

Deer impacts on forest ecosystems: a North American perspective

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Summary

White-tailed deer have increased in abundance and expanded their geographic range in North America over the past century, and now exist at higher densities than they have in the past several hundred years. This is having numerous impacts on the forest ecosystems they inhabit. Regional recruitment failure of eastern hemlock (*Tsuga canadensis*) and northern white cedar (*Thuja occidentalis*) trees can be explained in part by deer browsing. Deer also have significant negative effects on understorey plants, including wild lily-of-the-valley (*Maianthemum canadense*) and white-flowered trillium (*Trillium grandiflorum*). Long-term studies of primary, old-growth forest stands reveal a 48–81 per cent herb and shrub species loss accompanying increases in deer density. Graminoids, ferns and club mosses were more likely to persist in these stands than plants in all other taxonomic groups. Deer also exhibit indirect effects on forest communities by reducing host plant densities or altering forest structure. Because of their numerous direct and indirect effects on other species, and because of the magnitude of these effects, white-tailed deer act as a keystone herbivore. Natural regulation and maximum sustained yield management approaches have failed to alleviate deer impacts on forest ecosystems, but an ecosystem-based management approach offers promise.

Introduction

Deer impacts on woodlands and forests are not confined to Europe. Significant deer impacts on forests have been recorded in New Zealand (Stewart and Burrows, 1989), Japan (Shimoda *et al.*, 1994), and the United States (Alverson *et al.*, 1988; Stromayer and Warren, 1997; Waller and Alverson, 1997). This paper focuses on deer impacts in North America, and draws on my own research over the past 5 years.

There are three taxa of deer endemic to North America: the mule deer (*Odocoileus hemionus hemionus*), black-tailed deer (*Odocoileus hemionus columbianus*) and white-tailed deer (*Odocoileus virginianus*). Whereas the mule deer

and black-tailed deer are confined to western North America, the white-tailed deer is found throughout the temperate and north tropic zones of the western hemisphere. Both mule deer and black-tailed deer occasionally become overabundant in some places and in some years, particularly on predator-free islands and in urban parks (McCullough *et al.*, 1997). When their densities are high, mule deer have severe impacts on sagebrush (*Artemisia* spp.) communities (McArthur *et al.*, 1988; Singer and Renkin, 1995), and black-tailed deer damage unprotected tree seedlings (Sullivan *et al.*, 1985). Most studies of deer impacts in North America concern white-tailed deer, which generally achieve the highest densities.

Since European settlement, the white-tailed deer has expanded its geographic range and increased in abundance. While the exact range of population densities is not known, densities were certainly lower than at present. For example, McCabe and McCabe (1997) used archaeological, anthropological and historical data, and estimated an average density of 3.1–4.2 deer km⁻² throughout their North American range. Alverson *et al.* (1988) used a multivariate habitat model and estimated deer densities to be 2–4 deer km⁻² in deciduous and mixed deciduous–coniferous forests. In the year 2000, deer exceeded these pre-settlement densities by a factor of 2–12 in the deciduous and mixed coniferous forests of northern Wisconsin. Deer densities throughout the eastern United States are highly variable, but deer densities in excess of 10 deer km⁻² are common (Diefenbach *et al.*, 1997; Russell *et al.*, 2001).

The history of white-tailed deer populations in the United States and southern Canada can be divided into three stages: a pre-settlement stage, an exploitation stage and a present stage (see Leopold, 1943). During the pre-settlement stage (pre-1700), deer densities were low. The abundance of deer was probably regulated by three mechanisms. First, harsh winters every 10–20 years resulted in high mortality of overwintering animals, thereby reducing the population. Secondly, predators, including the wolf (*Canis lupus*), cougar (*Felis concolor*), and the estimated seven million Native Americans that lived within the range of white-tailed deer (McCabe and McCabe, 1997; Wilson, 1999), prevented deer population numbers from dramatically increasing following a severe winter die off. However, predators are only able to regulate deer populations if deer occur at low density (Eberhardt and Peterson, 1999; Mech and Nelson, 2000). Thirdly, the forest structure and composition constrained the amount of food available annually to the population (Dahlberg and Guettinger, 1956). It is difficult to determine retrospectively which of these factors operated most of the time. However, these factors undoubtedly worked together to affect deer populations (Leopold, 1943; Sinclair, 1997). The carrying capacity for white-tailed deer was most likely set by food availability, which is in turn determined by forest structure and composition (McCaffery, 1976). The direct and indirect effects of predators would have prevented

