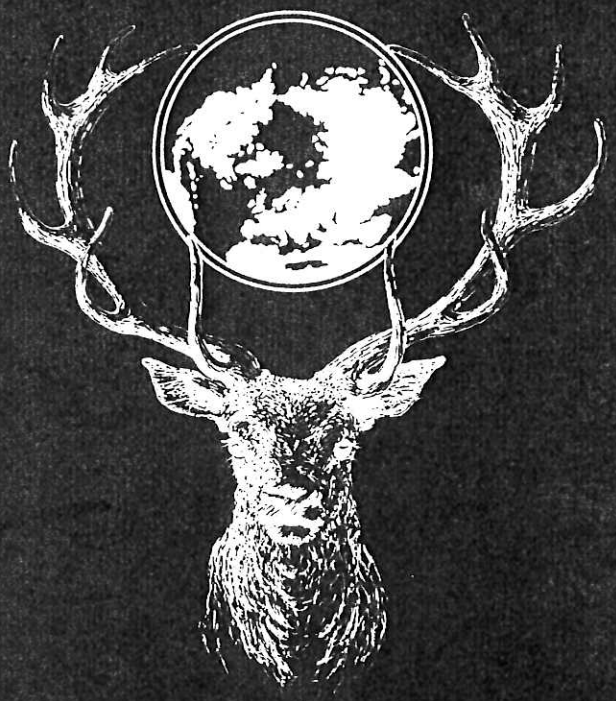
Recent Developments in Deer Biology



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The white-tailed deer (*Odocoileus virginianus*) - "the most managed and mismanaged species"

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Summary

Population estimates for 45 states in the United States indicated a white-tailed deer population of over 26 million in 1993. Management and population trends from prehistoric time to the present are described. Harvest data were acquired from deer biologists in each state and research and wildlife restoration project reports were searched for state-wide population data and trends. Major fluctuations in white-tailed deer habitat and populations have occurred since man first occupied North America. High populations of deer have changed forest communities. State harvest records indicate population growth for this species has not been controlled. Translocations have altered phenotypic and physiological parameters, and it is doubtful whether some subspecies are intact. Over-exploitation of males has caused truncated age structures, with few mature males. Distorted sex ratios have caused delayed breeding and fawning. It is proposed that sport hunting is the most efficient and viable means of controlling deer populations and that sex and age ratios, as well as numbers, require to be manipulated. Reduced harvest of males is required to obtain mature age-class bucks and allow deer populations to function as they had evolved prior to man's exploitation.

Introduction

The environment of the white-tailed deer *(Odocoileus virginianus)* and its populations have undergone continuous change since the arrival of man. Management policies also have continuously changed in response to political pressures and changing environments, and use of this species. As deer populations have increased, we believe that there is need to re-examine the management strategies for this species. The purpose of this paper is to review these changes, current management and the current population status of this species in the United States.

An analysis of white-tailed deer population and harvest trends within the United States was conducted. The individual responsible for deer management was contacted in 45 states where white-tailed deer reside. In addition wildlife restoration programme performance reports, state bulletins and documents, and research findings regarding deer population histories, harvest trends, and sex and age structure were examined. Telephone calls were used to acquire additional information or clarify interpretations of data. Most commonly available data included harvest by weapon type (viz., gun, shotgun, bow, etc.). There were few records on harvest age structure.

History of white-tailed deer and habitat modifications

The genus *Odocoileus* may date from the Pliocene (Putman, 1988) and up to one million years of its existence in North America may precede man. During this period, deer populations probably fluctuated greatly and were influenced by natural events and predators. Preferring intermediate seral

stages, deer would have been most abundant in transition areas between prairies and forest, and where forests had been recently altered by fire or violent storms.

With man's arrival in North America, less than 15,000 years ago (Fagan, 1991), the forests were radically altered. It is little known but the human density of North America prior to European colonization exceeded densely settled parts of western Europe, and 12 million or more people were present (Fagan, 1991; Williams, 1989). Prior to depopulation from disease, famine and warfare, the American Indians had altered the North American forests with a complex subsistence agriculture. The Indians also practised both harvest and habitat management (McGinnes & Reeves, 1958), and annually burned thousands of square miles for hunting, warfare and travel (Williams, 1989; McCabe & McCabe, 1984). Early explorers encountered large cleared tracts, forests with open understories and prairies (Williams, 1989). Abandoned Indian clearings and transition areas from the forest clearings and fires had created excellent habitat for deer.

