

HISTORY OF DEER POPULATION TRENDS AND FOREST CUTTING ON THE ALLEGHENY NATIONAL FOREST

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Abstract: The forests of the Allegheny Plateau section of northwestern Pennsylvania have been severely impacted for more than 70 years by selective browsing by white-tailed deer (*Odocoileus virginianus*). Historical and ecological interactions of deer and the forest ecosystem in this region from pre-settlement times to the present are presented based on data from the Allegheny National Forest area. The data suggest that deer impacts on forested ecosystems can be controlled through a combination of increased, sustained deer harvests and increased forage production through timber harvesting.

INTRODUCTION

As the second-growth forests on the Allegheny Plateau began to mature in the mid-1960's, foresters attempted to regenerate new stands by clearcutting, anticipating that species composition of the new stands would be similar to the second-growth forest that originated near the turn of the century. However, these harvest cuts resulted in a complete failure of woody species to regenerate or in understocked stands that lacked the hardwood species diversity of the second-growth forest.

Concern about the inability to obtain regeneration success led to the establishment of a regeneration research project conducted at the Northeastern Forest Experiment Station's Forestry Sciences Laboratory at Warren, Pennsylvania. Grisez and Peace (1973) showed that nearly half of all regeneration cuts in the 1960's failed to regenerate to woody species. The half that did regenerate successfully had well-established advance regeneration prior to cutting. Deer browsing was suspected as a primary cause of most regeneration failures. A series of deer exclosure studies was installed to test this hypothesis. Exclosures placed in recently failed clearcuts demonstrated that in 87 percent of the stands sampled, regeneration was satisfactory inside the fences but not outside (Marquis and Brenneman 1981). This finding supported the hypothesis that deer browsing was a direct factor in causing regeneration failures in the 1960's. But there were other indirect effects of deer browsing and other ecological factors that changed the entire dynamics of the regeneration process.

Four major components of the ecosystem had changed dramatically since the turn of the century, leading to the complex situation for regeneration that exists today. First, deer were nearly extinct in Pennsylvania at the turn of the century but at record levels in the 1960's (Horsley 1992). Second, species composition of the overstory and understory was different in second-growth forests than in the original forest. Much of the original forest contained overstories of large white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and chestnut (*Castanea dentata*), and small quantities of black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), oaks (*Quercus* spp.), and red maple (*Acer rubrum*) (Marquis 1975; Whitney 1990). The understories in the original forest contained many well-established advanced seedlings which were absent in the 1960's (Marquis 1973). The second-growth forest contained higher proportions of shade-intolerant species such as black cherry, white ash, and yellow-poplar (*Liriodendron tulipifera*) in the main crown canopy, with very shade-tolerant species such as American beech and sugar maple relegated to the lower canopy unless left as residual trees from the original forest (Marquis 1981). Species of intermediate tolerance such as red maple, basswood (*Tilia americana*), and cucumber (*Magnolia acuminata*) were in a third layer just below the main crown level.

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Third, the second-growth forest contained a species-altered and less diverse understory of shrubs and herbaceous plants because of decades of preferential browsing by an exceptionally large deer herd (Leopold 1943; Whitney 1984). Many of the shrub species that were abundant in the original forest, for example, greenbrier (*Smilax rotundifolia*), hobblebush (*Viburnum alnifolium*), wild raisin (*Viburnum cassinoides*), and other viburnums, were nearly lacking from the second-growth forest (Leopold 1943; Whitney 1984). Instead, the understory is dominated by species such as striped maple (*Acer pennsylvanicum*), root suckers of American beech, or by fern and grass. Fourth, seedbed conditions in the 1960's were different due to long periods without fire, years of heavy browsing, and a lack of dead and down course woody debris that had been present at the turn of the century (Mladenoff and Sterns 1993).

A look at long-term trends in deer densities and forage production suggests a strong relationship between the two (Whitney 1990; Marquis 1975). In this paper I have made the assumption that timber harvest can be used as a surrogate for forage production. This assumption is made with the knowledge that not all silvicultural treatments create the same quantity and quality of forage, and that forage production can vary within treatments. With these assumptions in mind, I present an historical overview of events from pre-settlement times to the present that shows how deer populations and forage availability have combined to create a deer impact on all forest communities on the Allegheny Plateau in Northwestern Pennsylvania.