white-tailed deer populations from reaching carrying capacity. The direct effects of predation are obvious – predators eat deer and reduce their numbers. The indirect effects of predators are less obvious. Deer show an avoidance response to predators, and avoid otherwise suitable habitat if predators are present (Brown *et al.*, 1999). In Minnesota, for example, deer tend to maintain home ranges in between wolf pack territories, where the risk of predation is lower (Lewis and Murray, 1993). Harsh winters that kill young, old and sick animals tend to reduce population sizes further (McCaffery, 1976).

European settlement brought major changes to North America, including widespread habitat modification, predator elimination and legislation that protected deer populations from hunting. The white-tailed deer population in northern Wisconsin started to increase in the early 1800s, in response to logging activities. Logging converted old-growth forest stands into young forest stands that provided more and higher quality food, thereby increasing carrying capacity for deer. Concurrently, densities of wolves and cougars declined due to bounty hunting. The loss of predators allowed deer to multiply rapidly. The deer population grew for a few decades, but then declined to near-extinction due to market hunting pressures. This decline marked the exploitation stage (1700–1900). The exploitation stage was followed by aggressive conservation measures, including restrictive hunting legislation and deer translocation (Schorger, 1953). During the present stage (1900–present), the deer population responded to better habitat conditions and fewer predators by growing in numbers and expanding its geographic range. Conditions for white-tailed deer in North America have never been better.

Deer impacts on plant species composition

Just like exotic species, native species can pose threats to ecosystems. In North America, many native species tolerant of anthropogenic environmental changes have increased their geographic range and/or abundance, and are having novel effects on ecosystems (Garrott *et al.*, 1993; Sinclair, 1997). White-tailed deer are among these thriving, opportunistic, overabundant species. In

recent years, I have examined white-tailed deer impacts on forest communities in the United States, and considered direct and indirect effects on forest taxa.

Direct effects

Eastern hemlock (*Tsuga canadensis*) is a long-lived conifer tree, and is a potential natural vegetation dominant throughout much of the eastern USA. This species has suffered decades of recruitment failure in New England and the Upper Great Lakes, and hemlock is no longer replacing itself. Hemlock forests support distinct bird and floral communities, so its decline is a conservation concern. Deer eat the needles of saplings and can cause recruitment failure at a local scale (Hough, 1965; Frelich and Lorimer, 1985; Alverson *et al.*, 1988). However, Mladenoff and Stearns (1993) warned against extrapolating from a few local sites to explain recruitment failure at a regional scale. Against this backdrop, Rooney *et al.* (2000) examined hemlock recruitment at 100 sites over a 10 000 km² area in the Upper Great Lakes region. Data were collected on four height classes of hemlock seedlings (4–9 cm, 10–29 cm, 30–99 cm, 100–300 cm), and a number of biotic and abiotic variables at each site. The goal was to determine which factors best explained the abundance of hemlock seedlings in each size class at a regional scale. Findings were summarized using path analysis. Abiotic factors, such as light and biogeographic location, were important for the two smaller hemlock sapling size classes. Deer had a negative direct effect on the 30–99 cm saplings (path coefficient = -0.245) and an

indirect effect on 100–300 cm saplings (path coefficient = -0.166). Demographic inertia was important for all size classes. These results demonstrated that deer play a significant role in limiting hemlock recruitment at a regional scale.

Northern white cedar (*Thuja occidentalis*) is another long-lived conifer tree. It is canopy-dominant in calcareous swamps in the boreal forest region. Cedar swamps support a number of rare plants, particularly orchids. Thus, cedar swamp viability is also of conservation concern. Like hemlock, northern white cedar exhibits widespread recruitment failure, and is a favoured food of white-tailed deer in winter. Northern white cedar recruitment at 49 sites over a broad geographical area was studied in northern Wisconsin and Michigan, and many biotic and abiotic factors were examined (T.P. Rooney, S.L. Solheim and D.M. Waller, unpublished). Results were summarized using path analysis, and patterns were very similar to those observed with eastern hemlock (Figure 1). Light and basal area (a surrogate for seed input) account for significant variation in seedling numbers, and deer significantly reduce the abundance of larger saplings. Deer had a significant direct effect on the 10–29 cm saplings (path coefficient = -0.39), and significant direct (path coefficient = -0.28) and indirect (path coefficient = -0.24) effects on the 30–300 cm saplings. Thus, deer significantly reduce cedar recruitment at a regional scale.

