

Overabundant White-tailed Deer and the Alteration of Forested Communities

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INTRODUCTION

Although exotic, invasive organisms have received a great deal of attention recently in the press and with conservation biologists, the negative impacts of overabundant native species are often overlooked. Many native generalists have flourished in the ever changing human dominated landscape, including white-tailed deer (*Odocoileus virginianus*) (Garrott et al. 1993). Prior to European settlement of North America, deer provided indigenous people with essentials for daily living like food and clothing. At reasonable densities, they also provide ecological benefits in ecosystems including providing a food source for predators and scavengers and low-level browsing which benefits plant diversity and seed dispersal (Drake et al. 2002). Current populations of white-tailed deer in North America far exceed the biological carrying capacity of the land, and natural communities are being extensively altered. Although other ungulates in North America occasionally become overabundant and severely impact the environments they inhabit, white-tailed deer achieve the highest densities. Therefore most research has centered on this species. What follows is a review of the literature that illustrates the

various direct and indirect effects white-tailed deer have on the alteration of forested plant communities and the associated faunal populations.

HISTORICAL INFORMATION

While population densities of white-tailed deer prior to European settlement are uncertain, it is generally accepted that they were much lower than current populations. Three distinct historical stages with regards to white-tailed deer populations can be delineated. The first stage, pre-European settlement prior to 1700, can be characterized by low deer densities. Deer populations were regulated by cyclical harsh winters (every 10-20 years) which resulted in elevated mortality. Predators inhibited deer populations from increasing significantly following severe winters. These predators included carnivores like wolves and mountain lions and the several million indigenous people that depended on deer for sustenance (Rooney 2001). These predators were only able to regulate white-tailed deer numbers at the low densities that occurred during this era (Eberhardt and Peterson, 1999). Finally, population growth was hampered by the depleted food resources made available by the composition and structure of the dense mature forests (Leopold, 1943; McCaffery 1976).

The second stage, which was triggered by the settlement of North America by Europeans (1700-1900), can be characterized by the vast land use changes that occurred across the landscape. Large-scale forest clearing by the logging industry and for agricultural purposes led to major habitat alteration. Less productive ancient forests were converted to early successional habitats and young forests. This conversion provided a

considerable increase in forage for deer which artificially elevated the carrying capacity of the land and allowed for range expansion by white-tailed deer. During this time, the predators that utilized deer as part of their diet were also rapidly declining due to wholesale eradication efforts begun because humans perceived these predators as threats to themselves and their domestic livestock. Deer populations swelled for a few decades but eventually ceased and severely regressed during this period because of overexploitation due to the demands of market hunting. Hunting not only led to declines that bordered on extirpation, but also led to a decrease in the overall range of white-tailed deer in North America.

Americans began to become alarmed at the loss of white-tailed deer and conservation measures such as the Lacey Act of 1900 were used to halt market hunting (McCabe and McCabe, 1984). These measures, along with game regulations limiting harvest numbers to allow harvest of only males and restricting hunting seasons to only a few months of the year, allowed deer populations to rebound. Many states translocated deer from private reserves and other states to restock areas devoid of deer, which further enhanced population expansion (NJ Division of Fish, Game, and Wildlife 1999). Another factor that allowed populations to expand was the diminished predator populations that formerly regulated deer populations. These conditions led to the third and current stage where deer densities are at critically high levels. Densities of deer (Alverson et al., 1988) have continually increased across much of their range and today estimates can reach as high as 80 deer per km² (Drake et al 2005). The negative impacts of such high deer densities on humans and ecological services are well known among wildlife biologists and the next section reviews these effects in detail.

