1-1966

International Union of Game Biologists

Richard D. Taber
University of Montana, Missoula

INTERNATIONAL UNION OF
GAME BIOLOGISTS

Reprint from

TRANSACTIONS OF THE VIth CONGRESS

Bournemouth 7 October – 12 October 1963

LAND USE AND NATIVE CERVID POPULATIONS IN AMERICA NORTH OF MEXICO

by

RICHARD D. TABER
University of Montana

Bulletin No. 29

January, 1966

Montana Forest and Conservation Experiment Station

THE NATURE CONSERVANCY
LONDON

LAND USE AND NATIVE CERVID POPULATIONS IN AMERICA NORTH OF MEXICO *

RICHARD D. TABER

MONTANA STATE UNIVERSITY

In summarizing the relations between land use and members of the deer family in North America one must be prepared to generalize. In this brief review, no attempt will be made to differentiate between the subspecies of the native cervid species: wapiti or elk *(Cervus canadensis)*, dwarf wapiti *(C. nannodes)* (Murie, 1958); mule or black-tailed deer *(Odocoileus hemionus)*, white-tailed deer *(O. virginianus)* (Burt and Grossenherder, 1952); moose *(Alces alces)* (Peterson, 1952); and caribou *(Rangifer tarandus)* (Banfield, 1961). The original and present ranges of these animals are shown in figures 2–6. In addition to the indigenous forms listed above, a number of cervids have been introduced into North America, but the latter have never been an important faunal element and will not be considered here.

Since animals are dependent upon plants for most requirements, animal distribution is closely connected with plant distribution and can best be discussed from the habitat, or ecological point of view. Space limits the detail with which the plant distribution of ecologically complex North America can be described, however, and we must in this report resort to a rather arbitrary categorization of broad vegetational zones. In placing various vegetation types in one zone or another, and in lumping several disparate types within some single zone, consideration has been given not only to the "original" vegetation (of the period before European settlement) but also to the vegetational changes attributable to man's use of the site over the past three centuries. This highly simplified scheme includes the following broad categories (shown in Fig. 1): tundra; boreal forest; cordilleran forest; northern, southern, and western temperate humid coniferous forest; temperate deciduous forest; and desert-scrub-grassland (here referred to as grazing lands).

Before even a general discussion of land use and its ecological effects on cervids can be presented, it is desirable to set the stage with the legal and social background of land use and wildlife conservation in America north of Mexico.

SETTLEMENT, LAND OWNERSHIP, AND KILL OF BIG GAME

The region covered by this report is under the governments of two nations, the United States of America and Canada. Since first white settlement in the 17th Century, the more fertile lands, especially those originally covered by temperate humid coniferous and deciduous forest and humid grassland, have passed gradually into private ownership. However, vast areas of less productive lands, especially tundra, boreal forest, cordilleran forest, and arid grazing lands, have remained in governmental ownership.

The ownership of wild animals has not parallelled the ownership of the land on which they live. Instead, all free wild animals are owned equally by the citizens of the state (U.S.A.) or Province (Canada) in which they are found. A game or fur-bearing animal passes into private ownership only when legally killed or captured (Wing, 1951). A landowner has only the right to protect himself from excessive damage by wildlife, and from unauthorized trespass.

The process of settlement in North America over the past three centuries has typically consisted of pioneering agriculture often preceded by fur-trapping, lumbering, or pastoralism. The settlers in a new area ordinarily had little in the way of livestock or stores of food. There was a lean

---

* Contribution from Montana Forest and Conservation Experiment Station and Montana Cooperative Wildlife Research Unit (Montana State University, Montana State Department of Fish and Game, U.S. Fish and Wildlife Service, and the Wildlife Management Institute cooperating). The author expresses his appreciation to the many colleagues who have made suggestions for the improvement of this manuscript.