Indians were dependant on venison and were proficient hunters, skilled in the use of drive traps and snares. It was common for individual hunters to kill 100 or more deer annually (McCabe & McCabe, 1984). With arrival of colonists, Indians went from subsistence to market hunting. Between 1500 and 1800 they, and the colonists, reduced deer populations from over 30 million to less than half of this (McCabe & McCabe, 1984). In the early 1800's deer populations rebounded, but a second exploitation period extended from the 1850s until about 1900. During this period, organized market hunting depleted remaining deer populations. In places, deer were exterminated over large areas, including the entire state of Indiana (Trefethen, 1975).

The mid-1800's also was the period of extensive timber harvest, first on the eastern seaboard, followed by almost complete deforestation of the Great Lake states by 1900, the mid-central states and then the South, with peak logging between 1910 and 1920 (Williams 1989). Deforestation, fire, livestock grazing and unregulated hunting combined to reduce the white-tailed deer to as low as 350,000 animals by the turn of the century (McCabe & McCabe, 1984).

State game laws to protect deer were initiated as early as 1846 in the state of Rhode Island (McCabe & McCabe, 1984). Early laws were ineffective and it was not until 1852 that Maine became the first to employ game wardens and enforce deer and moose hunting regulations (Trefethen, 1975). Most state seasons were liberal, and snares, traps, jacklighting, pitfalls and killing deer driven to water were generally legal until the turn of the century (Trefethen, 1975).

The 1900s brought protection and restoration efforts. Closed seasons and restocking were initiated as early as 1897 by Pennsylvania (Trefethen, 1975). Other states soon followed. By 1925. Pennsylvania's deer population had grown to such a point that massive starvation occurred and, despite public outcry, a liberal antlerless harvest was initiated in 1928 (Trefethen, 1975).

Recovery of deer populations in the U.S. closely followed the history of logging and the ideal forage conditions left from cutover forests. The states of Pennsylvania and New York were the first to witness population explosions of deer, followed by the Lake States of Michigan and Wisconsin and more recently the Southeastern States.

Leopold *et al.* (1947) expressed concern about the size of deer populations, suggesting steps immediately be taken to arrest population growth in problem areas. Specific areas with populations above carrying capacity were: Arkansas, Canada (Algonquin Park and Anticosti Island), Illinois, Iowa, Maine, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New York, North Carolina, Oklahoma, Pennsylvania, Texas, Vermont and Wisconsin. Numerous authors (Kroll, 1994; Eflingwood & Caturano, 1988; Teer, 1984) have since reported on deer population issues.

Population ecology

The white-tailed deer is considered a K species (McCullough, 1979), adapted to live in a relatively stable habitat, at or near carrying capacity (Pianka, 1970; Stubbs, 1977). Game management dogma is based on the concept of sustained yield (Caughley, 1976; McCullough, 1979). The

logistic population growth curve associated with K species can be used to derive a bell-shaped yield curve, in which maximum sustained yield occurs at I-carrying capacity or approximately 50% of K (McCullough, 1979; 1984) and, as Kroll (1991) pointed out, the condition, "in a stable habitat", either never existed or no longer holds true. Unfortunately, the theoretical model described above is based on the existence of a stable habitat. McCullough (1979) offered four possible explanations why populations rarely achieve dynamic equilibrium with the habitat-environment complex. These were that 1) the population varies in absence of environmental variation, 2) the population attempts to track K, but K is constantly shifting, 3) the population overshoots K because of time lags, thereby, altering carrying capacity and 4) one or more of the above factors combine to confound the model.

Even though litter size is small (viz., 1 or 2 fawns), relative longevity (6 or more years), early puberty (can breed at 6 months) and high fawn survival often result in eruptive populations. For example, the 464 ha George Reserve in Mitchigan was stocked in 1927 with two male and four female deer (Hickie, 1937; O'Roke & Hammerstrom, 1948). By 1933, the herd had increased to an estimated 220 animals, or one deer per 2.1 ha (McCullough, 1984). This same herd was reduced in 1975 to 10 deer to study population growth potential; increasing to 212 deer by 1980 (McCullough, 1984). This rapid growth, when combined with the vagaries of successional forces, increases opportunities for over-shooting K-carrying capacity.