The wild lily-of-the-valley (*Maianthemum canadense*: Liliaceae) is a short-statured, clonal herb with insect-pollinated flowers and bird-dispersed fruits. This plant is particularly abundant in northern hardwood forests. Browsing impacts

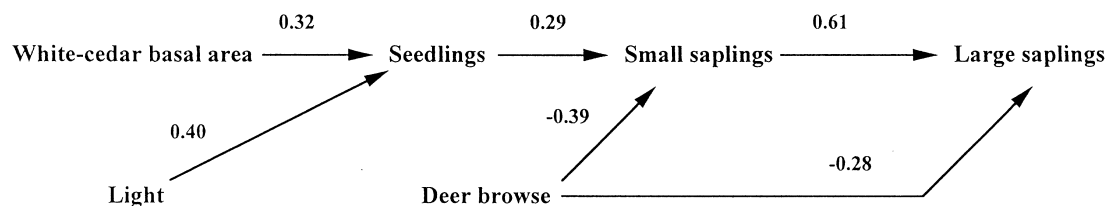


Figure 1. Path analysis of northern white cedar abundance in three height classes from 49 sites in northern Wisconsin and Michigan, in 1996. Cedar abundance is $(1 + \ln N)$ transformed prior to analysis. Numbers adjacent to arrows are path coefficients, and all are significant at the $P \leq 0.05$ level. From T.P. Rooney, S.L. Solheim and D.M. Waller (unpublished).

on this species were examined in the Allegheny Plateau region of north-western Pennsylvania, a region where deer have been overabundant since the 1920s (Marquis, 1975). A natural deer exclusion experiment was used to study browsing impacts on this species (Rooney, 1997). Plants growing on boulder tops were compared with plants growing on rocks at ground level. Deer were naturally excluded from the high boulders. Substrate was controlled for, since all plants examined occurred on rocks. Plants growing on boulder refugia were found to be 30 per cent larger, 3900 per cent more likely to flower, and had population densities 300 per cent larger than those growing on rocks at ground level. Wood sorrel (*Oxalis acetosella*), a species avoided by deer, showed no such differences.

The white-flowered trillium (*Trillium grandiflorum*: Liliaceae *sensu lato*) is a showy, non-clonal herb with insect-pollinated flowers and ant-dispersed seeds. The species is abundant in deciduous forests throughout the eastern USA, and is browsed by deer. The average height of plants in a population and the density of flowering plants increase when plants are protected from browsing (Anderson, 1994; Augustine and Frelich, 1998). Rooney (2000) demonstrated the mechanism underlying these patterns, using 80 plants in an artificial defoliation field experiment. Forty plants were clipped, and 40 plants were used as controls. Deer ate 21 plants before they could be measured, so the analysis was performed on 59 plants. Relative growth rate (RGR) was measured between 1998 and 1999. Experimentally defoliated plants had a RGR that was 50 per cent that of control plants. Effects due to site and site \times defoliation were also detected. Plant biomass was used as a covariate to soak up extraneous variation, because growth rates are inversely proportional to plant size. The loss of photosynthetic tissue resulting from defoliation reduces whole plant carbon budgets, and results in reduced RGR (Rooney, 2000).

Deer impacts on understorey communities

It is possible that deer browsing just affects a few species, and the four plants profiled above are unusual. Alternatively, deer browsing might alter the entire forest understorey. To examine deer impacts on forest understoreys, I will examine the

Heart's Content site in Pennsylvania, and the Piney Point site in Wisconsin. These two sites are unusual because (1) they are primary forests embedded within a forested landscape, (2) excellent baseline data exist on understorey species composition, and (3) the deer population has increased dramatically since the original survey. Neither of these forests have been affected by large-scale disturbances, natural or otherwise, that could account for changes in the ground flora.

