hunters to achieve management goals has come to be called “The North American model.”<sup>130</sup> This model has seven tenets that call for ethical hunting of a shared resource for sport and personal consumption. A modification on this model is “Quality Deer Management,” which engages the public more directly in population management by encouraging relatively low deer densities through high harvest rates on females, thereby allowing males to reach older age classes under optimal forage conditions.<sup>131</sup>

The North American model has been credited with expanding game populations in North America and creating a system of forest land that is accessible to the public.<sup>130</sup> It should be noted that game populations have also increased throughout Europe without the benefit of the model.<sup>129</sup> Wildlife managers and researchers have noted that the model has problems with expanding use of its revenues and effort beyond game species, developing a strong role for the nonhunting citizen, and replacing an aging constituency of hunters.<sup>132,133</sup> These socioeconomic changes, and safety concerns, result in increasing portions of private land in exurbia being closed to hunting either by individual landowners or homeowner associations.<sup>134</sup> The reliance on a volunteer hunter limits a manager’s ability to target deer harvest to specific forests, but some success can be achieved through incentive programs to encourage increased harvest of females.<sup>126</sup> Hunters go where they have the highest probability of obtaining a quality deer, even when they know the management intent is to reduce deer density.<sup>135</sup> Quality Deer Management guidelines do encourage lower densities, but it is limited to cooperatives where hunters agree to shared quotas.<sup>131</sup> Many suburban communities have gone to sharpshooters, usually professional companies, to accomplish goals due to safety concerns.<sup>121</sup>

A major limit to managing the impact of deer herds on forests in North America is that the multiple constituencies involved with deer management who do not all view the ecological role of white-tailed deer as their highest priority.<sup>14</sup> Whereas ecological damage and disease spread may be a direct function of high densities, states have not been able to reduce deer populations across a broad landscape. If state-wide reduction is not possible, then a primary concern of ecologists is that high densities of deer do not result in the homogenization

of forests.<sup>70,136</sup> To satisfy stakeholders demanding higher densities, specific areas may be able to “survive” high deer densities if we can shift these areas over time and allow plant communities a periodic release from heavy browsing pressure. In rangelands, livestock-grazing systems that promote both temporal and spatial variation have been shown to increase plant and bird biodiversity.<sup>137,138</sup> In unharvested forests, an effective stocking rate for oak seedlings can be achieved in three years of low deer density, and subsequent canopy disturbance would release seedlings to reach sufficient heights to escape damaging deer browsing within an additional five years.<sup>87,88</sup> Responses within harvested forests would be quicker, assuming seed banks are still viable.<sup>22</sup> It might be possible to create a three-tiered system of deer management for public lands composed of areas with >30, 15–30, and 5–15 deer/km<sup>2</sup>. Hunters could have access to the first two tiers, and the third tier would be maintained at lower densities through targeted management by either commercial or professional staff. Converting to a hybrid model of deer management, where citizen hunters are initially allowed to harvest deer under standard regulations, followed by subsequent years where regulated sale of meat from harvested deer is allowed, might provide incentive to lower deer densities into the third tier and below ecological carrying capacity. Without the economic incentive to remove deer from already low-density populations, managers probably will have to expend funds to recruit hunters. The goal of such management would be to bring deer densities as low as possible in the focal areas and create a heterogeneous deer density across the landscape.

Several researchers argue for creating ecological benchmarks and managing for impact rather than deer density.<sup>139–141</sup> Transition points between the three tiers of deer density outlined above can be converted to benchmarks, which are easier to measure than deer density and which trigger shifts in management prescription. These measures would manage deer on an ecological basis rather than on cultural carrying capacity. The support of conservationists and ecologists for deer management would be stronger if management was based on ecological principles.