Over-populated deer herds damage plant and animal communities (Dasmann 1971; 1981; Matschke *et al.*, 1984; McCullough, 1984; Ellingwood & Caturano, 1986; deCalesta, 1994; Witmer & deCalesta, 1991; LaBar, 1987; Finley & Brittingham, 1989; Dorio & Marquis, 1986; Redding, 1987; Wunz, 1987; Yahner *et al.*, 1987; Yahner, 1989). Some plants have been exterminated over portions of their range. Canada yew *(Taxus canadensis)* originally occurred throughout the Canadian Provinces south to Virginia, Kentucky and Iowa, as a common understorey plant in shady woods, but has been extirpated by deer through most of its range (Martell, 1974). Heavy browsing by deer affects both plant and animal community structure and species diversity (deCalesta, 1994). In addition to negative effects on ecosystem health, high deer populations may create disease threats. Lyme disease is vectored by deer ticks and of human health concern, with over 9,000 cases in 1991 (Conover, 1993). Bovine tuberculosis can be carried by white-tailed deer (Sockett, 1993) and establishment in free-ranging populations could cause major economic loss and public health threats. Though many parasites and diseases affect white-tailed deer, the most significant threat is that of foreign disease (Hayes, 1981). Deer densities now existing would allow for rapid spread and little hope of control for diseases like Foot and Mouth Disease and Rinderpest.

Economic issues

In 1980, 17.4 million U.S. hunters spent an estimated U.S. $8.5 billion (United States Department of the Interior, 1980). Deer hunters comprised 65% (11.4 million) of the total hunters, spending $5.6 billion. In Texas alone, hunting is a $3 billion per year industry (Kroll, 1991). The annual harvest of deer produced 44.1 million kg of venison, worth an estimated $108 million (Williamson & Doster, 1981). The total net annual worth of the white-tailed deer in the U.S. is $27.3 billion, using a 30% recruitment rate (Langenau *et al.*, 1982). Non-hunting values were $5.4 billion (Langenau *et al.*, 1982).

Negative economic impacts may be equally important as positive ones. In Pennsylvania in 1990, there were over 42,000 deer-vehicle collisions with losses of U.S. $40 million, and annual forest and crop losses were estimated at $208 million and between $36 and $86 million, respectively (Witiner & deCalesta, 1991). In the United States, over 200,000 reported automobile collisions result in an estimated annual loss of U.S. $1.3 billion, 16,000 human injuries and 114 deaths (Conover, 1993).

Current population status

Population estimates for 45 states indicated a U.S. white-tailed deer population of over 26

million in 1993 (Table 1), approaching or exceeding pre-Columbian population estimates (McCabe & McCabe, 1984). Most deer were harvested by hunters with guns. Analysis indicated all regions have undergone explosive increases in recent years (Fig. 1). Given similarity of these increases to the logistic growth curve, we believe most deer populations have exceeded McCullogh's "I" carrying capacity and are dangerously close to exceeding "K".

Many states indicated a management goal of maximum sustained yield. Yet, on examination of their historical data, the attained goal appeared to be maximization of "hunter opportunity." This strategy was manifested in high antlered harvests and surprisingly low antlerless harvests.

Population control

Several options for population control have been offered (Ellingwood & Caturano, 1988; Matschke *et al.,* 1984), including regulated hunting, trap and transfer to other locations, fencing and repellents, fertility control agents, re-introduction of predators, use of professional shooters and "letting nature take its course." Unfortunately, most population control options are either too expensive, infeasible, ecologically unsound or politically impractical (Ellingwood & Caturano, 1988; Ismael & Rongstad, 1984; O'Bryan & McCullough, 1985; Rongstad & McCabe; 1984; Ozaga & Verme, 1982; Baker & Hobbs, 1985). Fertility control has received attention as a popular alternative to lethal control methods. However, as pointed out by Guynn (1993), regulatory approval and registration of contraceptives as pesticides or vaccines will be required, health-related issues (non-target organism effects) and efficiency of population treatment will need to be determined, and effects on organism physiology and behaviour, addressed. Further, implementation of such strategies relegates white-tailed deer to "pest" status. These realities have led most biologists and managers to conclude that sport hunting, or a combination of sport hunting and one or more of the above strategies, are necessary to control deer population growth.