Actual data for estimates of the deer population taken in Warren, Forest, McKean, and Elk Counties, that encompass the Allegheny National Forest, are presented. These data were used rather than statewide averages because actual timber harvesting figures are available for the Allegheny since 1923. Comparing deer population and forage production levels reveal some important relationships that are not apparent when looking at the two separately.

The 4-county area encompassing the Allegheny National Forest is a part of the larger Allegheny Plateau region. Elevations on the Plateau range from about 1,500 to 2,500 feet (Hough 1959). The climate is generally cool and moist with precipitation well distributed throughout the summer months (Whitney 1990). Nearly all of the soils in the area are podzols derived from acid sandstone and shale. The forests of the area are primarily second-growth cherry-maple mixed hardwood forests and are listed as SAF type 28 (Marquis 1975).

Human influence on ecological processes in the Allegheny region has been divided into 6 distinct periods². I add a 7th period to reflect changes in forest management from 1980 to the present. Each period is discussed separately and summarized to show trends.

ECOLOGICAL PERIODS INFLUENCED BY HUMAN ACTIVITY

Pre-settlement Period: Pre-1800

Native Americans occupied northwestern Pennsylvania for many centuries prior to the arrival of the European settlers. The Allegheny River, Clarion River, and Conewango Creek served as major travelways and the rich river valleys provided sites for major Indian villages.

Vegetation conditions. Pre-settlement forests were a mosaic of forest stands in various stages of successional development. The largest share of the forest was mature or overmature hemlock-beech and beech-sugar maple (Illick 1923; Marquis 1975). There were scattered meadows and rough mountaintops void of forest cover but also vast stretches of unbroken timber (Whitney 1990). Areas of early successional ecosystems were created by natural disturbances such as hurricanes and tornadoes. A large area of blowdown was reported in what is now Alleghany State Park, just north of the present Allegheny National Forest, by a surveyor for the Holland Land Company in June 1805 (Gordon 1940). Understory conditions probably were variable due to human activity and periodic windstorms.

²Bennett, A. 1969. History of Allegheny Plateau Forest. Unpublished talk at Regeneration Conference on Allegheny Plateau Hardwoods, Bradford, PA.

Native Americans periodically burned forest understories near their villages to increase berry production and enhance hunting opportunities (Marquis 1973; McCabe and McCabe 1984). Shrub species such as the viburnums likely were present during pre-settlement times as they were noted in early surveys of the area in the late 1700's.

Forage availability. The amount and quality of forage used by white-tailed deer were highly variable, spatially and temporally, due to periodicity of windstorms and the abandonment of Indian villages as resources were depleted (Marquis 1973). Agricultural crops grown in or near these villages provided quality forage as did early successional ecosystems, for example, areas burned by Native Americans and those created by tornadoes.

Predation. Predators of deer included wolves (*Canis lupus*), mountain lions (*Felis concolor*), bobcats (*Felis rufus*), and bears (*Ursus americanus*). It is believed that these predators accounted for half of the annual deer mortality (McCabe and McCabe 1984). The remaining mortality was caused by hunting by Native Americans, disease, starvation and weather events.

Weather. Due to cyclic patterns of weather and the length of the pre-settlement period, the entire range of weather conditions was experienced.

Deer densities. Estimates cited from the literature of deer densities during pre-settlement times are for the entire range of white-tailed deer, which extends beyond northwestern Pennsylvania. Findings from numerous archeological middens show that deer were an important source of protein in the diets of Native Americans (McCabe and McCabe 1984). Using population models developed by Severinghaus and Maguire, estimates of deer densities were made using sex ratios and age-class structures of the population harvested by Native Americans (Severinghaus and Maguire 1955). These estimates in the range of 20 deer/square mile for the region, agrees with those of Seton based on suitable habitat within the range of eastern white-tailed deer (Seton 1909).

It is likely that deer populations in the 4-county area of this report differed from place to place and year to year. Populations likely were higher near Native American villages where agricultural crops were available and firewood cuttings and burned areas produced browse. Also, populations probably were higher in and around areas of early successional forest created by periodic weather events. Most of the four-county area was inaccessible and heavily forested resulting in low deer browse production during this period so the best estimate of average deer density is 10 to 15 per square mile.

Pioneer Period: 1800-1860

The first record of Europeans in northwestern Pennsylvania was an English trading post established in 1750 at Buckaloons along the Allegheny River near Warren, Pennsylvania³. The first permanent European settlers traveled from Susquehanna County to Warren County in 1795. Settlement of the area progressed slowly at first but then increased rapidly in the latter part of the 19th century. Warren County, for example, had a population of only 26 in 1810 (Marquis 1973). The last half of this period saw rapid growth in human populations.