DIRECT EFFECTS ON FORESTED COMMUNITIES

The majority of research on the direct effects of white-tailed deer focuses on herbivory. Deer can have profound effects on preferred woody and herbaceous browse species. The following discussion deals with each vegetation type independently because the overall effects to the forest are quite different. There are four distinct vertical layers above the forest floor in Northeastern North American forests that are widely recognized which include the canopy, subcanopy, shrub layer, and herbaceous layer. The overbrowsing of woody plant species can lead to the loss of the vertical structure and two layers of the forest. Deer browse of woody vegetation alters the subcanopy and the shrub layer which are made up of small understory trees, young recruits for future canopy openings, and shrubs. The overbrowsing of the herbaceous level affects one level and can virtually eradicate an entire plant during one browsing episode. Another direct effect applied by deer on a forest is conveyed through endozoochory, which is seed dispersal by an animal often in its digestive tract. Deposition of propagules, sometimes over fairly substantial distances and from diverse habitats, often fill the voids that remain following the overbrowsed native plant communities mentioned above. When these propagules are produced by exotic invasive plants, the forest herb layer and shrub layer can shift to being dominated by nonnative plants.

Woody Plant Regeneration

Several studies reveal that regeneration of certain tree species is inhibited where deer densities are elevated above the densities that occurred prior to European settlement of North America which is estimated to have been 3.1-4.2 deer/km² (McCabe and McCabe 1984). The effect of deer herbivory on woody plant regeneration differs temporally and spatially depending on the species of tree affected. For example, two evergreens, eastern hemlock (*Tsuga canadensis*) and northern white-cedar (*Thuja occidentalis*), are important winter food of white-tailed deer. Waller and colleagues (1996) conducted an extensive regeneration study of 142 hemlock sites and 77 cedar sites around the Great Lakes region during 1990-91. Their data revealed that regeneration of seedlings greater than 30 cm for both species declined as browsing pressure increased. Where browse was most severe regeneration failure was absolute (Waller et al. 1996). Deciduous tree species are targeted for browse by white-tailed deer during the growing season because the trees are flush with tender leaves. In a similar example, Rooney and Waller (2003) investigated regeneration with browsing pressure for red oak (*Quercus rubra*) and yellow birch (*Betula alleghaniensis*) with deer densities at 10/ km². This study revealed that regeneration of red oak is severely restricted by deer and seedling densities sharply decline with increasing pressure from browsing. The effect of white-tailed deer browsing on the yellow birch, however, was less clear.

When deer are introduced to formerly deer-free environments, the ecological consequences can be catastrophic. For example, white-tailed deer were introduced to Anticosti Island, located in the Gulf of St. Lawrence, Quebec, over 100 years ago and became numerous there by 1930. Prior to deer introduction, the island was dominated by

balsam fir (*Abies balsamea*), a typical boreal forest component. Balsam fir cover prior to 1930 was approximately 40% of the island. After decades of heavy browsing pressure from an artificially elevated deer population (16 deer per km²), the cover of fir was decreased by 50% and was being replaced by white spruce (*Picea glauca*). The future of the remaining stands of balsam fir on the island is certainly in question. The vast majority of the remaining fir trees are 90-100 years old and are thus near the end of their expected life span. Also, the regeneration tactic employed by balsam fir is to release scores of seeds that result in a copious seedling bank of this highly shade tolerant species. The older fir stands will eventually succumb to disease or old-age and the herbivory of seedlings by the introduced and abundant deer will prohibit establishment of new stands (Potvin et. al., 2003).

Herbaceous Plant Species

Trees are not the only plants in the forest community that are impacted by ungulate herbivory. The understory forbs are an important component of a functioning forest and encompass most of the plant diversity found in boreal and temperate forests. The understory herbs in particular are quite susceptible to browsing by white-tailed deer because they never grow above the browse level and thus never escape browsing pressure. For example, Augustine and Frelich (1998) conducted exclusion studies to determine the effect of high deer densities on *Trillium spp.* in the Big Woods of southeastern Minnesota. Herbivory on individual plants can be ruinous since one nibble can defoliate the plant and remove all reproductive parts of the plant. As no regrowth will occur in that season and they will not produce offspring clonally, that single bite will effectively stop the plant from reproducing. In the control forests where deer densities

were classified as high ($37/ \text{km}^2$), herbivory removed greater than 50% of reproductive plants from the overall population in consecutive years and reduced overall individual plant mass. The deer will most often select the plants in flower to graze on suggesting that elevated resident deer densities are thwarting many *Trillium* populations from recuperating. The enclosure portion of the study revealed fairly substantial growth response following only two growing seasons of release from deer herbivory. Also, the plants inside the enclosure flowered at a rate 19 times greater than those outside of the enclosure which in turn would allow for pollination and setting seeds for future generations. This process can be eliminated by white-tailed deer browse, which could lead to the eventual decimation of populations and recruitment.