We used a modification of the linked sex harvest technique (McCullough *et al.,* 1990) to evaluate how well states are controlling deer populations. They stated exploitation of females approaching 40% of the total harvest would be a desirable goal to prevent over-exploitation and maintain maximum sustained yield. States do not provide percent harvest by females, but do provide "antlerless harvest," which includes buck fawns in the total estimates. Antlerless harvest rates approaching 50% of the total harvest would give similar results in population control to that of the estimate of McCullough *et al.* (1990) of females comprising 40% of the total harvest. Under most 'antlerless harvest' conditions, fawn buck harvest generally constitutes about 10% of the total. In data recorded from public hunting at the Noxubee National Wildlife Refuge, Mississippi between 1973 and 1993, antlerless harvest averaged 48.4% of the total harvest of 7,640 deer and fawn bucks composed 9.8% of that total (H.A. Jacobson, unpublished data).

Two U.S. states have sustained a reputation for managing white-tailed deer: Texas and Pennsylvania. These states offer historical examples for private lands (Texas) and public (Pennsylvania) management strategies.

For many years, Texas was recognized as a leader in private lands deer management. Brothers & Ray (1975) were the first to draw attention to basic management principles for producing quality white-tailed deer. Teer (1984) discussed the history of the Texas herd. He documented numerous die-offs and range deterioration, concluding "reduction of the white-tailed population to half its average density in the period 1953-1961 still would result in production and increments larger than the harvests at the present rate of exploitation."

Prior to 1990, regulation of harvest was primarily under control of county commissioners, who were generally opposed to a doe harvest, and this resulted in a patchwork system of seasons and bag limits. Institution of uniform authority in the 1980's, however, placed the entire state under regulatory authority of the Texas Parks and Wildlife Department and a single harvest system. Unfortunately, strict regulation of antlerless harvest continued until 1987. Under these conditions, the herd peaked in

Table 1. Population and harvest estimates (1993-94) for 45 states in the US

State	Estimated Population	Estimated Harvest		Percent of Population	Percent Antlerless
		Gun	Bow		
Alabama	1,400,000	270,000	30,000	21.4	32.0
Arizona	90,000	4,200	200	4.9	0.0
Arkansas	500,000	106,119	15,944	24.4	35.0
Colorado	6,000	900	100	16.7	50.0
Connecticut	70,000	8,195	2,165	14.8	57.0
Delaware	20,000	6,917	548	37.3	40.0
Florida	800,000	80,000	-	10.0	18.0
Georgia	1,200,000	435,159	-	36.3	51.2
Idaho	35,000	18,500	500	54.3	30.0
Illinois	650,000	92,147	23,215	17.8	60.7
Indiana	319,000	77,226	23,988	31.7	56.0
Iowa	276,000	67,139	9,291	27.7	53.0
Kansas	300,000	34,000	5,500	13.2	34.3
Kentucky	380,467	85,135	9,000	24.7	40.8
Louisiana	1,000,000	193,000	*20,100*	*21.3*	55.0
Maine	262,000	26,720	682	10.5	38.9
Maryland	200,000	39,983	11,251	25.6	50.8
Massachusetts	70,000	6,952	1,387	11.9	46.9
Michigan	1,630,000	232,820	98,160	20.3	35.0
Minnesota	1,000,000	189,206	13,722	20.3	58.0
Mississippi	1,750,000	229,425	32,971	15.0	32.0
Missouri	764,280	156,725	14,696	22.4	55.1
Montana	500,000	58,269	2,100	12.1	47.5
Nebraska	160,000	23,327	3,281	16.6	27.8
New Hampshire	67,662	9,012	877	14.6	34.3
New Jersey	150,000	32,936	17,006	33.3	52.3
New Mexico	10,000	-	-	-	00.0
New York	900,000	200,240	20,048	24.5	53.5
North Carolina	975,000	187,000	14,000	20.6	44.0
North Dakota	180,000	58,163	4,089	34.6	53.4
Ohio	400,000	115,592	23,160	34.7	61.7
Oklahoma	300,000	50,248	7,853	19.4	29.0
Oregon	5,000	594	-	11.9	42.4
Pennsylvania	1,178,000	359,285	49,409	34.7	59.6
Rhode Island	5,500	945	378	24.1	34.3
South Carolina	1,000,000	137,927	-	13.8	*50.1*
South Dakota	250,000	45,394	3,000	19.4	48.9
Tennessee	780,000	120,194	19,648	17.9	44.0
Texas	3,364,188	437,509	15,000	13.5	44.0
Vermont	130,000	10,300	3,000	10.2	9.0
Virginia	950,000	201,122	-	21.2	41.1
Washington	80,000	10,000	1,500	13.1	28.0
West Virginia	800,000	142,589	26,425	21.1	46.6
Wisconsin	1,100,000	217,484	52,935	24.6	45.6
Wyoming	50,000	10,132	300	20.8	43.0
Total Mean (S.E.)	**26,058,097**	**4,788,730**	**577,429**	**21.1 (1.4)**	**41.6 (2.2)**