Vegetation conditions. Overall, vegetation changed little from pre-settlement times. The impact of humans on vegetation was restricted to the major drainages as most of the Plateau remained much as it was for centuries prior to settlement. A slight increase in agricultural land and timber harvesting resulted in modest increases in early successional vegetation along the drainages.

Forage availability. During the first 20 years of this period, little timber cutting took place. The few European settlers there were cut small quantities of wood for cabins, barns, and firewood, and cleared land for gardens. Forage availability during this time likely was similar to that of pre-settlement times.

³Stotz, L. 1973. A country supposed uninhabitable, Senecas and Settlers on the Allegheny National Forest. In: Allegheny Nat. For. Spec. 50th Anniversary Pub. Article #3. Schuler, N. (ed.)

After 1820, water-powered mills were common and there was some commercial timber cutting along the major drainages where logs could be floated easily to the mill. During the last half of this period, forage production increased as timber cutting accelerated to meet the demands of an expanding population.

Predation. There was a gradual, continuing decline of major deer predators during this period, culminating in the near extirpation of some natural species toward the latter portion. Predators such as the gray wolf, wolverine, mountain lion, and lynx were not extirpated, but their numbers declined steadily as human populations increased (Merritt 1987). Deer populations also were reduced by Native Americans and European settlers.

Weather. The only major documented event was a large tornado that occurred in what is now the Tionesta Scenic and Research Natural Area in 1808 (Bjorkbom and Larson 1977). Winters likely were much as they are today.

Deer Density. During the first 20 years of this period, deer densities likely were similar to those of pre-settlement times as human populations increased little and timber harvesting remained about the same and were restricted to lands along the major drainages. As the period progressed, human populations and timber harvesting increased while natural predators decreased, resulting in a probable increase in deer populations. Speculative estimates of deer densities for this period are 10 to 15 per square mile early in the period and 25 to 35 per square mile toward the end of the period.

Steampower Period: 1860-1890

The 1860's saw the beginning of industrialization of the Allegheny Plateau. Steam replaced water as the major source of power. Steam-powered sawmills, railroads, log loaders, and other logging equipment became common during this period (Marquis 1975). This equipment was capable of processing huge quantities of timber. Tanneries were common during this time and used large quantities of hemlock bark for tannin.

Vegetation conditions. Major changes in vegetation began to take place. White pine was the major species being harvested by 1875, and was almost gone by 1892. Pine and hemlock were replaced with shade-intolerant, early successional hardwood species. Once the pine was depleted, hemlock became the major species harvested, for its bark for the tanning industry and for sawlogs cut into construction lumber. Most of the pine and hemlock harvests was small patchy cuts that were heaviest along the major drainages. Most of the forest remained intact.

Forage availability. Forage production resulting from the harvest cuts along the major drainages increased greatly. Encroachment by white settlers increased with better access to the region afforded by railroads, and more land was cleared for agriculture. But forage on the plateau top remained essentially unchanged.

Predation. By the end of this period, all of the major natural predators were extirpated. Wolverines, mountain lions, and lynx were gone by the late 1800's (Merritt 1987), and the last gray wolf was reported in 1892 in Clearfield County, southeast of the Allegheny region (Merritt 1987). Humans continued to play a large role in the annual mortality as there were no laws to protect deer..

Weather. There are no detailed records for this period. A large tornado was recorded in 1870 in the Tionesta Scenic and Research Natural Area (Bjorkbom and Larson 1977).

Deer Density. Although forage was increasing, especially near the major drainages, so too was human harvest of the deer herd as year-round hunting prevented the herd from becoming excessive. Knowing what we know about forage availability and the effects of hunting, I estimate the deer population was 20 to 25 deer/square mile during this period.

Chemical Wood Clearcutting Period: 1890-1930

Until this time, steam locomotives were used primarily for transportation. During this period specially designed narrow gauge locomotives were developed to traverse the most rugged terrain, and were located in nearly every

drainage making nearly all of the Plateau accessible. Chemical wood plants utilized wood of all species, quality, and size to produce charcoal, acetic acid, wood alcohol, and other distillation products (Marquis 1975). The combination of markets utilizing trees of all species and quality, and the heightened access afforded by logging railroads resulted in an extremely high degree of utilization of the wood resource. Most of the area was clearcut down to stems 1 or 2 inches in diameter, resulting in a species conversion from true northern hardwoods to the second-growth cherry-maple forests that cover the area today. Along major drainages, stands of pine, chestnut, and oak, were converted to chestnut-oak-red maple.