Heart's Content is a 50 ha white pine (*Pinus strobus* L.)–hemlock–beech (*Fagus grandifolia* Ehrh.) forest in north-western Pennsylvania. A ground layer survey was conducted in 1929 (Lutz, 1930), and the frequency and relative abundance of herbs and shrubs were recorded. Deer populations increased by a factor of 2–6 over the next several decades (Marquis, 1975). The site was resurveyed in 1995, using the same methods and same sampling intensity as the original survey. Species losses between the two time periods were dramatic (Rooney and Dress, 1997). There were no new species present, but 81 per cent of the species had disappeared from the hemlock–beech stand and 59 per cent had disappeared from the hemlock stand. The hypothesis that graminoids (grasses, sedges and rushes), ferns and club mosses were less likely to disappear than all other taxonomic groups was tested using a G-test for goodness-of-fit. While the losses were less severe in the graminoid–fern–club moss group, the results were not significant in the hemlock–beech stand (d.f. = 1; $G = 2.63$; $P = 0.10$) or the hemlock stand (d.f. = 1; $G = 0.93$; $P = 0.33$).

Piney Point is a 5 ha red pine (*Pinus resinosa* Aiton)–white pine forest in northern Wisconsin. A ground layer survey was conducted in 1949, and the frequency of herbs and shrubs was recorded. For decades afterwards, deer hunting was prohibited on the property. The site was resurveyed in 1999, using the same methods and the same sampling intensity as for the original survey. Species losses between the two time periods were again dramatic (Rooney and Millam, 2000). There was a 48 per cent net species loss between the two time periods. Here, graminoids, ferns and club mosses were more likely to persist than all other taxonomic groups (d.f. = 1; $G = 8.41$; $P < 0.01$).

Data from Heart's Content and Piney Point indicate that deer impacts can affect many taxa. Between 48 and 81 per cent of the understorey species disappeared within a few decades. Graminoids, ferns and club mosses seemed less susceptible to deer than the other taxonomic groups were. A *G*-test for heterogeneity was used to perform a meta-analysis of species loss based on taxonomic grouping using data from Piney Point and both of the Heart's Content stands. Taxonomic grouping is a significant predictor of species loss, as indicated by the significance of *G*-total (d.f. = 3; *G* = 11.97; *P* < 0.01), and a lack of significance for *G*-heterogeneity (d.f. = 2; *G* = 4.11; *P* > 0.10). Plants classified in the graminoid, fern and club moss group are more likely to persist in heavily browsed communities than the group of plants containing all other taxa.

Indirect effects

Deer browsing can affect a species in two ways. Browsing can have direct effects on plants – the removal of photosynthetic tissue reduces a plant's capacity for growth and reproduction. As the proportion of reproductive individuals declines, the population becomes increasingly reliant on seed immigration to maintain population densities. Often, immigration is sufficiently low that plant population densities decline. However, deer browsing impacts are not confined to the plants that they feed on. Deer can give rise to indirect, or cascading effects, in forest ecosystems. These indirect effects are not well studied, but still merit discussion.

Deer browsing can reduce the size and population density of the species consumed. This can have numerous adverse effects on other taxa that rely on these same plant species. Generally, specialists should be more affected than generalists. Several types of host plant specialists can be considered. Monophagous insects (insects that feed on a single genus or species of plant) compete with deer for food. In the USA, population declines of the endangered Karner blue butterfly (*Lycaeides melissa samulis*: Lepidoptera) have been linked to deer browsing in New England (Miller *et al.*, 1992). Both deer and butterfly larvae feed on lupins (*Lupinus perennis*). Unlike white-tailed deer, the Karner blue is a feeding specialist and relies exclusively on lupins for food.

Deer browsing caused a decline in lupin densities, thereby adversely affecting Karner blue populations. However, monophagous herbivores are not the only species dependent on host plants. Some species of parasitic fungi are highly species-specific, often occurring on a single species (Greene, 1951). If specialist parasitoids or parasites rely on monophagous herbivores, they could be adversely affected by deer browsing as well.

When deer densities are sufficiently great, deer reduce vertical habitat complexity by reducing or eliminating understorey herbs, shrubs and saplings. This results in reduced nesting habitats for shrub-nesting birds and feeding habitats for insectivorous birds that feed in forest understoreys (deCalesta, 1994; McShea *et al.*, 1995; McShea and Rappole, 1997). Deer browsing can reduce the amount of forest floor vegetation cover, thereby making small mammals more visible and thus more susceptible to predation by avian predators.

