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To cite this article: David G. Hewitt (2015) Hunters and the conservation and management of white-tailed deer (*Odocoileus virginianus*), *International Journal of Environmental Studies*, 72:5, 839-849, DOI: [10.1080/00207233.2015.1073473](https://doi.org/10.1080/00207233.2015.1073473)

To link to this article: <http://dx.doi.org/10.1080/00207233.2015.1073473>



Published online: 05 Nov 2015.



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Hunters and the conservation and management of white-tailed deer (*Odocoileus virginianus*)

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White-tailed deer are widely distributed in North America and for at least 10,000 years have been important to human beings for food, clothing, and tools. Market hunting and habitat changes in the 1800s caused a precipitous decline in the number of white-tailed deer in North America. Hunters acted to restore deer populations. By promoting and helping to enforce hunting regulations, transplanting deer, and funding conservation and management programs, hunters were the primary reason deer populations grew during the 1900s from 500,000 to nearly 30 million. Today white-tailed deer are the most popular big game animal in North America and hunters continue to fund deer management and research. Hunters help wildlife agencies to manage white-tailed deer populations within ecological and cultural carrying capacity by harvesting deer. Thus, hunters, with their interest in viable deer populations, are integral to the conservation and management of white-tailed deer in North America.

Keywords: Hunting; Management; White-tailed deer

Introduction

White-tailed deer (*Odocoileus virginianus*) are a medium-sized cervid that evolved in North America. The species' range extends from the Yukon and Northwest Territories in Canada, south through the United States, Mexico, and Central America, into South America as far south as Peru and Bolivia [1]. With such a vast range, white-tailed deer are obviously highly adaptable. They are found in boreal, deciduous, and rain forest as well as prairies, mountains, rangelands, and swamps. White-tailed deer prosper in subarctic, temperate, semiarid, and highly mesic climatic conditions. In recent times, the whitetail's adaptability has enabled it to thrive in areas heavily influenced by people, such as agricultural and suburban landscapes.

Using the criteria of number of hunters and annual harvest, white-tailed deer are North America's premier big game animal. Annually during 2010–2013, about 10 million hunters harvested over 6 million white-tailed deer in the United States [2,3]. An additional 1.2 million hunters pursued big game in Canada during 2012 [4], a significant number of whom hunted white-tailed deer. The whitetail's distribution partly explains the species' popularity among hunters because whitetails are abundant in eastern North America where most of the populace lives. White-tailed deer are also popular game animals because they are wary and challenging. The meat is excellent and mature males can grow large, complex antlers

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that are desirable trophies. Finally, white-tailed deer are beautiful, elegant animals that are enjoyed by hunters and non-hunters alike. This paper aims to describe the importance of white-tailed deer to various cultures in North America and explain why hunters have been an essential component of the management system that has resulted in the record populations of white-tailed deer in North America today.

Cultural importance of white-tailed deer

White-tailed deer have been prominent in human cultures in North America for thousands of years, likely gaining importance after most species of mammalian megafauna went extinct during the Pleistocene, 12,000–15,000 years ago [5]. Compared to the dozen other large terrestrial herbivores that survived in North America, white-tailed deer have many attractive characteristics. First, white-tailed deer are widely distributed and much of the species' range includes some of the most productive habitats on the continent, especially the Mississippi River valley, prairie and forest biomes of the upper Midwest and central Canada, and the coastal plains and piedmont regions of the eastern United States. These regions, where agriculture was possible, also supported large human populations before Europeans arrived [6]. A second reason white-tailed deer have been especially important to human cultures is that they have a high biotic potential. Female white-tailed deer can breed at 6 months of age where high quality forage is available and breeding at 18 months of age is common [7]. The average litter size of adult white-tailed deer is 1.5–2 fawns, depending on the nutritional state of the doe, and adult deer typically reproduce every year [7]. The annual rate of increase of white-tailed deer in optimal conditions may be as high as 89% [8], enabling whitetails to sustain a large annual harvest. Finally, white-tailed deer are highly adaptable and therefore can exist and even thrive despite dramatic landscape changes brought about by prehistoric and modern human cultures [9,10].