Vegetation conditions. Nearly the entire area was in early successional stage vegetation consisting of a mixture of species of various tolerance to shade. Many shrub species such as hobblebush were abundant. By the late 1920's, about half of the cut areas had grown into sapling or small poletimber trees.

Forage availability. Vast quantities of forage were available to deer throughout this period. The midpoint of the period provided the most forage. By the late 1920's, many stands were growing out of the reach of deer.

Predation. All natural predators were absent during this period. From 1890 to 1900, deer were hunted for venison and hides and to supply meat for logging camps. By 1900, deer were all but extirpated from the entire state. The Pennsylvania Game Commission was established in 1896 primarily to establish laws to protect what few deer remained (Winecoff 1930). Salt licks and the use of dogs for hunting deer were prohibited after 1898. The first game refuge, known as State Gamelands today, was established in 1905. A "bucks only" law was enacted in 1907 and remained in effect for the next 16 years. A hunting license law was enacted in 1913 to raise money to restock deer from other states. During the period, 700 deer were purchased and restocked in Pennsylvania.

Weather. No unusual or extreme weather events are recorded for this period.

Deer density. Deer densities went from near extinction at the turn of the century to near record highs at the end of this period. Laws to protect deer, a lack of natural predators, and vast forage production resulting from chemical wood cuts led to an irruption of the deer population. Densities increased from nearly zero to more than 40 deer/square mile by the end of this period.

Figure 1 shows the pattern of timber harvest and deer density on the Allegheny National Forest from 1900 to 1992. Forage production was greatest during the chemical wood harvest and sawtimber-modern eras. Circles mark actual data points listed in Table 1, and are connected by arbitrary straight lines. Timber harvest data are actual annual figures for the Allegheny National Forest for 1941-92. The crashes in deer densities in the early 1940's and again in the late 1970's occurred after successive severe winters and a sharp decrease in forage production (timber cut).

Second-Growth Poletimber Period: 1930-1950

By the early 1930's, trees on the chemical wood clearcuts had grown into the large sapling-small pole size classes. Much of the land in the 4-county area was under protection and management by the USDA Forest Service. Although the Allegheny National Forest was established in 1923, little management other than fire protection took place until the 1950's.

Vegetation conditions. Much of the shrub layer of vegetation began to decline in number during the early part of this period and many species were absent by 1950. Fern, grass, striped maple seedlings, and small root suckers of American beech made up a large portion of the understory toward the end of this period. The overstory consisted of dense sapling and poletimber stands composed of shade-intolerant species such as black cherry, yellow-poplar, and white ash, with red maple poles growing in the intermediate canopy. Sugar maple and American beech saplings were found beneath the main canopy. By 1942, nearly all of the hemlock advance regeneration had been eliminated from the Tionesta Natural Area by deer browsing (Hough 1965). Most of the hemlock in the second-growth forest was left as residual trees from the original forest. Stems of sugar maple and American beech in the same crown layer as the shade intolerants also were residuals from the original forest and represented an older age class.