Deer browsing can also degrade horizontal forest structure. I will highlight two examples: 'fern parks' and 'deer savannas'. Excessive deer browsing can create forests dominated by ferns in the understorey and no shrub or sapling layer – a condition termed a fern park. Such areas have an aesthetically pleasing appearance (hence the term 'park'), but they are biologically impoverished. In north-western Pennsylvania, overbrowsing by deer has eliminated most species from forest understoreys, although hay-scented fern (*Dennstaedtia punctilobula*) persists. Rooney and Dress (1997) report that plots containing high densities (>50 stems m⁻²) of hay-scented fern have lower plant species richness than plots with lower fern densities. Hay-scented fern also suppresses the growth of tree seedlings, and inhibits the reforestation of logged sites (Horsley and Marquis, 1983). In such areas, a few seedlings manage to survive and grow, but the nature of the community changes. It takes on a more open, savanna-like structure (Stromayer and Warren, 1997). Because deer drive this shift from forest to savanna, the resultant areas have been termed deer savannas.

Deer as a keystone herbivore

Because of their numerous direct and indirect effects on forest structure and composition, and

the magnitude of these effects, deer act as a keystone herbivore (McShea and Rappole, 1992; Waller and Alverson, 1997). The effects of deer are far-reaching and not always immediately obvious. In New York, for example, a large deer population reduced the size of white-footed mouse (*Peromyscus leucopus*) populations where they co-occurred. Both species fed on acorns (Ostfeld *et al.*, 1996), and deer probably reduced the extent of vegetation cover for the mice. White-footed mice are important predators of gypsy moths (*Lymantria dispar*: Lepidoptera), an invasive exotic species established in the north-eastern USA. By reducing mouse populations, deer effectively facilitate severe outbreaks of gypsy moths. Deer populations are also strongly associated with deer ticks (*Ixodes scapularis*: Acari) – the ticks that carry Lyme disease. Where deer are completely absent, tick populations decline as well (Duffy *et al.*, 1994). Lyme disease transmission to humans increases as deer populations increase, indicating a complex interaction among people, deer, ticks and the disease-causing bacteria.

Managing deer impacts

Because deer are a major threat to forest species composition, policies are needed to balance the needs of deer with the needs of the forest. There are three dominant competing policies for deer management in the USA, which are referred to here as natural regulation, wildlife management and ecosystem management.

The first of these is the natural regulation approach, which can best be summarized as ‘let nature take its course’. This approach is popular with many of the animal rights organizations and some environmental groups. It reflects an underlying anti-interventionist philosophy and, given the history of land management in the USA and Canada, that is understandable. Unfortunately, this approach is inconsistent with protecting species diversity. Natural regulation has been practised for the past five decades at Piney Point, which lost 48 per cent of its understorey plant species during this interval.

The second approach is the wildlife management approach, which aims to maintain a large deer herd. This approach is advocated by many

wildlife managers and hunters. It is based on maximum sustained yield theory. Maximum sustained yield aims to maintain the deer population at 50 per cent of carrying capacity, which ensures the maximum possible harvest for an infinite period of time. Unfortunately, maximum sustained yield theory does not take into account the environmental impacts associated with maintaining a population at 50 per cent of carrying capacity. Deer can begin reducing biological diversity when their densities are at less than 25 per cent of carrying capacity (deCalesta and Stout, 1997). Further, because wildlife managers rely on hunter effort to maintain deer populations at 50 per cent of carrying capacity, they have little direct management control. Often, wildlife managers fail to maintain deer populations at the optimum density, and deer impacts increase as the deer population grows. The wildlife management approach has been the land management policy at Heart’s Content for decades, and this resulted in massive species losses.

The final approach is the ecosystem management approach, which aims to integrate ecological theory and socio-political values to protect ecosystems. Ecosystem management permits commodity and amenity production, but only if biological diversity is not compromised (Grumbine, 1994). This approach is currently espoused by federal and state land management agencies, but it is practised mostly in private nature reserves. Under an ecosystem management approach, researchers identify deer densities that are compatible with maintaining biological diversity. Under this approach, both deer populations and indicator species are monitored on an ongoing basis (Waller and Alverson, 1997). Indicator species should be selected on the basis of their sensitivity to changes in deer densities. Lilies such as *Maianthemum canadense* and *Trillium grandiflorum* show negative responses to elevated deer densities. Indicator species need not show a negative response to deer browsing pressure, though. Species that increase in density with rising deer densities, such as graminoids, ferns, lycophytes or deer ticks, might also be used as indicators, particularly in areas where deer have been overabundant for decades and most browse-sensitive species have been eliminated (Waller and Alverson, 1997). Indicator species can be used to set management thresholds, such that a decline

(or increase) in an indicator by x per cent signals that the deer population must be lowered to avoid adverse impacts to biological diversity. Of the three management approaches presented, the ecosystem management-based approach seems the most promising for effectively integrating deer management and biological conservation.