Native Americans

Native Americans in central and eastern North America hunted deer for food, clothing, and tools. Whitetail remains are common in archeological sites and venison may have comprised 25% of the diet of Native Americans living in the species' range [9]. In some instances, whitetails were such an important resource that deer distribution and abundance influenced tribal boundaries, disputes, and alliances [9]. Native Americans used a dizzying array of techniques to hunt deer, including driving deer over cliffs or into traps or water using groups of people or fire. Deer were stalked and killed with spears or arrows, caught in pitfall traps or snares, or pursued until exhausted [9]. Deer not only provided sustenance, but also the hides, bones, sinew, antlers, gastro-intestinal tract, and hooves, which were used for clothing, tools, preparing and storing food, and ornamentation.

With the arrival of Europeans, deer hides became a commodity that could be traded for European wares. Such trade grew to 85,000 skins annually in the late 1600s and to over 500,000 in the middle 1700s [11]. By 1800, Native Americans' role in trading deer hides declined because deer had been overharvested in areas near the markets and a tide of European immigrants moving west over the Appalachian Mountains had displaced Native Americans into areas where white-tailed deer were less abundant.

European immigrants

White-tailed deer were important to European immigrants in much the same way they were important to Native Americans. Deer provided food, clothing, tools, and commodities, especially hides and venison, for trade. Immigrants and commercial logging and mining operations relied on venison for sustenance. Market hunters shot deer to meet these needs and, with the expansion of railroads in the mid and late 1800s, sent increasingly large amounts of meat to markets in the upper Midwest and Eastern United States [9]. After the Civil War, repeating rifles improved the efficiency of market hunters dramatically and when combined with hunting using dogs, night-lighting, traps, pitfalls, and snares, deer populations through most of the species' range declined to no more than 500,000 by 1900 [12].

Contemporary North America

White-tailed deer, from being foremost a resource for exploitation, have become a wildlife species for which people have a complex set of positive and negative values. Hunting remains a prominent value, and while only 4.3% of the United States population hunts deer, support among the general populace for hunting to obtain food is 85% [13]. Even non-hunters are increasingly interested in consuming locally harvested deer for health and ecological reasons [14]. Whitetails have great esthetic value. Many people value the beauty and grace of deer and enjoy viewing, photographing, and painting them. White-tailed deer are the face of nature for many suburban and small town residents who otherwise may take little notice of local wildlife. White-tailed deer hunting is an autumn ritual that forges and strengthens ties among family and friends in rural areas across North America [13,15].

The ecological value of deer has become widely recognized with the improved understanding of ecosystems and their functioning. Deer are prey for large carnivores, influence vegetation communities through herbivory and seed dispersal, and impact important ecological processes such as nitrogen cycling, fire regimes, and plant succession [16–18]. The ecological value of deer can be positive or negative, depending on the deer density and people's perceptions of deer impacts [19]. Negative values of deer have grown in recent decades because high-density deer populations conflict with people through agricultural damage, deer-vehicle collisions, zoonoses, and damage to landscape plants. Balancing the positive and negative values of white-tailed deer is a daily challenge for state wildlife management agencies.

White-tailed deer hunting has economic value. Big game hunters in the United States during 2011 spent US\$16.9 billion on trip related expenses and equipment [2]. Eighty percent of hunters come from metropolitan areas with >50,000 residents (and 42% from cities with >250,000 residents). Thus, deer hunting results in a transfer of income from cities to rural communities; many of which rely heavily on hunting-generated revenue. Accounting for all the economic activity from hunting in the United States, hunters support over 500,000 jobs [20]. The net economic value of a species is the total positive minus the total negative economic value. Conover [19] calculated the net economic value of deer [white-tailed and mule deer (*O. hemionus*)] in 2008 US dollars as the positive economic activity from hunting (\$12.0 billion) and deer viewing (\$4.6 billion) minus the negative economic effects from deer-vehicle collisions (\$1.7 billion), losses to agricultural (\$0.6 billion) and timber (\$1.6 billion) production, and damage to households (\$0.5 billion). Using these numbers, the annual net economic value of deer is \$12.2 billion. These calculations do not

account for the positive and negative ecological values of deer, the existence, empathic, or historic value of deer, nor the cost of zoonotic diseases from deer. Nonetheless, white-tailed deer are clearly of high value in North America.