Populations of uncommon herbaceous plants can be decimated by overabundant deer browsing. For example, in a study conducted by Fletcher et al. (2001), two of five perennial wildflowers, under persistent excessive herbivory by white-tailed deer ($35/ \text{km}^2$), were far less abundant in the areas outside of 9-year old deer enclosures than they were inside. Both species were in the *Liliaceae* family; bellwort, (*Uvularia* spp.) and false Solomon's seal, (*Smilacina* spp.) Miller and colleagues (1992) surveyed nearly 100 threatened and endangered vascular plants that are eaten by deer and those in the *Liliaceae* were among the most dominant (Miller et al. 1992). Four of the five tested perennials had suppressed growth outside of the enclosure and all of the plants had higher reproductive rates when protected from the excessive browsing by elevated densities of deer. One final example of how long-term browsing pressure can directly affect single plant species is from a study completed in New Jersey. Jack-in-the-pulpit (*Arisaema triphyllum*) was shown to be particularly susceptible to repeated herbivory from an

overabundant deer population with densities that ranged from 60-76/ km². White-tailed deer were shown to utilize this perennial at a substantial rate (27.2%) over one season. Continual browsing indirectly altered the sex ratios and halted reproduction of this sequential hermaphrodite (Ruhren and Handel 2000).

Seed Dispersal through Endozoochory

Although many facets of the white-tailed deer ecology and their role as a keystone herbivore have been well studied, their ability to disperse seeds across the landscape has been somewhat overlooked until fairly recently. There exists a gap in the understanding of how plant species migrate over long distances and swiftly invade new areas (Myers et al. 2004). Research to date has only shown short distance dispersal of seeds in most species in eastern North America despite that observation that many plants spread into areas well-beyond these distances. Two studies were conducted to investigate if this information gap could be explained by endozoochory, the dispersal of diaspores by means of the digestive system of animals, and the implications of such a mechanism.

Myers et al. (2004) completed the first thorough study of seed dispersal by white-tailed deer through endozoochory. Their study included collecting deer feces, also known as pellets, in a study area in central New York that resembles much of the eastern North America in its species composition and spatial structure, being a blend of suburban development, agriculture, and forested stands. Myers et al. (2004) collected seeds from white-tailed deer pellets from a population density which was estimated at 20/km² and allowed them to germinate to ascertain which species could be dispersed by direct consumption of a diaspore. Over 70 different species germinated including both exotic

and native forbs, trees, and shrubs. The majority (38%) of these were exotic herbs derived from open areas including purple loosestrife (*Lythrum salicaria*), a major noxious weed of New York's wetlands. The seeds of purple loosestrife do not have any special features for dispersing and are thought to spread by water. The work of Myers et al. (2004) illustrates that this plant may instead rely on herbivores as dispersal agents. An earlier study by Velland et al., (2003), suggests that of all loosestrife seeds that are dispersed, 95% are deposited at more than 100 m and up to 30% would be carried more than 1 km by deer. This demonstrates that white-tailed deer herbivory could carry loosestrife seeds upstream and to other wetlands and thus provide a major vector for the spread of this invasive species. There were other notable invasive plant species that germinated in the Velland et al. (2003) experiment including multiflora rose (*Rosa multiflora*), exotic honeysuckles (*Lonicera* spp.), and common buckthorn (*Rhamnus cathartica*). Although exotic species dominated the samples, Velland et al. (2003) also demonstrated that a native ant-dispersed forest forb, *Trillium grandiflorum*, could rapidly establish and be dispersed far beyond its expected rate and range by deer.