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References

- Alverson, W.S., Waller, D.M. and Solheim, S.L. 1988 Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2, 348–358.
- Anderson, R.C. 1994 Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. *Ecol. Appl.* 4, 104–109.
- Augustine, D.J. and Frelich, L.E. 1998 Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conserv. Biol.* 12, 995–1004.
- Brown, J.S., Laundré, J.W. and Gurung, M. 1999 The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80, 385–399.
- Dahlberg, B.L. and Guettinger, R.C. 1956 *The White-tailed Deer in Wisconsin*. Game Management Division, Wisconsin Conservation Department, Madison, WI.
- deCalesta, D.S. 1994 Effects of white-tailed deer on songbirds within managed forests in Pennsylvania. *J. Wildl. Manage.* 58, 711–718.
- deCalesta, D.S. and Stout, S.L. 1997 Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildl. Soc. Bull.* 25, 252–258.
- Diefenbach, D.R., Palmer, W.L. and Shope, W.K. 1997 Attitudes of Pennsylvania sportsmen towards managing white-tailed deer to protect the ecological integrity of forests. *Wildl. Soc. Bull.* 25, 244–251.
- Duffy, D.C., Campbell, S.R., Clark, D., DiMotta, C. and Gurney, S. 1994 *Ixodes scapularis* (Acari: Ixodidae) deer tick mesoscale populations in natural areas: effects of deer, area, and location. *J. Med. Entomol.* 31, 152–158.
- Eberhardt, L.L. and Peterson, R.O. 1999 Predicting the wolf-prey equilibrium point. *Can. J. Zool.* 77, 494–498.
- Frelich, L.E. and Lorimer, C.G. 1985 Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. *Biol. Conserv.* 34, 99–120.
- Garrott, R.C., White, P.J. and White, C.A.V. 1993 Overabundance: an issue for conservation biologists? *Conserv. Biol.* 7, 946–949.
- Greene, H.C. 1951 *Host Index of Parasitic Fungi Collected on Plants in Wisconsin, 1880–1950*. Edward Bros., Ann Arbor, MI.
- Grumbine, R.E. 1994 What is ecosystem management? *Conserv. Biol.* 8, 27–38.
- Horsley, S.B. and Marquis, D.A. 1983 Interference by weeds and deer with Allegheny hardwood production. *Can. J. For. Res.* 13, 61–69.
- Hough, A.F. 1965 A twenty-year record of understory vegetational change in a virgin Pennsylvania forest. *Ecology* 46, 370–373.
- Leopold, A. 1943 Deer irruptions. *Wisconsin Conserv. Bull.* 8 (8), 2–11.
- Lewis, M.A. and Murray, J.D. 1993 Modelling territoriality and wolf-deer interactions. *Nature* 366, 738–740.
- Lutz, H.J. 1930 The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. *Ecology* 11, 1–29.
- Marquis, D.A. 1975 *The Allegheny Hardwood Forests of Pennsylvania*. US Forest Service General Technical Report NE-15, Upper Darby, PA.
- McArthur, E.D., Blauer, A.C. and Sanderson, S.C. 1988 Mule deer-induced mortality of mountain big sagebrush. *J. Range Manage.* 41, 114–117.
- McCabe, T.R. and McCabe, R.E. 1997 Recounting whitetails past. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood and J.H. Rappole (eds). Smithsonian Press, Washington, DC, pp. 11–26.
- McCaffery, K.R. 1976 Deer trail counts as an index to populations and habitat use. *J. Wildl. Manage.* 40, 308–316.
- McCullough, D.R., Jennings, K.W., Gates, N.B., Elliott, B.G. and DiDonato, J.E. 1997 Overabundant deer populations in California. *Wildl. Soc. Bull.* 25, 478–483.
- McShea, W.J. and Rappole, J.H. 1992 White-tailed deer as keystone species within forested habitats in Virginia. *Virginia J. Sci.* 43, 177–186.
- McShea, W.J. and Rappole, J.H. 1997 Herbivores and the ecology of forest understory birds. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood and J.H. Rappole (eds). Smithsonian Press, Washington, DC, pp. 298–309.
- McShea, W.J., McDonald M.V., Morton, E.S., Rose, M.