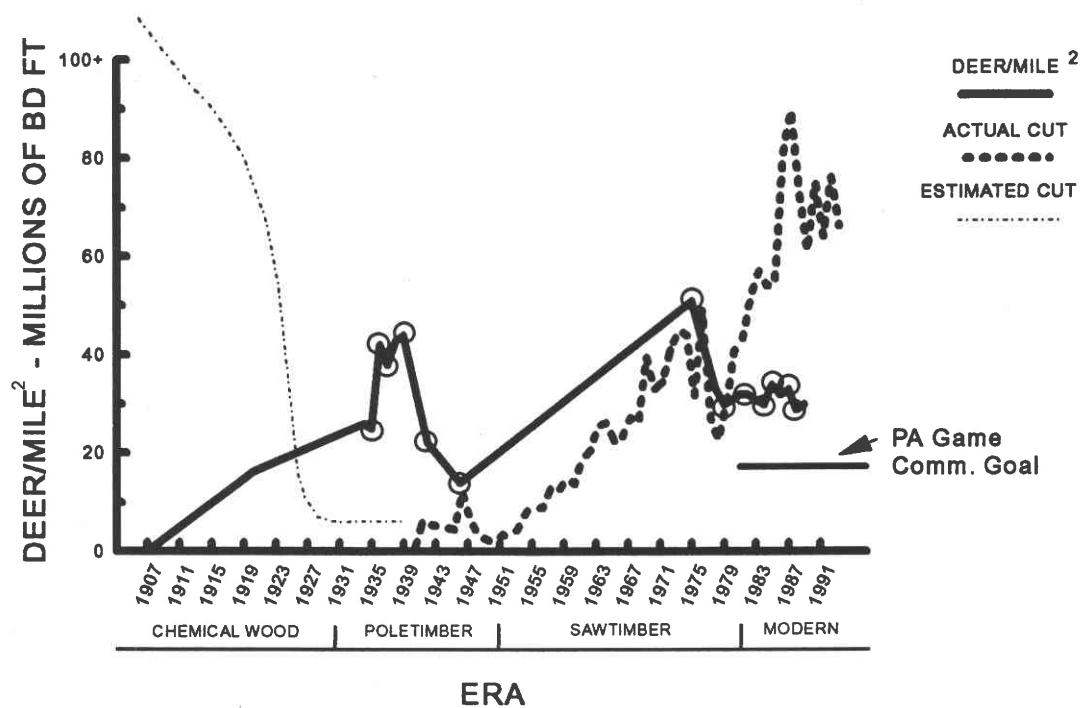


Figure 1. Deer population and timber cutting trends on the Allegheny National Forest.

Table 1. Data sources reported in Figure 1.

Source	Date	Deer/square mile
McCain	1935	23
McCain	1936	27
McCain	1937	34
McCain	1938	23
Hough	1936	29
Hough	1938	42
Hough	1946	14
Jordan	1974	15 ^a
Jordan	1975	43
Jordan	1976	35
Jordan	1977	29
PA Game Comm.	1980 - 1992	30
deCalesta	1992	31

^a Jordan's 1974 estimate was reduced by 30 percent due to consistent error found in the sampling technique used.

Forage availability. Due to the young age class of most of the forest, there was little timber cutting during this period (Fig. 1). Some selection cutting removed sawtimber left during the chemical wood cuts and some stands were thinned for pulpwood in the late 1940's. Little browse or mast was being produced during the period.

Predation. The natural predators that became extinct before the turn of the century remained absent during this period. Doe seasons were introduced periodically to reduce the deer herd which had irrupted before this time and remained high. Concerns for orchards and agricultural crops led to public pressure to control the deer population. The first concern in the forestry community was for plantation failures presumably caused by heavy deer browsing. The deer herd had become so large that hunting mortality no longer kept pace with recruitment.

Weather. Weather in the form of severe winters coupled with declining forage availability caused massive starvation of deer in the late 1930's and early 1940's (Fig. 1).

Deer density. This period witnessed the first attempts to quantify deer density. Deer drives were conducted using Civilian Conservation Corps crews; actual counts of deer on known areas were made in four consecutive years. In total, 8,124 acres of the Allegheny National Forest were driven, resulting in estimates of deer density for 1935 through 1938 of 23, 27, 34, and 23 per square mile, respectively (McCain 1939).

Estimates of carrying capacity during the mid-1930's indicated that the forest could support no more than 18 deer/square mile, and that many areas of the forest were overstocked by as much as 220 percent (Clepper 1931). As a result of too many deer, forage growing out of their reach, and successive severe winters in the late 1930's and early 1940's, mass starvation reduced population levels to a 20th century low (Fig 1). In one drainage alone, more than 200 deer were found starved to death⁴.

Second-growth Sawtimber Period: 1950-1980

By 1950, some of the stands that regenerated around the turn of the century, though not yet mature, were yielding sawlog-size black cherry, white ash, and yellow-poplar. The timber industry, which had left the area during the 1930's, was small in 1950 but beginning to grow. Stands were managed using the single-tree selection system until 1960. A change to even-age systems of management was initiated in 1960; clearcuts were not to exceed 1 percent per year of all operable timber stands, and no single cut was to exceed 50 acres⁵.

A new deer management era in Pennsylvania was initiated during the 1950's. Deer and habitat management were placed on a scientific basis, and food plots were established on the Allegheny National Forest by the Pennsylvania Game Commission under cooperative agreement. Sex ratios and age structure of the harvested deer were used to assess the condition of the herd and antlerless seasons became an annual occurrence.