Hunters and deer conservation, management, and research

From the low deer densities at the end of the nineteenth century, white-tailed deer populations blossomed. Land-use changes, including regenerating forests and abandoned farm fields, provided excellent habitat for deer. The primary reason whitetails were able to recover was a change in people's relationship with wildlife. As in previous generations, people enjoyed seeing deer, pursuing deer, and eating venison. But, there were fewer places to enjoy deer in the early 1900s. In fact, deer in the United States were limited to inaccessible areas in northern Maine, pockets of the Adirondacks, southeastern Massachusetts, the Ozarks, and undeveloped regions of the Gulf Coast and the Mid-Atlantic States [12]. The low populations of deer made market hunting economically infeasible, but instead of working to increase deer populations, market hunters simply changed livelihoods. The dearth of deer was noticed by others in North America, but did not concern urban dwellers or farmers. The people most impacted by the scarcity of deer were deer hunters. The fact the deer shortage was important to hunters is evident in their efforts to recover deer populations. Many of these hunters not only had the interest, but also had the means to influence deer populations using their political connections, professional and governmental positions, and private resources. Sport hunters, from the late 1800s to date, are the key component in white-tailed deer conservation, management, and research.

Hunters in deer conservation

Early efforts to conserve deer were initiated when deer became scarce around colonial settlements. The first legislative initiative on low deer densities occurred in 1646 when Rhode Island outlawed harvest of deer between May and November [12]. Like most early hunting regulations, this law was enacted, not in answer to a higher conservation ethic, but because deer hides and venison were economically important and their loss would limit the colony's prosperity. Most colonies followed with their own hunting regulations by the mid-1700s, but the laws were generally not enforced. Further, the laws only set hunting seasons; they did not regulate the number of deer that could be harvested [9].

The stark decline of deer populations through the 1800s motivated conservation-minded sportsmen to act. The New York Sportsmen's Club was organized in 1844 to stop the take of game animals for the market, the spring shooting of gamebirds, and poor enforcement of game laws [12]. The effectiveness of this group, composed primarily of attorneys, in establishing and prosecuting local game laws spawned similar sportsmen's groups in most major eastern cities. Many of these groups hired game wardens to enforce hunting regulations. Hunters not only established and enforced hunting regulations, but deer hunters bought or leased land on which deer populations could be protected or even propagated. Blooming Grove Park in Pennsylvania, the Bisby Club and later Adirondack League Club in New York, and George Vanderbilt's Biltmore Estate in North Carolina are prominent examples of hunters protecting large areas from unregulated hunting and forest destruction [21]. These three preserves were important in restoring deer. They were also among the first places in the country where European forestry practices were applied in North

America, to use forests sustainably to the benefit of people and wildlife. This model of wildlife and habitat protection was followed, albeit on a smaller scale, in many areas across the eastern United States.

Sportsmen used the Press of the early 1870s in their efforts to conserve wildlife. *American Sportsman*, *Forest and Stream*, and *Field and Stream* were periodicals established then. These papers not only related hunting and fishing stories, but described the natural history of wildlife and published articles defining the character of a sportsman, extolling the virtues of fair chase, and lambasting market hunters for destroying North America's wildlife heritage [21]. These papers supported legislation to limit deer harvest, and to change public attitudes from a strictly utilitarian view of wildlife to a richer set of values celebrating the virtues of sport hunting.

In the late 1800s the Boone and Crockett Club (B&CC) promoted wildlife and habitat conservation, especially North American big game. In addition to securing National Parks, National Forests, and National Wildlife Refuges that supported conservation of white-tailed deer, the B&CC acted specifically on behalf of deer. In the 1890s, Club members worked through the New York state legislative process to eliminate night- and hound-hunting of deer, actions that soon cascaded through other eastern states to limit these controversial hunting methods [12].