### Management conclusions

The ecological evidence is compelling that deer populations in eastern North America need to be man-

aged significantly below biological carrying capacity to maintain intact, diverse forested ecosystems, but that this regulation is not likely to be accomplished under the present suite of natural predators or through significant habitat modification. For the immediate future, managers must rely on hunters to reduce deer populations. Two issues hinder the ability of managers to achieve their goals. First, the current wildlife management system (i.e., the North American model) was developed to grow wildlife populations and may not have enough incentives to meet the current challenges of reducing deer populations. Second, state wildlife managers have adopted a paradigm of cultural carry capacity for setting population levels, and this qualitative measure does not insure densities below biological carry capacity. The primary function of management should be stewardship of the public’s natural resources, and any system not based on quantifiable measures will not be able to withstand careful scrutiny by opposing groups. Adoption of a management plan based on biological carrying capacity relies on cross-agency cooperation and buy-in by stakeholder groups, which includes the continued support of the citizen hunter and by gaining the support of other conservationists.

### Conflicts of interest

The author declares no conflicts of interest.

### References

- McNaughton, S.J., D.A. Oesterheld, D.A. Frank & K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitat. *Nature* **341**: 142–144.
- Hobbs, N.T. 1996. Modification of ecosystems by ungulates. *J. Wildl. Manage.* **60**: 695–713.
- Danell, K., R. Bergstrom, P. Duncan & J. Pastor, eds. 2006. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. Cambridge University Press. Cambridge, UK.
- Ray, J.C., K.H. Redford, R.S. Stenbeck & J. Berger, eds. 2005. *Large Carnivores and the Conservation of Biodiversity*. Island Press. Washington, DC.
- Beschta, R.L. & W.J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biol. Conserv.* **142**: 2401–2414.
- Terbourgh, J. & J. A. Estes. 2010. *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature*. Island Press. New York, NY.
- Hester, A.J., M. Bergman, G.R. Iason & J. Moen. 2006. Impacts of large herbivores on plant community structure and dynamics. In *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. K. Danell, R. Bergstrom,