The other study that was conducted to better understand the efficacy of the notion that white-tailed deer have the ability to broadcast seeds by the mechanism of endozoochory was conducted in suburban southern Connecticut. Williams and Ward (2006) hypothesized that on the suburban/woodland interface, overabundant deer populations were responsible for some of the plant invasions by exotic species in the neighboring natural areas. Deer herds in suburban areas not only benefit from the protective nature of housing developments (no hunting zones) but gain added forage from landscape and ornamental plantings. The study area was a fairly large, 2800 ha, and

included a natural area owned by a water authority adjacent to a medium-density housing development. Deer densities were buoyed in the study area by the ban on hunting since the 1920s and were estimated at 23 deer per km² during the time of this research. Williams and Ward (2006) followed the same procedure of Meyers and colleagues; pellets were collected, vernalized, covered with a growing medium, and allowed to germinate. Pellet groups were maintained and watered until the time when any germinating plant could be conclusively identified. Of the 57 different plant species identified, 56% (32) were exotic and the greatest exotic plant diversity in collected pellet groups was recovered at an average of 500m from the source, which was assumed to be the landscape/ornamental plants found in the adjacent human development. At the existing deer density, these authors calculated the herd could potentially disperse as many as 586-1,040 viable exotic seeds/day/ km². Their research illustrates the capability white-tailed deer have of dispersing a great deal of seeds particularly from potentially invasive plants into natural areas. This broad scale dispersal could eventually lead to an altered plant community in the natural area and ultimately an entirely new forest community.

INDIRECT EFFECTS ON FORESTED COMMUNITIES

As was detailed above, herbivory by white-tailed deer at elevated densities can directly affect individual plant species and, to a lesser degree, communities. The indirect effects imposed may better illustrate the potential that high deer densities assert on altering forested communities. These effects develop when the impact of a single species, known as the donor, is conveyed via a second species, the transmitter, to a third species, the

receiver (Morin 1999). This can lead to cascading trophic effects on ecosystems and have deleterious consequences, ultimately terminating in an altered stable state. This is a situation where individual species that were part of the former community are restricted from reestablishing. The following section details the potential indirect effects that white-tailed deer overabundance and herbivory can have on different elements of the forested community. Interspecific competition between plants can be transformed sometimes allowing for unpalatable subordinate species to dominate, shifting the successional stage sometimes to an altered stable state. Deer herbivory can also indirectly affect the animals that compete for the same resource including vegetation, mast, or fruits. The fauna that is influenced can range from an invertebrate such as a butterfly to a large mammal like a bear. The avian community associated with forests is indirectly affected by overbrowsing through loss of nesting sites and elevated predation from the lack of cover and refugia.

Altered Plant Community Competition

White-tailed deer can act as a donor species for these indirect interactions through selective foraging, eventually altering plant community structure. One mechanism for such changes is an alteration of interspecific competitive relationships between the plant species in a community. Selective foraging can either decrease or increase forest cover and diversity, which ultimately depends on whether or not the choice of browse species by the herbivore is a dominant species in the forest community and the density of the herbivore. Schütz et al., 2003 showed that red deer (*Cervus elaphus*), an ungulate in the same family (Cervidae) as white-tailed deer, selectively foraged on the dominant, taller plants in an alpine meadow community. This selective deer browsing from a population

density of 39.7/km² led to increased overall species richness in the meadow by increasing the abundance and variety of the smaller, understory plants (Schütz et al., 2003). This effect, however, occurred at normal ungulate densities.