The patchy distribution of white-tailed deer across the continent during the late 1800s and early 1900s meant there were large areas of suitable habitat devoid of deer. Scattered reintroductions of white-tailed deer into these areas began in the 1870s and 1880s [22]. Early reintroductions in eight states were conducted by private individuals interested in establishing deer herds that could eventually be hunted. Restocking efforts picked up in the early 1900s as state game agencies became established. The Pisgah National Game Preserve in western North Carolina, established in 1916 from property of George Vanderbilt, was instrumental in helping reestablish deer in at least eight states from Pennsylvania to Mississippi [22]. After the Pittman-Robertson Federal Aid in Wildlife Restoration Act in 1937, restocking efforts expanded greatly because hunter-generated funds were now available to support wildlife restoration. Translocations of over 105,000 white-tailed deer have been documented in the United States since 1878, with about 100,000 occurring after 1937 [22]. All these reintroductions were promoted and financially supported by hunters.

In the 1940s, the Key deer, a diminutive race of white-tailed deer in the Florida Keys, had declined to fewer than 50 individuals [1]. The B&CC recognized that poaching and a poor understanding of the population's ecology threatened to extirpate this unique subspecies. In 1950 the B&CC put US\$5000 toward hiring a biologist to patrol the islands where Key deer were found until more permanent protection could be secured. Although it took seven more years, authorization for a National Wildlife Refuge was passed by the US Congress and with additional funds from the B&CC and other conservation organizations to purchase land, the Florida Key deer population was secure [12].

Like other remote areas, the rangelands of southern Texas supported viable populations of white-tailed deer through the era of market hunting exploitation of the late 1800s. One critically important area in the early 1900s was a portion of the King Ranch near the Gulf Coast about 100 km north of the Mexico border. The King Ranch was founded in 1853 and viable deer populations remained because the area was inaccessible and the King Ranch family had a strong conservation ethic. Members of the King Ranch family were motivated not only by wildlife conservation, but by a love of the outdoors and hunting. R.J. Kleberg, Sr. and Caesar Kleberg, family members with a passion for wildlife conservation, established hunting rules for the King Ranch before state harvest regulations

existed and which were more restrictive than the state regulations that were eventually passed. The rules were designed to prevent overharvest, especially during the frequent droughts that stressed all wildlife in Texas [23]. For example, the annual bag limit on the King Ranch was one male deer with at least eight antler points and the hunting season closed on 15 December when the breeding season began. Furthermore, no hunting was allowed around water sources or other places where deer naturally concentrated and hunting was stopped altogether during drought when deer were especially stressed [23]. These voluntary efforts not only served the interest of the hunters on King Ranch, but benefitted conservation of white-tailed deer through much of the country. From the 1920s through the 1980s King Ranch provided deer for relocation efforts across Texas and in several states in the southeastern United States, with over 12,000 white-tailed deer trapped and relocated in the 1960s and 1970s alone [23,24].

Hunters in deer management

Hunters were essential in white-tailed deer conservation in the early 1900s. They remained essential to deer management as restoration efforts bore fruit and white-tailed deer numbers surged past 15 million in the 1970s on their way to 30 million today [10]. Hunters' contributions were largely funding. Later, hunters assisted state wildlife agencies in controlling deer populations. Hunters have taken on a large share of management efforts during the past 25 years.

Wildlife management is expensive and as state wildlife agencies were established in the early 1900s, money was needed to survey deer populations, establish and enforce annual harvest regulations, monitor the size and composition of the annual harvest, and otherwise manage the growing deer population. Funding came largely from hunters. The Pittman–Robertson Federal Aid in Wildlife Restoration Act of 1937 was achieved with the support of sportsmen. This Act levied a 10% tax on ammunition and firearms. Thus, hunters and shooters carry much of the burden of wildlife management in the United States. The Act has since been amended to include archery equipment. It provided US\$336 million for wildlife management in 2009 [25]. These funds are used to support restoration and management of many wildlife species, but deer hunters, as the largest proportion of the hunting public, generate a large portion of these funds. Additional revenue was pumped directly into state wildlife agencies through hunting license fees.