- P. Duncan & J. Pastor, Eds.: 97–141. Cambridge University Press. Cambridge, UK.
8. Karath, K.U., J.D. Nichols, N.S. Kumar & J.E. Hines. 2004. Tigers and their prey; predicting carnivore densities from prey abundance. *Proc. Natl. Acad. Sci. USA* **101**: 4854–4858.
  9. Vera, F.W.M., E.S. Bakker & H. Olff. 2006. Large herbivores: missing patterns of western European light-demanding tree and shrub species. In *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. K. Danell, R. Bergstrom, P. Duncan & J. Pastor, Eds.: 203–231. Cambridge University Press. Cambridge, UK.
  10. Pastor, J. & Y. Cohen. 1997. Herbivores, the functional diversity of plant species and the cycling of nutrients in ecosystems. *Theor. Popul. Biol.* **51**: 165–179.
  11. McCabe, T.R. & R.E. McCabe. 1997. Recounting whitetails past. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood & J.H. Rappole, Eds.: 11–26. Smithsonian Institution Press. Washington, DC.
  12. Hickey, L. 2008. Assessing re-colonization of moose in New York with HIS models. *Alces* **44**: 117–126.
  13. Larkin, J.L., R.A. Grims, L. Cornicelli, et al. 2001. Returning elk to Appalachia: foiling Murphy's law. In *Large Mammal Restoration; Ecological and Sociological Challenges in the 21<sup>st</sup> Century*. D.S. Maehr, R.F. Noss & J.L. Larkin, Eds.: 101–117. Island Press. Washington, DC.
  14. Leong, K.M., D.J. Decker, T.B. Lauber, et al. 2009. Overcoming jurisdictional boundaries through stakeholder engagement and collaborative governance: lessons learned from white-tailed deer management in the U.S. *Res. Rural Sociol. Dev.* **14**: 221–247.
  15. Ruggiero, L.F. 2010. Scientific independence and credibility in sociopolitical processes. *J. Wildl. Manage.* **74**: 1179–1182.
  16. Warren, R.J. 2011. Deer overabundance in the USA: recent advances in population control. *Anim. Prod. Sci.* **51**: 259–266.
  17. Braun, E.L. 1950. *Deciduous Forests of Eastern North America*. The Blakiston Co. Philadelphia, PA.
  18. Bailey, R. G. 2009. *Ecosystem Geography*. Springer-Verlag. New York, NY.
  19. Augustine, D.J. & P.A. Jordon. 1998. Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. *J. Wildl. Manage.* **62**: 1076–1085.
  20. Morissette, E.M., C. Lavoie & J. Huot. 2009. Fairy slipper (*Calypso bulbosa*) on Anticosti Island: the occurrence of a rare plant in an environment strongly modified by white-tailed deer. *Botany* **87**: 1223–1231.
  21. Alverson, W.S. & D.M. Waller. 1997. Deer population and widespread failure of hemlock regeneration in northern forests. In *The Science of Overabundance: Deer Population Ecology and Management*. W.J. McShea, H.B. Underwood & J.H. Rappole, Eds.: 280–297. Smithsonian Institution Press. Washington, DC.
  22. Mallik, A.U. 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keystone species change. *Crit. Rev. Plant Sci.* **22**: 341–366.
  23. Sauve, D.G. & S.D. Cote. 2010. Winter foraging selection in white-tailed deer at high densities: balsam fir is the best of a bad choice. *J. Wildl. Manage.* **71**: 911–914.
  24. Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry* **74**: 201–208.
  25. Rooney T.P. & D.M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *For. Ecol. Manage.* **181**: 165–176.
  26. Cote, S.D., T.P. Rooney, J. Tremblay, et al. 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* **35**: 113–147.
  27. McShea, W.J. 2005. Forest ecosystems without carnivores: when ungulates rule the world. In *Large Carnivores and the Conservation of Biodiversity*. J.C. Ray, K. Redford, R.S. Stenbeck & J. Berger, Eds.: 138–153. Island Press. Washington, DC.
  28. Geist, V. 1998. *Deer of the World: Their Evolution, Behavior and Ecology*. Stackpole Books. Mechanicsburg, PA.
  29. McCaffery, K.R., J. Tranetzki & T. Piechura, Jr. 1974. Summer food of deer in Northern Wisconsin. *J. Wildl. Manage.* **38**: 215–219.
  30. Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* **62**: 1041–1051.
  31. Royo, A.R., R. Collins, M.B. Adams, et al. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* **91**: 93–105.
  32. Hansen, L.P., C.M. Nixon & J. Beringer. 1997. Role of refuges in the dynamics of outlying deer populations. In *The Science of Overabundance: Deer Population Ecology and Management*. W.J. McShea, H.B. Underwood & J.H. Rappole, Eds.: 327–345. Smithsonian Institution Press. Washington, DC.
  33. Etter, D.R., K.M. Hollis, T.R. Van Deelen, et al. 2002. Survival and movements of whitetailed deer in suburban Chicago, Illinois. *J. Wildl. Manage.* **66**: 500–510.
  34. Storm, D.J., C.K. Nielson, E.M. Schaubert & A. Woolf. 2007. Deer–human conflict and hunter access in an exurban landscape. *Hum. Wildl. Inter.* **1**: 53–59.
  35. Stewart, C.M., W.J. McShea & B.P. Piccolo. 2007. The impact of white-tailed deer foraging on agricultural resources at 3 National Historical Parks in Maryland. *J. Wildl. Manage.* **71**: 1525–1530.
  36. Retamosa, M. I., L.A. Humberg, J.C. Beasley & O.E. Rhodes, Jr. 2008. Modeling wildlife damage to crops in northern Indiana. *Hum. Wildl. Inter.* **2**: 225–239.
  37. Meier, A.J., S.P. Bratton & D.C. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecol. Appl.* **5**: 935–946.
  38. Miller, B.F., T.A. Campbell, B.R. Laseter, et al. 2009. White-tailed deer herbivory and timber harvesting rates: implications for regeneration success. *For. Ecol. Manage.* **258**: 1067–1072.
  39. Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J. Wildl. Manage.* **53**: 524–532.
  40. Anderson, R.C. & A.J. Katz. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer (*Odocoileus virginianus* Zimmerman) browsing pressure. *Biol. Conserv.* **63**: 203–208.