When deer densities are much higher, the indirect effects of deer browsing can lead to reduced diversity. For example, several studies have shown a reduction in diversity within forests of the Alleghany Plateau in northwest Pennsylvania due to heavy deer herbivory. Population density estimates for the sites used for study were estimated at 22.6/km². When a forest opening is created through a weather-related event or human disturbance in a typical forest of that region, it is often first colonized by Allegheny blackberry (*Rubus allegheniensis*). The thorny shrub protects tree seedlings from herbivores thereby encouraging an increase in tree seedling survival. Unfortunately, the white-tailed deer find the blackberry shrub highly appetizing, reducing its abundance and the ability to protect the tree seedlings from herbivores. By selecting these shrubs to browse upon, the deer indirectly augment the competitive edge of hay-scented fern (*Dennstaedia punctilobula*), which the deer find unpalatable. As the fern increases in abundance and begins to dominate the forest floor, forest herbs and tree seedlings are excluded and will probably never become well-established again (Horsely and Marquis 1983). Another study showed that plots with abundant densities of hay-scented fern have much lower species richness than in other plots with lower fern densities (Rooney and Dress 1997). Other plant species are given a competitive advantage because of the selectivity of feeding by deer. As with the hay-scented fern example, this will lead to a shift in the relative abundance of species that comprise a forest community. Those plants that have the ability to avoid browse will become more abundant and those that cannot

will decrease. Many ferns, probably because of the chemical composition in the leaves and various graminoids, due to tough silica in their leaves and their basal meristems, are the winners in this scenario.

Faunal Community

The indirect effects of deer herbivory are not exclusive to the plant community of a forested ecosystem. Many insects, birds and mammals can be impacted by the herbivory of overabundant white-tailed deer (Rooney and Waller 2003). Deer can have a negative impact on these organisms by utilizing the same resources or by altering the structural heterogeneity of the habitat.

For example, competition between invertebrate herbivores and deer ensues when they utilize the same plant species for food. Specialist invertebrates would inherently be affected at a more severe level than a generalist who has many other food options. This is the case, for if the plant species being competed for is completely browsed by deer, it would be unavailable for the specialist who may exclusively feed on the plant.

Sometimes these monophagous species are endangered by other forces, and thus further drops in their numbers could lead to extirpation or even extinction. One such species, the federally endangered Karner blue butterfly (*Lycaeides melissa samulis*), utilizes wild blue lupine (*Lupinus perennis*) exclusively, which is itself an endangered plant in New England. Overbrowsing of lupine by white-tailed deer has led to the loss of lupine with cascading effects on the Karner blue (Miller et al., 1992). Deer can also indirectly affect invertebrates through selective browsing and habitat alteration. As was mentioned

earlier, deer can shift the abundance of browse tolerant species, creating a situation where a subordinate species now dominates the understory (i.e. graminoids and ferns). Since these plant guilds are subject to little invertebrate herbivory and offer no rewards to pollinating insects, their dominance may result in a decline in the species richness of invertebrates in the forest they reign over (Stewart 2001).

Often the cascade continues, from the loss of vegetation, to a decrease in invertebrate abundance and finally to a reduction in insectivorous avian species and other birds that utilize the understory for nesting and/or foraging. Allombert et al. (2005) conducted a field study in the Haida Gwaii archipelago in British Columbia, Canada that uncovered just such a cascading effect. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), a cogener of the white-tailed deer, were introduced on certain islands of the archipelago in 1878 and have colonized many others on their own since. Six islands were chosen for Allombert and colleagues' research: two with no deer populations, two with less than a 20 year deer presence, and two that were subjected to heavy browse and inhabited for over 50 years. When compared to the deer-free islands, those islands with a 50+ year browsing history and deer densities estimated to range between 21-36/km² showed that alpha-diversity decreased as browsing history increased. One substantial finding was a 70% overall reduction in the density of avian breeding pairs compared to the islands with no deer. When only considering bird species whose life histories are closely associated with understory vegetation, the reduction in breeding pairs was 92%, which corresponds to an 83% reduction in understory vegetation and an 87.5% decline of invertebrate abundance that is associated with this same vegetation.

Illustrating these results are two species of birds, the rufous hummingbird (*Selaphorous rufus*) that primarily forages in the understory and the fox sparrow (*Passarella iliaca*) that nests exclusively in understory vegetation. Both species were commonly encountered by Allombert and colleagues on deer-free islands and on the islands with less than 20-year exposure to introduced deer. They were completely absent from those islands with 50+ year of inhabitation of the introduced ungulate, however.