Hunters not only funded the deer management programs of state agencies, however; they also became the primary mechanism by which agencies manipulated deer numbers. Agencies could increase, stabilize, or reduce deer populations by altering the number and sex of deer that could be harvested, season dates, method of take, and many other factors [26]. During the early- to mid-1900s when whitetail populations were depleted and far below population objectives, state agencies used regulations and educational campaigns to encourage hunters to shoot only male deer. This approach worked well when the objective was to increase deer populations and soon became established as a standard of good hunting practice. In areas of good habitat where the high reproductive capacity of white-tailed deer could be fully expressed, deer populations increased rapidly. Deer became overabundant in portions of Pennsylvania as early as the 1930s and deer managers had considerable difficulty in encouraging hunters to harvest female deer also. This cultural reluctance by hunters to harvest females posed a challenge for the next 50 years of deer management [27]. Hunters had been taught to shoot only male deer and once harvest of females became necessary, hunters were reluctant to participate [10].

By the 1970s deer populations in many areas were overabundant, were numerically heavily dominated by females and because of the heavy harvest of male deer, had few if any mature males. Regulations, such as the earn-a-buck approach in which hunters had to harvest a female deer before they could hunt a male, and special seasons directed to harvesting female deer exclusively, did help to increase the harvest of female deer. In addition, educational efforts by state agencies and by private NGOs such as the Quality Deer Management Association explained that harvesting female deer was actually in the hunter's self-interest and was essential if deer populations were to avoid depletion of their primary forage species and cause wider ecological damage through habitat impacts. The Kinzua Quality Deer Cooperative in Pennsylvania provides an example of hunters working with a wide variety of stakeholder groups to control white-tailed deer populations to reduce problems caused by the deer, although not all hunters are satisfied with the lower deer densities [27]. These approaches eventually worked and in 1999, the number of antlerless deer harvested in the United States surpassed the harvest of antlered deer [10]. In 2013, more antlerless deer are still harvested than antlered deer, but the antlerless harvest has declined in the past 3 years in part because deer populations in many areas are nearing population objectives [3].

These population management efforts also helped reduce socio-economic problems caused by overabundant deer numbers. Deer damage is acute in suburban areas where deer-vehicle collisions are common and deer eat landscape vegetation and gardens. The threat of zoonosis also increases in suburban areas with high deer densities. Special deer hunts were used successfully in areas of Connecticut to reduce the incidence of deer-vehicle collisions, a significant concern because such collisions are frequent, highly expensive in direct damage to vehicles and insurance claims, and can result in human injury or death [20]. Archery and firearm hunts in four suburban areas of New Jersey and Pennsylvania over 3–10 years reduced deer densities from 30–80 to 17–18 deer/km² [28]. The expense of removing deer using traditional deer hunting is borne by the hunters. Organized recreational hunts in suburban areas cost US\$14–177/deer, depending on organizational and law enforcement costs whereas removing deer by trapping (greater than US \$1000/deer) or using sharpshooters (US\$90–260/deer) is expensive and finding places to release trapped deer is increasingly difficult [29].

It is not only through their ability and willingness to harvest animals that hunters assist in management of deer populations. Beginning with their early efforts to protect and reintroduce deer when populations were at their lowest, hunters have now invested vast resources to otherwise help manage deer throughout their range [10]. Hunters assist in deer census efforts using cameras, spotlights, and helicopters. They provide forage for deer by improving habitat, planting food plots, or providing various supplements. Additionally, hunters increasingly make harvest decisions by choosing the age of male deer to harvest and when and where female deer should be harvested [30]. State agencies have responded to this increased sophistication and capacity of deer hunters to help meet management goals and carry out important management practices. In several states, wildlife management agencies are provided with reliable deer census and harvest data from properties directly managed by hunters who either lease or own the land outright. In many cases, the state agencies work closely with the hunters involved and often permit considerable flexibility in deer harvest protocols. Such cooperative efforts produce far more refined approaches to deer conservation and management than would be otherwise possible. State and provincial wildlife agencies are everywhere challenged by the many demands for their services and can only allocate human and financial resources within their means.