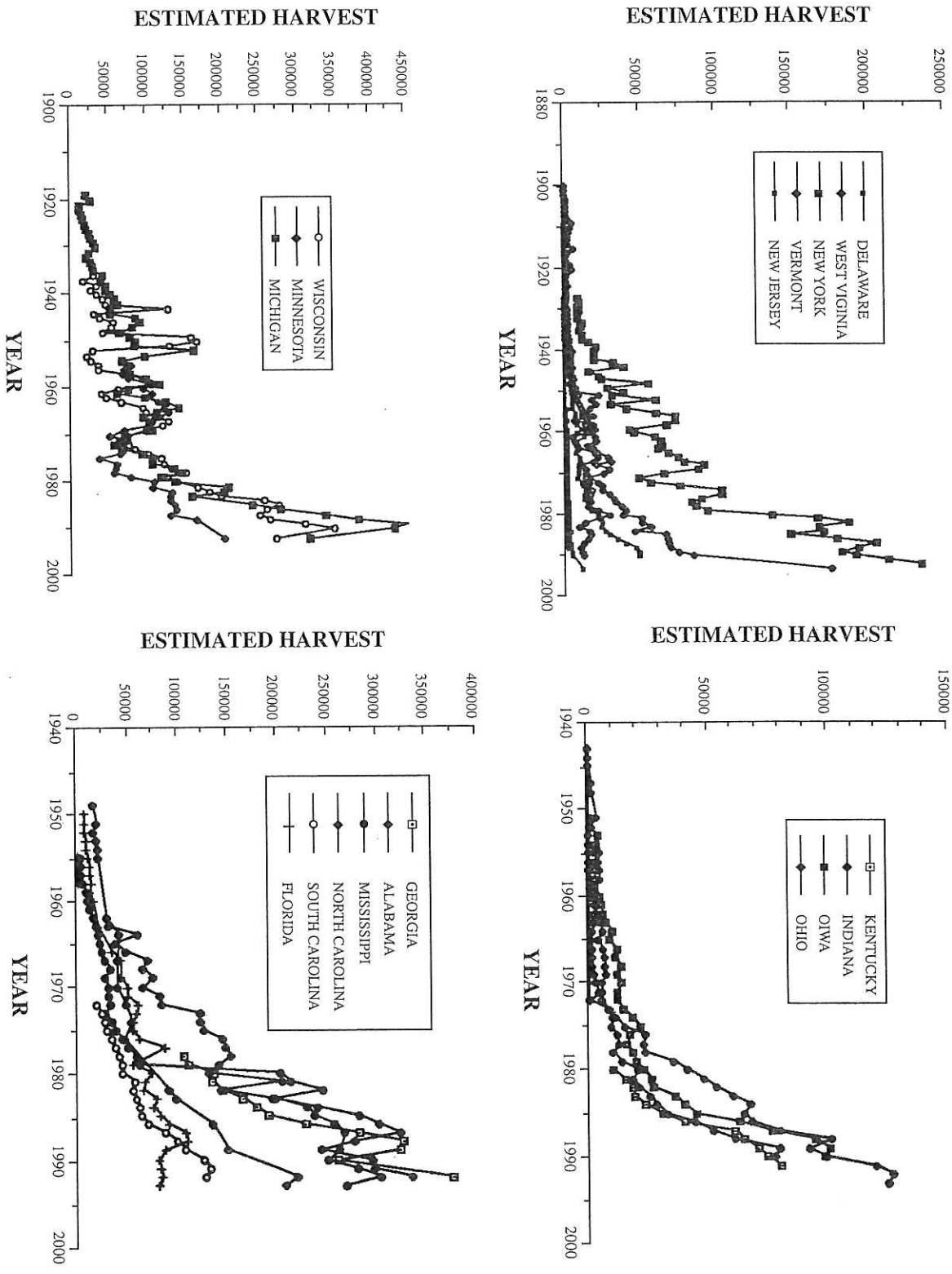


Figure 1. Estimated harvest of white-tailed deer by hunting in four regions of the United States

1987 to more than 4 million animals and has declined by more than 1 million animals since (Fig. 2). During 1984-1993, antlerless harvest more than doubled. However, Texas is only harvesting about 13% of the population, of which 44% is antlerless deer. Teer's (1984) admonition for increased harvest to control the Texas population clearly has not been heeded.

Pennsylvania was the first to recognize deer population and range problems and took dramatic action as early as 1928 to reduce deer numbers. Antlerless harvest reported for Pennsylvania since 1915 has averaged 50.4% of the total harvest (Fig. 3). In spite of its progressive action to reduce deer numbers, this level of antlerless harvest failed to prevent growth in the Pennsylvania deer herd (Fig. 3).

No other state has had an antlerless harvest history approaching Pennsylvania. However, some states have recently attempted to stabilize or reduce deer populations. Thirteen states had antlerless harvest in 1993 that exceeded 50% of the total harvest (Table 1). In 1993, antlerless deer composed 41.1% of state harvests.