Vegetation conditions. By the early 1950's, many of the second-growth stands that regenerated from cuttings between 1890 and 1910 had grown to sawtimber size. Individual trees were selectively harvested for sawtimber. Gaps created by these single-tree selection cuts generally were filled by beech, striped maple, or ferns. Understories remained fairly sparse throughout the forest. With a switch to even-age management in 1960, some stands regenerated to early successional stages of woody vegetation consisting primarily of black cherry and red maple. About half of these regeneration cuts regenerated to savannah stands of herbaceous cover along with isolated black cherry and red maple trees (Marquis 1973).

⁴Curnutt, W.C. 1973. More than 1000 acres a year, the "new look" in reforestation on Allegheny National Forest. In: National Forest Special 50th Anniversary Pub. Warren, PA. Schuler, N. (ed.). Article #8

⁵Stotz, L. 1973. Crosscut'n doublebit, timber sales and timber utilization on the Allegheny National Forest. In: National Forest Special 50th Anniversary Pub. Warren, PA. Schuler, N. (ed.). Article #7

Forage availability. As a result of a steady increase in timber harvesting, forage production increased throughout the period as a whole (Fig. 1). An exception occurred during the early 1970's when there was a drop in timber harvesting due to a lack of stands with adequate advanced regeneration. Techniques for establishing adequate advanced seedlings were being developed at the Forestry Sciences Laboratory at Warren and not yet available. The sharp increase in harvest from 1976 through 1980 initially was the result of a large tornado salvage in 1976-78. By 1980, the use of guidelines for establishing advance reproduction using an herbicide-shelterwood technique made more stands eligible for final harvest. Both the quantity and quality of forage produced by regeneration and intermediate cuts was much less than that produced by cuttings at the turn of the century. Forage produced during this period tended to be of a single species such as black cherry or fern, both of which are low in nutrition and in preference by deer. Species of higher nutritional quality such as sugar maple, white ash, and yellow-poplar were preferentially browsed and eliminated or greatly reduced in abundance by white-tailed deer.

Predation. Hunting and highway accidents involving deer were the major causes of mortality during this period.

Weather. Severe winter weather played a major role in reducing deer numbers during this period. The winters of 1976 and 1977 were long and cold and characterized by heavy snowfall. A series of tornadoes occurred on the Allegheny National Forest during the summer of 1976.

Deer density. From 1950 through 1976, deer populations increased steadily as forage availability increased due to increased final harvest cuts (Fig 1.). In the mid-1970's pre-fawn estimates were made on 2154 acres of the Allegheny National Forest during 1974 through 1977 (Jordan 1977). These estimates, made using the belt-transect pellet-group method, were 50, 43, 35, and 29 deer/square mile, respectively. Three additional National Forest areas totaling 48 square miles that were sampled in 1974 had population estimates of 28, 35, and 41 deer/square mile (Jordan 1977). The deer population declined drastically during the late 1970's due to 2 consecutive severe winters and a sharp decrease in the annual cut on the Forest (Fig. 1).

Modern Period: 1980-Present

In response to an increasing deer herd the Pennsylvania Game Commission adopted a system of issuing doe permits in 1979 that was based on the overwinter carrying capacity of each county. Carrying capacity was determined by a formula involving amount of woodland in the seedling-sapling, poletimber, and sawtimber stage. This resulted in an increase in antlerless permits. A saturation point of 500,000 to 550,000 antlerless licenses annually was not enough to reduce populations to a goal of 18 deer/square mile on the Forest (Pa. Game Comm. 1991). To increase harvests, a bonus deer program was initiated in 1988 to allow hunters to harvest more than one deer. During this period, the Allegheny National Forest was increasing its annual timber harvest substantially due to the maturing of the forest. Annual cuts in the 1980's and early 1990's were more than double those of the 1970's.

Studies by Forest Service scientists at Warren showed that deer also could influence other portions of the ecosystem--songbirds, wildflowers, and other herbaceous plants (deCalesta 1992). Public awareness of the impact of deer on the entire ecosystem has been heightened as a result of these studies.