41. Russell, F.L., D.B. Zippin & N.L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *Am. Midl. Nat.* **146**: 1–26.
42. Pedersen, B.S. & A.M. Wallis. 2004. Effects of white-tailed deer herbivory on forest gap dynamics in a wildlife preserve, Pennsylvania, USA. *Nat. Areas J.* **24**: 82–94.
43. Royo, A.A. & W.P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can. J. For. Res.* **36**: 1345–1362.
44. Huebner, C.D., K.W. Gottschalk, G.W. Miller & P.H. Brose. 2011. Restoration of three forest herbs in the Liliaceae family by manipulating deer herbivory and overstorey and understorey vegetation. *Plant Ecol. Divers.* **3**: 259–272.
45. Eschtruth, A.K. & J.J. Battles. 2008. Deer herbivory alters forest response to canopy decline caused by an exotic insect pest. *Ecol. Appl.* **18**: 360–376.
46. Schmitz, O.J. & A.R.E. Sinclair. 1997. Rethinking the role of deer in forests. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood & J.H. Rappole, Eds.: 201–223. Smithsonian Institution Press. Washington, DC.
47. Stromayer, K.A.K. & R.J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildl. Soc. Bull.* **25**: 227–34.
48. Horsley, S.B., S.L. Stout & D.S. DeCalesta. 2003. Whitetailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* **13**: 98–118.
49. Tremblay, J.P., J. Huot & F. Potvin. 2006. Divergent non-linear responses of the boreal forest field layer along an experimental gradient of deer densities. *Oecologia* **150**: 78–88.
50. Webster, C.R., M.A. Jenkins & J.H. Rock. 2005. Longterm response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biol. Conserv.* **125**: 297–307.
51. Taverna, K., R.K. Peet & L.C. Phillips. 2005. Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. *J. Ecol.* **93**: 202–213.
52. Knight, T.M., J.L. Dunn, L.A. Smith, *et al.* 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Nat. Areas J.* **29**: 110–116.
53. Myers, J.A., M. Vellend, S. Gardescu & P.L. Marks. 2004. Seed dispersal by white-tailed deer: implications for long distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* **139**: 35–44.
54. Fletcher, J.D., W.J. McShea, L.A. Shipley & D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Nat. Areas J.* **21**: 172–176.
55. Augustine, D.J. & D. deCalesta. 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. *Ecoscience* **10**: 472–486.
56. Heckel, C.D., N.A. Bourg, W.J. McShea & S. Kalisz. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* **91**: 319–326.
57. Waller, D.M. & W.S. Alverson. 1997. The white-tailed deer: a keystone herbivore. *Wildl. Soc. Bull.* **25**: 217–226.
58. Ostfeld, R.S., C.G. Jones & J. O. Wolff. 1996. Of mice and mast; ecological connections in eastern deciduous forests. *Bioscience* **46**: 323–330.
59. McShea, W.J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* **81**: 228–238.
60. Martin, J.L., S.A. Stockton, S. Allombert & A.J. Gaston. 2010. Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: lessons from a deer introduction. *Biol. Invasions* **12**: 353–371.
61. Pringle, R.M., T.P. Young, D.I. Rubenstein & D.J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proc. Natl. Acad. Sci. USA* **104**: 193–197.
62. McShea, W.J. & J.H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. *Conserv. Biol.* **14**: 1161–1170.
63. Martin, T.G., P. Arcese & N. Scheerder. 2011. Browsing down our natural heritage: deer impact on vegetation structure and songbird populations on across an island archipelago. *Biol. Conserv.* **144**: 459–469.
64. Jones, C.G., R.S. Ostfeld, M.P. Richard, *et al.* 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease. *Risk Sci.* **279**: 1023–1026.
65. Illius, A.W. 2004. Linking functional responses and foraging to population dynamics. In *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. K. Danell, R. Bergstrom, P. Duncan & J. Pastore, Eds.: 71–96. Cambridge University Press. Cambridge, UK.
66. Ward, D. 2006. Long-term effects of herbivory on plant diversity and functional types in arid ecosystems. In *Large Herbivore Ecology, Ecosystem Dynamics and Conservation*. K. Danell, R. Bergstrom, P. Duncan & J. Pastor, Eds.: 142–169. Cambridge University Press. Cambridge, UK.
67. Augustine, D.J., L.E. Frelich & P.A. Jordon. 1998. Evidence for two alternative stable states in an ungulate grazing system. *Ecol. Appl.* **8**: 1260–1269.
68. Ripple, W.J. & R.L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *For. Ecol. Manage.* **184**: 299–313.
69. Parker, J.D., J-P Salminen & A.A. Agrawal. 2010. Herbivory enhances positive effects of plant genetic diversity. *Ecol. Lett.* **13**: 553–563.
70. Rooney, T.P., S.M. Wiegmann, D.A. Rogers & D.M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conserv. Biol.* **18**: 787–798.
71. Southwick, R. 2009. The economic contributions of hunting in the United States. 199–211 In *Transactions of the Seventy-third North American Wildlife and Natural Resources Conference*, Wildlife Management Institute. Washington, DC.
72. Virginia Department of Game and Inland Fisheries. 2007. Virginia Deer Management Plan 2006–2015. Wildl. Inform. Publ. 07–1. Richmond, VA.