MacShea and Rappole (2000) suggested that an appropriate method to approximate the impact potential of overabundant deer on songbird populations is through qualitative analysis of understory vegetation cover and structural heterogeneity. Many other studies have attained the same results and have attributed the loss of birds to diminished nesting habitats and foraging areas for avian species closely linked to understory vegetation to complete their life cycles (deCalesta 1994; McShea and Rappole 1997; Hino 2006.)

Predation increases with the loss of cover. When ground cover is low due to deer herbivory, avian predators become increasingly successful at hunting small mammals, and small mammals have an increased ability to find bird nests to prey upon. This increase in predation pressure can lead to a decrease in the population numbers of both species, and an overall decrease in diversity and increase in evenness (Flowerdew and Ellwood 2001).

McShea (2000) hypothesized that annual variation in acorn densities affected many species including weevils, birds, and several mammalian species. He further hypothesized that the strength of these relations was mediated by white-tailed deer. He

recorded production of acorns at 12 sites in Virginia for 12 years and measured the impact on understory vegetation and the abundance of small mammals. Populations of white-footed mice (*Peromyscus leucopus*), gray squirrel (*Sciurus carolinensis*), and eastern chipmunk (*Tamias striatus*) were notably associated with the annual variations in the size of the acorn crops. Half of the studies sites were deer-free (excluded by fencing) and at these sites, populations of *P. leucopus* and *T. striatus* were significantly greater following low mast years than at the control sites.

Ostfeld et al. (1996) conducted a similar study in New York, which revealed that an elevated white-tailed deer population effectively reduced the populations of *P. leucopus* where they coexisted by competing for a food resource (acorns) and reducing the vegetative protective cover for the mice. In addition, if white-footed mice populations are severely reduced through competition with deer, populations of the invasive gypsy moth (*Lymantria dispar*) can explode to outbreak status. White-footed mice prey upon the introduced invasive moth and play an important role in their population regulation (Ostfeld et al., 1996).

The most startling evidence of the potential indirect effects of white-tailed deer can have on other mammals comes again from Anacosti Island in Quebec. As was detailed earlier, the island historically had no resident deer until they were introduced in the late 1800s. By the 1930s the population exceeded 50,000 and alteration to the plant communities had already begun, including the loss of common shrubs that produce edible fruits (berries). Côté (2005) believes he has made the connection between the extirpation of black bears and the overabundant population of white-tailed deer (7.5-15.1/km²) on the island. Previous studies from western Canada revealed that black bears require a berry

abundance of at least 66/m² to maintain their current mass (Pelchat and Ruff 1986). Côté and his colleagues canvassed the island in search of the most historically common deciduous shrub species for two consecutive summers. What they found was a depauperate shrub component and a mere 0.28 berries/m². At these incredibly low berry concentrations the bears would not be able to maintain weight let alone put on the additional mass necessary to enter hibernation for a few months. Black bears that inhabit the northern forests require a great deal of berries, currants, and other fruits during the end of the summer and growing season. They will in fact overindulge by eating as much as one-third of their body weight in fruits per day to attain the mass needed for a couple of months slumber (Welch et al., 1997). Côté suggests that because the overabundant deer population so thoroughly outcompeted the bears for this vital resource and virtually eliminated shrubs from the island, they are responsible for the indirect extirpation of these large carnivores.

OPTIONS FOR POPULATION CONTROL

Non-lethal alternatives

Trap and translocation is an option for population control that includes capturing deer in nets, box traps, corrals, or tranquilizer darting and moving them to a different site.

Although this method is an opportunity for population control, there are many reasons it is not truly a viable solution. Cromwell et al. (1999) showed that this technique is exceptionally taxing on the captured deer frequently resulting in mortality. A second factor is the elevated costs necessary to sustain a trap and translocation project. On one two-year project in suburban central New Jersey, the estimated cost was

\$1,385/translocated deer including initial expenditures (Aquila 2006). Estimates from other projects have ranged to as high as \$2,391/deer. These differences in cost derive from the varying techniques utilized and the distance required for relocation (Ishmael et al., 1995).