- and Rappole, J.H. 1995 Long-term trends in habitat selection by Kentucky warblers. *Auk* **112**, 375–381.
- Mech, L.D. and Nelson, M.E. 2000 Do wolves affect white-tailed buck harvest in northeastern Minnesota? *J. Wildl. Manage.* **64**, 129–136.
- Miller, S.G., Bratton, S.P. and Hadidian, J. 1992 Impacts of white-tailed deer on endangered plants. *Nat. Areas J.* **12**, 67–74.
- Mladenoff, D.J. and Stearns, F. 1993 Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: a re-examination and model simulation. *Conserv. Biol.* **7**, 889–900.
- Ostfeld, R.S., Jones, C.G. and Wolff, J.O. 1996 Of mice and mast. *BioScience* **46**, 323–330.
- Rooney, T.P. 1997 Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. *J. Torrey Bot. Soc.* **124**, 280–285.
- Rooney, T.P. 2000 *Influence of light, soil fertility, and deer browsing on the spatial structure, relative growth rates, and population demography of Trillium grandiflorum*. Ph.D. dissertation, University of Wisconsin, Madison.
- Rooney, T.P. and Dress, W.J. 1997 Species loss over sixty-six years in the ground layer vegetation of Heart's Content, an old-growth forest in Pennsylvania USA. *Nat. Areas J.* **17**, 297–305.
- Rooney, T. and Millam, K. 2000 *White-tailed Deer Impact Assessment for the Dairymen's Club*. Department of Botany, University of Wisconsin–Madison. Unpublished report.
- Rooney, T.P., McCormick, R.J., Solheim, S.L. and Waller, D.M. 2000 Regional variation in recruitment of hemlock seedlings and saplings in the upper Great Lakes, USA. *Ecol. Appl.* **10**, 1119–1132.
- Russell, F.L., Zippin, D.B. and Fowler, N.L. 2001 Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations, and communities: a review. *Am. Midl. Nat.* **146**, 1–26.
- Schorger, A.W. 1953 The white-tailed deer in Wisconsin. *Trans. Wis. Acad. Sci. Arts Lett.* **42**, 197–247.
- Shimoda, K., Kimura, K., Kanzaki, M. and Yoda, K. 1994 The regeneration of pioneer tree species under browsing pressure in an evergreen oak forest. *Ecol. Res.* **9**, 85–92.
- Sinclair, A.R.E. 1997 Carrying capacity and the overabundance of deer: a framework for management. In *The Science of Overabundance: Deer Ecology and Population Management*. W.J. McShea, H.B. Underwood and J.H. Rappole (eds). Smithsonian Press, Washington DC, pp. 380–394.
- Singer, F.J. and Renkin, R.A. 1995 Effects of browsing by native ungulates on the shrubs in big sagebrush communities in Yellowstone National Park. *Great Basin Nat.* **55**, 201–212.
- Stewart, G.H. and Burrows, L.E. 1989 The impact of white-tailed deer *Odocoileus virginianus* on regeneration in the coastal forests of Stewart Island, New Zealand. *Biol. Conserv.* **49**, 275–293.
- Stromayer, K.A.K. and Warren, R.J. 1997 Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildl. Soc. Bull.* **25**, 227–234.
- Sullivan, T.P., Nordstrom, L.O. and Sullivan, D.S. 1985 Use of predator odors as repellents to reduce feeding damage by herbivores: 2. Black-tailed deer (*Odocoileus hemionus columbianus*). *J. Chem. Ecol.* **11**, 921–936.
- Waller, D.M. and Alverson, W.S. 1997 The white-tailed deer: a keystone herbivore. *Wildl. Soc. Bull.* **25**, 217–226.
- Wilson, J. 1999 *The Earth Shall Weep: a History of Native America*. Atlantic Monthly Press, New York.