The proportion of the estimated population harvested by individual states in 1993 averaged 21.1%. This average is considerably below established recruitment rates which can reach 50% (McCullough, 1984). Sport hunting, as implemented in the past, has not controlled deer populations. Indeed, our study suggests uncontrolled population growth throughout the range.

When harvest histories for states from four geographic regions (Northeast, South, Midwest and Lake States) are examined, harvest can be seen to have increased at an exponential rate but with some states (Alabama, Michigan and Wisconsin) showing a recent decline in harvest (Fig. 1). In most cases, harvest curves imply that sustained yield has not been achieved and that no degree of population control attained.

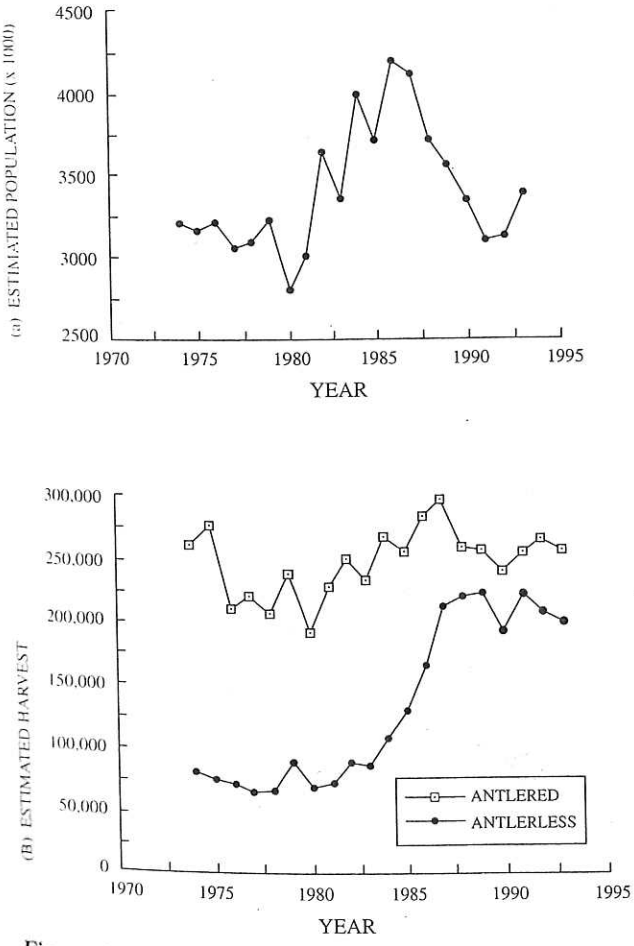


Figure 2. Estimation of (a) population and (b) harvest by hunting of white-tailed deer in Texas between 1973 and 1993.