Another non-lethal option for managing deer populations is reproductive controls. There are currently three methods by which white-tailed deer reproduction can be suppressed. The most effective and permanent method is sterilization through gonadectomy in females and vasectomy in males. However this requires surgery performed on an immobilized deer, which is very time consuming and requires a trained veterinarian. This method requires no further treatment of the individual deer, but research on the effectiveness of the method for population control is sparse (Drake et al. 2002). A second method is contragestation which causes infertility with gestation. Drugs like prostaglandin and Gonadotropin-releasing hormone (GnRH) are remotely delivered to females, which terminates their pregnancies (DeNicola et al., 1997, Miller et al. 1998). There are certain negative aspects of this methodology that may arise because of public sensitivity issues regarding the use of what is essentially an abortion drug. Another disadvantage is the restricted time frame at which contragestation can be effective on pregnant does and the necessity to treat individuals yearly. The timing is such that if the contragestation agent is administered too prematurely the female may abort the fetus, resume estrous, and breed within the same season (Drake et al 2002). If the agent is delivered too late in the gestation cycle, the fetus appears more like a fawn and may be objectionable (Warren 2000). Additionally, viability as a population control

has not been shown and this method will only ever be feasible as a part of an integrated long term management plan (DeNicola et al. 2000).

Immunocontraception is the third and most widely studied reproductive control measure. This method utilizes the animal's own immune system, which blocks the reception of sperm by the unfertilized egg. The two chief immunocontraceptives being researched are (PZP) Porcine Zona Pellucida and the aforementioned GnRH (Miller et al., 1998). There are a few published field experiments where PZP was utilized as an immunocontraception and applied to free-ranging white-tailed deer populations. Research in Ohio, Connecticut, and in upstate New York determined that PZP immunocontraception was extremely time-consuming and expensive (Warren 2000). Costs associated with the projects ranged from \$802-1,100 per treated female (Warren 2000). Underwood and Verret (1998) studied the use of PZP for immunocontraception, and they revealed another disadvantage of this method: inability to control white-tailed deer at the population level. The authors found that there was no drop in the deer population following five years of treating females. Based on this result, Underwood (2005) states that fertility control utilizing immunocontraception that lowers abundance in a free-ranging deer herd is probably decades away (Underwood 2005).

Lethal Alternatives

Conventional hunting, sometimes referred to as sport hunting, is the oldest and most recognized effective method for white-tailed deer population control (McCullough 1979). Under the modern system, most hunting is regulated by the state agencies responsible for wildlife management. This method is constrained by the bag limits and hunting seasons

established by these agencies. Even with these constraints, regulated hunting is the most efficient and economical system for reducing deer abundance (Drake et al., 2002). The biologists within these state agencies consider it a principal management tool and can alter harvest results by controlling various regulation parameters. This management technique can be tailored to suit specific social desires and biological requirements by limiting/increasing the number of permits, altering the hunting season length and/or timing, and controlling the sex ratio and volume of the harvest.

Often there are mitigating circumstances that will not allow for the utilization of regulated hunting as an option. Where it is deemed necessary to control deer population outside of regulated hunting seasons, particularly if agricultural crop damage is occurring, other opportunities for hunting are available. Deer depredation permits or permit-to-shoot programs can be utilized throughout the United States (86% of states allow such programs). These programs allow landowners who are experiencing crop losses to obtain a permit to hunt deer during any part of the year. This method can be very effective at reducing white-tailed deer populations on a local scale but there is insufficient evidence to support the efficacy of the method to reduce deer numbers on a landscape scale.