73. State Farm. 2009. Deer- vehicle collision frequency jumps 18 percent in five years. Available at: [http://www.statefarm.com/aboutus/\\_pressreleases/2009/deer\\_vehicle\\_collision\\_frequency\\_jumps.asp](http://www.statefarm.com/aboutus/_pressreleases/2009/deer_vehicle_collision_frequency_jumps.asp) accessed Dec. 29, 2011.
74. McShea, W.J., C.M. Stewart, L.J. Kearns, *et al.* 2008. Factors affecting autumn deer/vehicle collisions in a rural Virginia county. *Hum. Wildl. Confl.* **2**: 110–121.
75. Conover, M.R. & D.J. Decker. 1991. Wildlife damage to crops: perceptions of agricultural and wildlife professionals in 1957 and 1987. *Wildl. Soc. Bull.* **19**: 46–52.
76. Drake, D., J.B. Paulin, P.D. Curstis, *et al.* 2005. Assessment of negative economic impacts from deer in the northeastern United States. *J. Ext.* **43**. Available at: <http://www.joe.org/joe/2005february/rb5.php> accessed Dec. 29, 2011.
77. West, B.C. & J.A. Parkhurst. 2002. Interactions between deer damage, deer density, and stakeholder attitudes in Virginia. *Wildl. Soc. Bull.* **30**: 139–147.
78. Marquis, D.A. 1974. *The Impact of Deer Browsing on Allegheny Hardwood Regeneration*. USDA Forest Service Research Paper NE-308, Northeastern Forest Experiment Station, Upper Darby, PA.
79. Horsely, S.B. & D.A. Marquis. 1983. Interference of deer and weeds with Allegheny hardwood reproduction. *Can. J. For. Res.* **13**: 61–69.
80. Conner, M.M., M.R. Ebinger, J. A. Blanchong, & P.C. Cross. 2008. Infectious disease in cervids of North America. *Ann. N. Y. Acad. Sci.* **1134**: 146–172.
81. Centers for Disease Control and Prevention. 2011. *Summary statistics*. Available at: <http://www.cdc.gov/lyme/stats/index.html> accessed Dec. 29, 2011.
82. Ostfeld, R.S., C.D. Canham, K. Oggenfuss, *et al.* 2006. Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biol.* **4**: 1058–1068.
83. Ostfeld, R.S., F. Keesing, C.G. Jones, *et al.* 1998. Integrative ecology and the dynamics of species in oak forests. *Inter. Biol.* **1**: 178–186.
84. Fish, D. & J.E. Childs. 2009. Community-based prevention of Lyme disease and other tick-borne diseases through topical application of acaricide to white-tailed deer: background and rationale. *Vector-borne Zoonotic Dis.* **4**: 357–364.
85. Abrams, M.D. 2003. Where have all the white oak gone? *Bioscience* **53**: 927–939.
86. McShea, W.J., W.M. Healy, P. Devers, *et al.* 2007. Forestry Matters: decline of oaks will impact wildlife in hardwood forests. *J. Wildl. Manage.* **71**: 1717–1728.
87. Dey, D. 2002. The ecological basis for oak silviculture in eastern North America. In *Oak Forest Ecosystems; Ecology and Management for Wildlife*. W.J. McShea & W.M. Healy, Eds.: 60–79. Johns Hopkins Press. Baltimore, MD.
88. Healy, W.M. & W.J. McShea. 2002. Goals and guidelines for ecosystem management of oak forests. In *Oak Forest Ecosystems: Ecology and Management for Wildlife*. W.J. McShea & W.M. Healy, Eds.: 33–340. John Hopkins University Press. Baltimore, MD.
89. Suding, K.N., K.L. Gross & G.R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* **19**: 46–53.
90. Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. In *Applied Biology*. T.H. Coaker, Eds.: 183–246. Academic Press. New York, NY.
91. Sinclair, A.R.E. 1997. Carrying capacity and the overabundance of deer. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood & J.H. Rappole, Eds.: 80–394. Smithsonian Institution Press. Washington, DC.
92. McCullough, D.R. 1979. *The George Reserve Deer Herd*. Michigan State University Press. Ann Arbor, MI.
93. Lancia, R.A., K.H. Pollock, J.W. Bishir & M.C. Conner. 1988. A white-tailed deer harvest strategy. *J. Wildl. Manage.* **52**: 589–595.
94. Leopold, A. 1943. Deer irruptions. *Trans. Wisc. Acad. Sci. Arts Lett.* **35**: 351–366.
95. Leopold, A., L.K. Sowls & D.L. Spencer. 1947. A survey of over-populated deer ranges in the U.S. *J. Wildl. Manage.* **11**: 162–177.
96. McNab, J. 1985. Carrying capacity and related slippery shibboleths. *Wildl. Soc. Bull.* **13**: 403–410.
97. Latham, R.E., J. Beyea, M. Benner, *et al.* 2005. *Managing white-tailed deer in forest habitat from an ecosystem perspective: Pennsylvania case study*. Audubon Pennsylvania and the Pennsylvania Habitat Alliance, Harrisburg, PA.
98. Banta, J.A., A.A. Royo, C. Kirschbaum & W.P. Carson. 2005. Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. *Nat. Areas J.* **25**: 10–18.
99. Knox, M.W. 1997. Historical changes in the abundance and distribution of deer in Virginia. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood & J.H. Rappole, Eds.: 27–36. Smithsonian Institution Press. Washington, DC.
100. McGraw, J.B. & M.A. Furedi. 2004. Deer browsing and population viability of a forest understory plant. *Science* **307**: 920–922.
101. Nixon, C.M., L.P. Hansen, P.A. Brewer & J.E. Chelmsvig. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildl. Monogr.* **188**: 1–77.
102. Nowak, R.M. 1999. *Walker's Mammals of the World*. 6th ed. Johns Hopkins Press. Baltimore, MD.
103. Cote, S.D. 2005. Extirpation of a large black bear population by introduced white-tailed deer. *Conserv. Biol.* **19**: 1668–1671.
104. Walter, W.D., K.C. VerCauteren, J.M. Gilsdorf, & S.E. Hynstrom. 2009. Crop, native vegetation, and biofuel: response of white-tailed deer to changes in management priorities. *J. Wildl. Manage.* **73**: 339–344.
105. de la Cretaz, A.L. & M.J. Kelty. 1999. Establishment and control of hay-scented fern: a native invasive species. *Biol. Invasions* **1**: 223–236.
106. McShea, W.J., S.L. Monfort, S. Hakim, *et al.* 1997. The effect of immunocontraception on the behavior and reproduction of white-tailed deer. *J. Wildl. Manage.* **41**: 560–569.
107. Fraker, M.A., R.G. Brown, G.E. Grant, *et al.* 2002. Long-lasting, single-dose immunocontraception of feral fallow deer in British Columbia. *J. Wildl. Manage.* **66**: 1141–1147.
108. Miller, L.A., J.P. Gionfriddo, K.A. Fagerstone, *et al.* 2008. The single-shot GnRH immunocontraceptive vaccine (GonaCon) in whitetailed deer: comparison of several GnRH preparations. *Am. J. Reprod. Immunol.* **60**: 214–23.