Management for population age and sex structure

Most states do not provide information on harvest age and sex structure but, when such data are available, harvest is generally heavily skewed towards yearling bucks with few bucks ever reaching a mature age class of five or more years. It is common in most of the white-tailed deer's range to have 60 to 80 percent of the antlered bucks harvested annually. Because this situation is generally accompanied by low harvest rates on females, distorted sex ratios are common. Distorted sex ratios from over-exploitation of males leads to delayed breeding and late fawning (Jacobson, 1990; Cassels, 1992).

Because of high male exploitation, most breeding is accomplished by immature (<4 year old) males. Data from Indian middens and current state data indicate deer ≥ 6-years made up 20-25%, 3-11% and < 2% of the harvest in prehistoric, historic and modern times, respectively (Elder, 1965). Prior to 1700, Indians exercised restraint in harvesting younger animals, but acquisition of the rifle and involvement by the Indian in market hunting caused a shift in harvest age structure (McGinnes & Reeves, 1958).

Other management practices

At least 25 states translocated and released deer from other geographic localities (McDonald & Miller, 1993). We believe that, because of unauthorized and unrecorded releases by private individuals and groups, extent of restocking and translocation has been even greater.

Originally, 30 subspecies of white-tailed deer were described (Baker, 1984). With population reduction at the turn of the century and translocation efforts, we believe some subspecies are no longer intact. A contributing factor to gene-pool mixing has been movement of deer by private individuals and groups, with the hope of producing "bigger and better bucks" on their properties. Little concern has been given to the genetic effects of such translocations on phenotypic and physiological traits besides body size or antler development. Timing of breeding and other physiological characteristics have been demonstrated to be genetically controlled for white-tailed deer (Jacobson *et al.*, 1993).

Trophy harvest and maximum sustained yield may have similarly degraded gene pools of the white-tailed deer. The social status achieved and monetary awards provided to individual hunters from "big buck" contests have contributed to