The effectiveness of hunting could be maximized by incorporating it into an integrated deer management approach (Horton and Craven 1997). With ever increasing open space losses to development, particularly to housing, deer populations continue to increase as they can inhabit these communities. The presence of deer in housing developments requires special control measures if population control is deemed necessary. The New Jersey Department of Environmental Protection Division of Fish,

Game and Wildlife has fairly recently (1995) implemented a program to manage urban/suburban overabundant populations and is known as Community-Based Deer Management Permit (CBDMP) program. This program is designed to test and utilize alternative methods for population control other than traditional sport hunting, which is not feasible in these types of environments. Some of the CBDMP methods include controlled hunting, sharpshooting or shooting by an authorized agent, trap and euthanize, trap and transfer, and fertility control methods. Private landowners can not use a CBDMP. Only boroughs, townships, airports, or County Boards of Agriculture may apply for this program and must establish a Special Deer Management Area that can be a specific area or the entire township. The applicant must be able to demonstrate that there is an overabundant deer situation and that the deer are causing significant deer-vehicles accidents (DVAs), are causing severe property damage to landscape plantings and crops, or, in the case of airports, are introducing safety issues to airplanes landing or taking off.

An important part of the process is that all CMDMP Programs are open to public comment prior to initiation. This requirement often leads to intense and passionate philosophical debates between polarizing interest groups ranging from sport hunters to animal-rights activists. Despite this, there have been several CMDMP programs in New Jersey that have been successful at reducing the populations within these Special Deer Management Areas. Actual effects on reduction of DVAs and browse damage on crops and/or ornamental plantings have not yet been quantified, but should certainly be researched.

IMPLICATIONS FOR THE FUTURE AND WHAT KNOWLEDGE IS LACKING

White-tailed deer act as a keystone herbivore because of the copious effects they have on forest composition and structure (Waller and Alverson, 1997). When the number of deer surpass the biological carrying capacity of their ecosystems alteration of the forest community is inevitable. For numerous reasons, white-tailed deer populations in North America, particularly the northeastern portion of their range, have exploded. Unrelenting development, lack of natural predators, and increased forest edge that creates additional habitat, are but a few of the reasons for this nearly exponential growth. At the same time, the ecosystems of the world are going through a great upheaval in stability due to universal climatic change and from the homogenization of communities by invasive plants (Olden et al, 2004). Overabundant deer can play a key role in exacerbating these issues.

For example, it has been well documented that trees and forests are efficient at sequestering atmospheric carbon (Malhi et al. 2002). The ability of excessive deer populations to negatively effect regeneration, survival and growth of trees is well known. If forests continue to age and lose old trees without recruitment, the capacity to capture and sequester atmospheric carbon is drastically diminished.

Similarly, as was revealed in the endozoochory studies reviewed above, white-tailed deer are capable of spreading invasive plant propogules far from the point of origin and at alarming rates. As invasive plants take over ecosystems, natural diversity is lost, leading to a more homogenized community (Lockwood and McKinney 2001).

Finally, white-tailed deer, at current population sizes, are acting as ecosystem engineers. “Ecosystem engineers are species that create, modify, and maintain habitats by causing physical state changes in biotic and abiotic materials that, directly or indirectly, modulate the availability of resources to other species” (Jones 1997). White-tailed deer have demonstrated their ability to transform a forest plant community and shift it to an alternate stable state (Stromayer and Warren 1997). These hungry herds create “deer savannas” that are maintained by repeated selective browsing.

This review has detailed many studies that describe the negative ecological impacts of overabundant deer herbivory. However, many questions and gaps in understanding still exist despite the breadth of research on white-tailed deer ecology. Biological carrying capacity or threshold densities where significant impacts occur are still needed if managers are to design appropriate control strategies. Studies designed to manipulate deer densities across different forest types would be certainly beneficial in implementing management goals and understanding the densities at which native plant diversity is maintained or is necessary for recovery of degraded habitats. Also lacking is the knowledge of how deer at different grazing intensities affect community composition and structure across various forest associated taxa, thereby advancing the understanding of how they influence biodiversity. As with many ecological connections, the ecology of white-tailed deer, although well studied, is still quite challenging to grasp. At no fault of the species itself, *Odocoileus virginiana* has reached high densities and is utilizing available resources, often depleting them at the expense of other species. Much like the human population and the effects of thousands of years of “progress” white-tailed deer are degrading the land that is left to them, especially in the fragmented natural areas of

the developed northeastern United States. Without proper management, they will continue to negatively impact ecosystems, cause economic loss, disease spread, and loss of ecosystem services and biodiversity.

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