109. Rutberg, A.T. & R.E. Nagle. 2007. Population-level effects of immunocontraception in white-tailed deer (*Odocoileus virginianus*). *Wildl. Res.* **35**: 494–501.
110. Gionfriddo, J.P., J.D. Eisemann, K.J. Sullivan, *et al.* 2009. Field test of a single-injection gonadotrophin releasing hormone immunocontraceptive vaccine in female white-tailed deer. *Wildl. Res.* **36**: 177–84.
111. Porter, W.F., H.B. Underwood & J.L. Woodward. 2004. Movement behavior, dispersal, and the potential for localized management of deer in a suburban environment. *J. Wildl. Manage.* **68**: 247–256.
112. Davidson, W.R. & G.L. Doster. 1997. Health characteristics and white-tailed deer populations in the southeastern United States. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood & J.H. Rappole, Eds.: 164–184. Smithsonian Institution Press. Washington, DC.
113. Sharp, A. & J. Pastor. 2011. Stable limit cycles and the paradox of enrichment in a model of chronic wasting disease. *Ecol. Appl.* **21**: 1024–1030.
114. Laundré, J.W., L. Hernandez & K.B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Can. J. Zool.* **79**: 1401–1409.
115. Creel S., D. Christianson, S. Liley & J.A. Winnie. 2007. Predation risk affects reproductive physiology and demography of elk. *Science* **315**: 960.
116. Creel S., J.A. Winnie & D. Christianson. 2009. Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proc. Natl. Acad. Sci. USA* **106**: 388–393.
117. DelGiudice, G.D., M.R. Riggs, P. Joly & W. Pan. 2002. Winter severity, survival and cause of specific mortality in female white-tailed deer in north-central Minnesota. *J. Wildl. Manage.* **66**: 698–717.
118. Ripple, W.J. & R.L. Beschta. 2008. Trophic cascade involving cougar, mule deer and black oaks in Yosemite National Park. *Biol. Conserv.* **141**: 1249–1256.
119. Ballard, W.B., H.A. Whitlaw, S.J. Young, *et al.* 1999. Predation and survival of white-tailed deer fawns in north central New Brunswick. *J. Wildl. Manage.* **63**: 574–579.
120. Kilgo, J.C., H.S. Ray, C. Ruth & K.V. Miller. 2010. Can coyotes affect deer populations in southeastern North America? *J. Wildl. Manage.* **74**: 929–933.
121. Fish and Wildlife Service. 2011. *Hunting Summary Statistics*. Available at: <http://www.fws.gov/hunting/huntingstats.html> accessed Dec. 29, 2011.
122. Killmaster, C.H., D.A. Osborn, R.J. Warren, *et al.* 2007. Deer and understory plant responses to a large-scale herd reduction on a Georgia state park. *Nat. Areas J.* **27**: 161–168.
123. DeNicola, A.J. & S.C. Williams. 2008. Sharpshooting suburban white-tailed deer reduces deer-vehicle collisions. *Hum. Wildl. Confl.* **2**: 28–33.
124. Winchcombe, R.J. 2010. Hunting for balance: a long-term effort to control local deer abundance. *Wildl. Prof.* **4**: 48–50.
125. Berger J. 2005. Hunting by carnivores and humans: does functional redundancy occur and does it matter? In *Large Carnivores and the Conservation of Biodiversity*. J.C. Ray, K.H. Redford, R.S. Steneck & J. Berger, Eds.: 315–341. Island Press. Washington, DC.