The vast privately owned lands in southern Texas are a remarkable example of hunters providing a level of management that would be financially impossible for a state wildlife management agency. The King Ranch is an example. In addition to contributing to the restoration of white-tailed deer across a large portion of the species' range, the ranch began its wildlife management programme when Val Lehmann was hired in 1945, one of the first wildlife biologists to work for a private ranch anywhere in North America [23]. A series of biologists have been hired by the King Ranch ever since. These biologists experimented with helicopter surveys to count deer in the early 1960s and by the late 1990s had established 5646 km of helicopter transects that were flown annually to estimate deer numbers on the ranch's 333,865 ha [24]. As Caesar Kleberg himself had established long before, these biologists continued to implement harvest regulations appropriate to the ranch's deer management goals, based upon habitat availability and an understanding of deer-forage interactions. Ranch biologists now have extensive databases of past harvest and survey records for making total harvest recommendations. Additional harvest criteria for male deer based on age and antler size are also applied and are designed to ensure deer live long enough to express their full antler potential by growing to maturity. Many pastures on the King Ranch are leased for deer hunting and each lessee is required to have a professional biologist on staff to ensure that the location, age, weight, and antler size of all harvested deer is recorded. These harvest records are compiled annually and serve as a resource for the King Ranch to use in refining future harvest guidelines.

The King Ranch has been a leader in managing white-tailed deer on private land in southern Texas, but it is by no means alone. In 2011, deer hunters in Texas flew helicopter surveys on 4 million ha costing about US\$3 million [31]. Following guidelines established by the state wildlife agency, hunters captured over 12,000 deer using helicopters in support of privately funded management projects [31]. Untold hours were invested in camera and spot-light surveys, but such activities are more difficult to track because they do not require authorization by the state. Clearly hunters are a significant force in white-tailed deer management.

Hunters in deer research

Hunters are not only motivated to conserve and manage deer, but they relish knowledge about deer and are generous with their time, money, land, and other resources in supporting research on white-tailed deer. Funds for deer research come from the Pittman–Robertson Federal Aid in Wildlife Restoration Act. Other funds are given directly to deer research. The importance of deer hunting in Texas is illustrated by the US\$5 million that hunters have given to the Caesar Kleberg Wildlife Research Institute (CKWRI) in Kingsville, Texas, USA to support deer research projects from 2005 to 2015. These funds are in addition to the US\$1.2 million provided by state and federal agencies and the US\$1.4 million provided by private foundations with an interest in hunting to support deer research through the CKWRI. These project-specific funds are added to US\$5.1 million in endowment funds given by hunters to the CKWRI to support a funded chair in white-tailed deer research, four graduate student fellowships in deer research, and a captive animal facility where deer nutrition, physiology, and behaviour can be studied. The South Texas landscape is a laboratory for deer research and dozens of research projects on the ecology and management of white-tailed deer have been hosted on private property in the region. The hunters who own or lease the property have bolstered their financial support

of deer research with millions of dollars of in-kind support. For example, the King Ranch has allowed its property to be used for studies of white-tailed deer breeding ecology, antler growth patterns, home range and movement patterns, aging techniques, and survival and movements of translocated deer [24].

Hunters also contribute time and effort that are essential to answering important questions about deer ecology and management. For example, hunters in the state of Mississippi have been recording data on harvested deer for decades and those data have been used to learn about effects of landscape characteristics on deer body and antler size [32,33] and the effects of selective harvest on antler size of male cohorts as those cohorts mature [34].

Conclusion

Conservation is the preservation, protection, or restoration of the natural environment, natural ecosystems, vegetation, and wildlife. Clearly the unregulated market and subsistence hunting of the 1800s was the antithesis of conservation for white-tailed deer and many other wildlife species. The genius of conservation in contemporary North America is its explicit link to hunting, a link that paradoxically arose out of the near extermination of many wildlife species in the 1800s [35]. This system, called the North American Model of Wildlife Conservation, relies on the self-interest of sport hunters to allocate wildlife to legitimate purposes through legislation and regulation and to fund much of the continent's wildlife conservation activities. Under this model, hunters have been the engine behind the conservation, management, and research of white-tailed deer, the most important big game animal in North America.

Acknowledgements

Earlier drafts were reviewed by M.J. Schnupp and S.P. Mahoney. Support for writing this paper was provided by the Caesar Kleberg Wildlife Research Institute and the Stuart Stedman Chair for White-tailed Deer Research. This is publication number 15-117 of the Caesar Kleberg Wildlife Research Institute.

Disclosure statement

No potential conflict of interest was reported by the author.

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