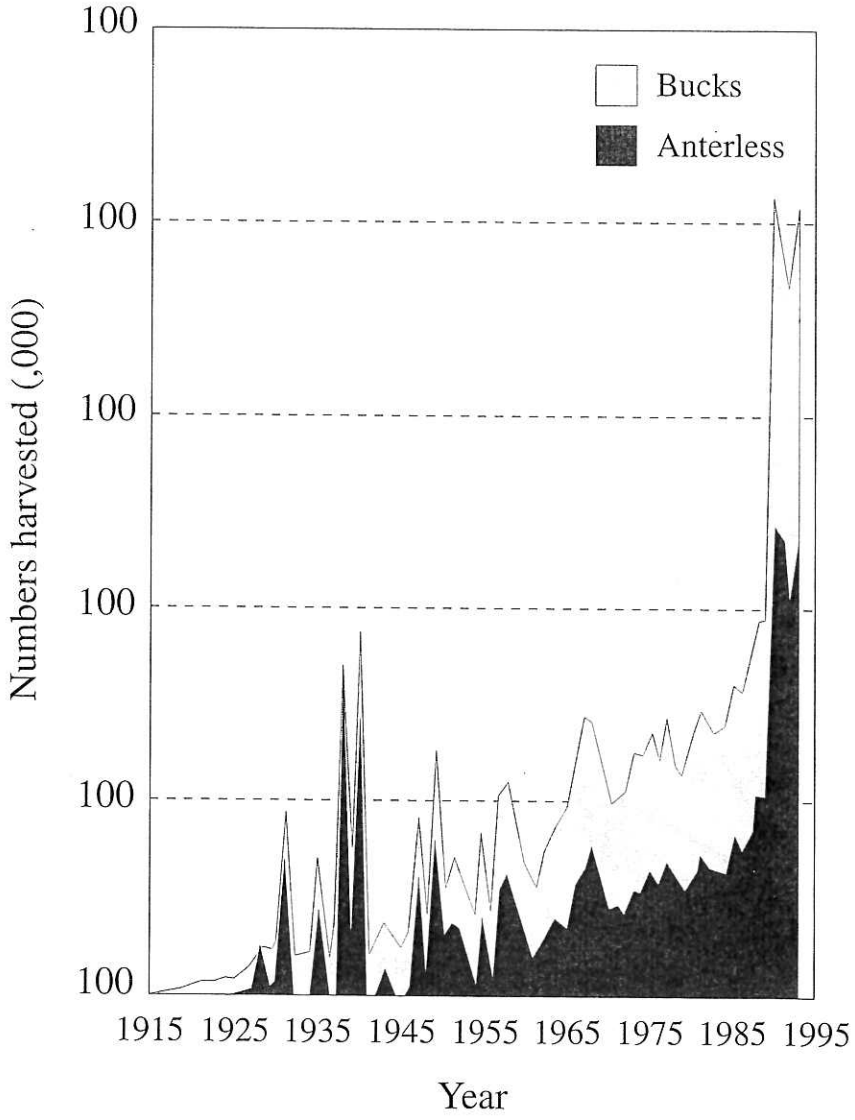


Figure 3. Estimated harvest of white-tailed deer by hunting in Pennsylvania between 1915 and 1993

selective removal of animals with the largest antlers (Jacobson, 1994). Likewise, maximum sustained yield and maximum buck harvest management strategies result in few animals reaching the mature age class where individual fitness might dictate which members of the population compete for breeding rights. Instead, breeding rights are essentially conveyed on the basis of age. In most areas, the individual buck that survives harvest until two years of age will be dominant, because of lack of any mature age class bucks to prevent him from breeding.

Farming of white-tailed deer is likely to additionally impact biology and ecology of this species. Several states (Arkansas, Louisiana, Michigan, Missouri, New York, Ohio, Pennsylvania, Texas and Wisconsin) allow commerce and farming of white-tailed deer. In some instances, individual game and fish agencies have sold the deer and the rights to management of those animals to private landowners. Domestication and translocation of domestic gene pools and the potential for these animals mixing will further complicate an already complex management policy.

Conclusions

Our study provides basis for concern for the future of the species, and poses serious questions about the efficacy of modern deer management. In spite of a broad array of regulations and harvest strategies, deer population growth remains unchecked in almost all states surveyed while there are excessive buck harvest rates in most states.

It is apparent that proactive management solutions are needed. Some examples do exist. New Jersey has established a system of citizen-based action groups to deal with growing urban deer conflicts (Kuser, 1993). Alabama, Arkansas, Louisiana, Michigan, Mississippi, South Carolina, Texas and Virginia have established deer management assistance programmes with special antlerless permits that allow individual private landowners and sportsmen clubs the ability to achieve deer management goals. Quality deer management programme have been initiated on private lands which have had substantial success in changing age structure and sex ratios of their deer populations (Brothers & Ray, 1975; Jacobson, 1990; 1994). Public management areas have been established in Mississippi, Georgia and Michigan with goals for quality deer management instead of the traditional sustained yield or maximum hunter recreation (Jacobson, 1994). Texas has established management areas that provide increased opportunity for public hunters to harvest antlerless deer on private lands through cooperative agreements with large landowners, and has initiated herd control priorities.

It is apparent when we examine harvest trends of white-tailed deer that state agencies have been ineffective in their management of this resource. Management policies have emphasized maximizing hunter recreational opportunity and buck harvest over ecosystem management.

In examination of all state harvest records, the state that obtained the highest proportion of antlerless harvest overall years was Pennsylvania, but even this state has not been able to control growth of its deer population (Fig. 2). It seems elementary, but to stabilize or decrease populations requires that harvests must equal or exceed annual recruitment of the female segment. Unless buck harvest is declining due to lowered recruitment (as opposed to change in regulations or hunter selection), this means as many or more does have to be harvested as bucks.

In most areas of its range, the sex ratio of deer is significantly skewed towards females, and male age structures are significantly skewed towards immature males. Most state and federal agencies have shown little interest in regulating the sex or age structures of their deer herd. We believe that to reverse the current situation will require a major policy change for State and Federal wildlife agencies.

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