126. Van Deelen, T.R., B.J. Dhuey, C.N. Jacques, *et al.* 2010. Effects of earn-a-buck and special antlerless-only season on Wisconsin's deer herd. *J. Wildl. Manage.* **74**: 1693–1700.
127. Apollonio, M., R. Anderson & R. Putman. 2010. *European Ungulates and their management in the 21<sup>st</sup> Century*. Cambridge University Press. New York, NY.
128. Apollonio, M., R. Anderson & R. Putman. 2010. Recent status and future challenges for European ungulate management. In *European Ungulates and their management in the 21<sup>st</sup> Century*. M. Apollonio, R. Anderson & R. Putman, Eds.: 578–604. Cambridge University Press. New York, NY.
129. Brainerd, S.M. & B. Kaltenborn. 2010. The Scandinavian model: a different path to wildlife management. *Wildl. Prof.* **4**: 52–55.
130. Organ, J.F., S.H. Mahoney & V. Geist. 2010. Born in the hands of hunters: the North American model of wildlife conservation. *Wildl. Prof.* **4**: 22–27.
131. Miller, K.V. & R.L. Marchinton, eds. 1995. *Quality White-tails: The Why and How of Quality Deer Management*. Stackpole Books. Mechanicsburg, PA.
132. Dratch, P. & R. Kahn. 2011. Moving beyond the model: our ethical responsibility as the top trophic predators. *Wildl. Prof.* **5**: 58–60.
133. Nelson, M.P., J.A. Vucetich, P.C. Paquet & J.K. Bump. 2011. An inadequate construct? North American model: what's flawed, what's missing, what's needed. *Wildl. Prof.* **5**: 58–60.
134. Harden, C.D., A. Woolf & J. Roseberry. 2005. Influence of exurban development on hunting opportunity, hunter distribution, and harvest efficiency of white-tailed deer. *Wildl. Soc. Bull.* **33**: 233–242.
135. Blanchong, J.A., D.O. Joly, M.D. Samuel, *et al.* 2006. White-tailed deer harvest from the chronic wasting disease eradication zone in South-Central Wisconsin. *Wildl. Soc. Bull.* **34**: 725–731.
136. McKinney, M.L. & J.L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* **14**: 450–453.
137. Derner, J.D., W.K. Lauenroth, P. Stapp & D.J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the Western Great Plains of North America. *Range. Ecol. Manag.* **62**: 111–118.
138. Nelson, K.S., E.M. Gray & J.R. Evans. 2011. Finding solutions for bird restoration and livestock management: comparing grazing exclusion levels. *Ecol. Appl.* **21**: 547–554.
139. Morellet, N., J.M. Gaillard, A.J.M. Hewison, *et al.* 2007. Indicators of ecological change: new tools for managing populations of large herbivores. *J. Appl. Ecol.* **44**: 634–643.
140. deCalesta, D.S. & S.L. Stout. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildl. Soc. Bull.* **25**: 252–258.
141. Tierney, G.L., D. Faber-Langendoen, B.R. Mitchell, *et al.* 2009. Monitoring and evaluating the ecological integrity of forest ecosystems. *Front. Ecol. Environ.* **7**: 308–316.