Vegetation conditions. Salvage from the 1985 tornadoes coincided with increased harvest levels when the Allegheny National Forest Land and Resource Management Plan was implemented in 1986 (USDA For. Serv. 1986). This increased the proportion of the land area in early successional stages, usually in communities dominated by one or several tree species. Partial cutting also increased and was supplemented by a series of insect and disease infestations, including invasion by the gypsy moth (*Porthetria dispar*), elm spanworm (*Ennomos subsignarius*), pear thrips (*Taeniothrips inconsequens*), beech bark disease complex, and a sugar maple decline complex. In understories exposed to increased light as a result of these forces, fern, grass, striped maple, and root suckers of beech often increased in dominance. Toward the end of the period there was increasing anecdotal evidence of increases in the regeneration of birch and of the limited recovery of at least one shrub species (hobblebush).

Forage availability. Although the quantity of forage has increased since the 1970's, quality has remained about the same. Regeneration cuts are restricted to stands with adequate advanced regeneration, generally black cherry. As a result, harvest cuts tend to regenerate to pure black cherry stands. In areas where there are insufficient advance seedlings, the understories generally are occupied by species not preferred by deer, for example fern, grass, striped maple, and beech. Forage availability increased substantially following a number of large tornadoes that struck the region in May 1985.

Predation. As mentioned previously, the Pennsylvania Game Commission attempted to reduce deer populations through increased antlerless license allocation and bonus tags. Road kills continue to be a major source of mortality in the state. In 1992, more deer were killed by motor vehicles on Pennsylvania highways (43,000) than were harvested through hunting in Vermont, Massachusetts Connecticut, and Rhode Island combined (38,520) (David S. deCalesta, pers. commun., 1994).

Weather. Winters during the early 1980's were more severe than normal; these were followed by 8 winters that were much milder and more snow free than normal. The winter of 1994 was the most severe snowfall for the period. As mentioned, tornadoes swept the region in 1985.

Deer density. Deer densities for the Allegheny plateau have remained fairly constant throughout the period. Estimates by the Pennsylvania Game Commission for the 4-county area remained at about 30 deer/square mile for the entire period (Palmer, Wm. Pa. Game Comm. pers. commun. 1994). In 1992, data from 11 sites on the Allegheny National Forest obtained by the transect/pellet method showed a range across the forest of 19 to 49 deer/square mile, averaging 29 deer/square mile, which agrees with the Pennsylvania Game Commission's 1990 estimate (Pers. Comm. D.deCalesta 1994).

CONCLUSION

Human activity in northwestern Pennsylvania has shaped and influenced factors that affect species composition, age, and structure of plant communities from pre-settlement time to the present. Pre-settlement forests were characterized by vast expanses of unbroken mature forests intermixed with early successional stages created by natural disturbances such as tornados, hurricanes, and natural fires, and by Native Americans who cleared land for villages and agriculture, and burned the woods repeatedly for berry production and to facilitate hunting and travel.

Since the arrival of European settlers in the region around 1800, man, has manipulated the forests of northwestern Pennsylvania changing their character at an accelerated pace. In particular, human activity has altered the conditions under which forests of the region regenerate. Timber harvesting has increased forage availability for deer which, in turn, have increased from near extinction at the turn of the century to record levels during the mid-1970's (Fig. 1). Laws to protect deer, seasons and bag limits, and a lack of natural predators also have contributed to the overpopulation of deer. With deer densities well above ecological carrying capacity for more than 70 years, all forest communities have been affected as animal-plant, and plant-plant interactions have been influenced. The result is a less diverse ecosystem.

Through the first 6 historical periods reviewed in this paper, there was a tight link between forage availability, as represented by timber harvesting and deer density. The experience of the modern period suggests that this link is not unbreakable. Although current deer densities are well above goal levels, the herd has been stabilized at about 30 deer/square mile throughout the modern period due to Pennsylvania Game Commission's program of antlerless deer harvest and despite a dramatic increase in forage availability.

The experience of the modern period also allows us to focus on the challenge of managing deer and forested ecosystems on a landscape scale. We can anticipate cyclic fluctuations in forage availability as forest and ecosystem managers attempt to achieve a balance in age classes. At the same time, both the number of hunters have declined steadily since peaking in 1982 and the number of new hunters as reflected by the number of people taking hunter-

training has also experienced a steady drop in numbers (deCalesta and Whitmer 1992). Careful coordination of management of both forage and deer density will be required if the region's forests are to recover from decades of overbrowsing during this century. The best short-term solution is to maintain high forage production through sustainable harvest levels while increasing hunting pressure to reduce density to 18 deer/square mile in the Allegheny region.

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