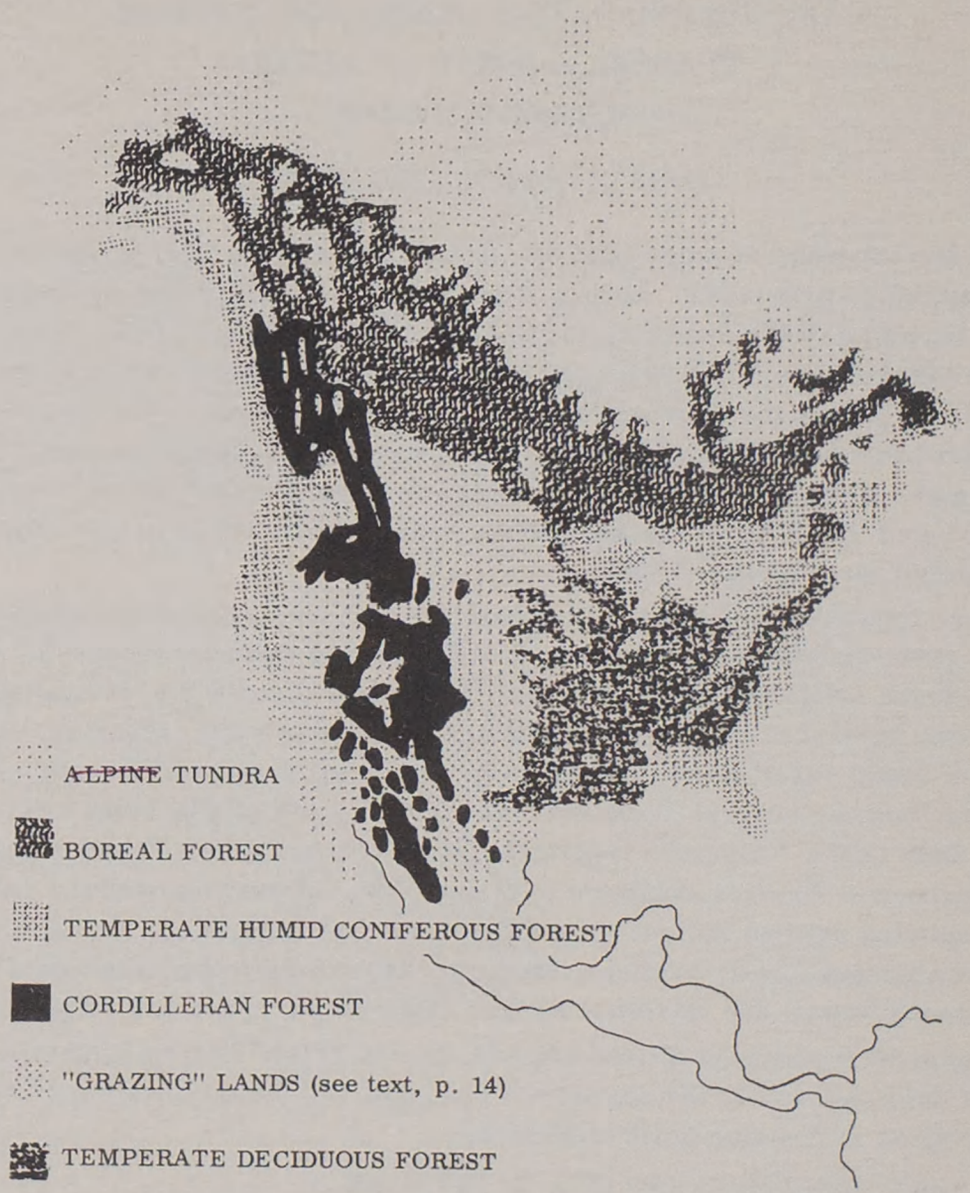

Figure 1. Broad original vegetation types in America north of Mexico (based on Oosting, 1956)

period while the land was being cleared and the first crop planted. During this interval, wild game was an important food supply. There were practically no effective restrictions on the season of hunting or the amount of game killed, either for family use or for sale. Early railroad men, loggers, etc., as well as farmers, lived on wild game. A heavy hunting pressure was usually maintained long after the need for wild meat for food had passed. Free hunting (that is, hunting without charge on all public and private lands) was accepted as almost a perquisite of citizenship. This excessive hunting severely reduced all big game animals in North America (and particularly in the United States) up to the turn of the century. There were many regulations intended to curb this hunting and allow wildlife populations to recover, but they were not enforced and so were ineffective.

This situation continued until about 1900–1915, during which period States and Provinces adopted the practice of charging their citizens a small fee (the hunting license) for the privilege of hunting. Revenue from the sale of licences was often used (in the United States) to support a body of enforcement officers - game wardens. Such officers had existed previously, but without such strong and reliable financial support. In Canada, enforcement officers were, and are, paid from the general treasury. Now for the first time (1900–1915) conservation regulations began to

be regularly enforced. In spite of initial public resistance to enforcement, those wildlife species for which suitable habitat existed began to increase toward the carrying capacity of that habitat. Remnant stocks spread into adjacent habitats from which they had been previously exterminated. Occasionally this process was speeded by man, who trapped and transplanted animals from surviving populations into suitable but untenanted habitat. Among the cervids, wapiti (elk), mule deer, white-tailed deer, and moose were able to adapt to the altered habitats. Only the dwarf wapiti and, to a smaller extent, the caribou, had suffered significantly from substantial losses of suitable habitat.

Among the various restrictive measures evolved in the early days of the century to help rebuild cervid populations was the "buck law". Under this regulation, which was applied to wapiti, deer, and moose, only mature males were legal game. Complete legal protection of females and young naturally permitted an unrestricted population increase wherever the habitat was suitable. The control of populations of the larger carnivores, particularly the wolf *(Canis lupus)*, and the establishment of refuges where all hunting was forbidden also encouraged big game population increase.

As a result, many populations of mule and white-tailed deer had filled their available habitat by 1930–40. At the same time, however, much suitable winter range had been destroyed or pre-empted by agriculture. Thereafter (and even before in a few cases) there were frequent losses due to over-use of forage and consequent starvation (Leopold *et al.*). As an understanding of the nature of the problem deepened, there were efforts to halt these starvation losses.

Artificial feeding was often attempted, but the following considerations have since led to its virtual abandonment as a regular wildlife management measure in North America: (1) it is difficult to obtain (at least for deer) an acceptable, digestible, nutritious, economical food; (2) it is impossible to spread the supplemental food over the entire winter range, so animals learned to concentrate at the feeding grounds, increasing the chance of transmitting disease; (3) since the bulk of the food must continue to come from natural forage, maintaining high game populations through artificial feeding merely serves to increase damage to native forage plants, especially around the feeding-site; (4) the expense of artificial feeding is greater than public agencies can afford, and support by private individuals, even if financially feasible, has no guarantee of continuity.

Another approach to the problem of local overpopulations of deer and wapiti was to trap the excess animals and move them to new range. This was carried out extensively in Yellowstone National Park, which had a surplus of wapiti as early as the 1920s, when wapiti herds outside the Park were still at low levels. Ultimately however, the suitable habitat in new ranges contained all the big game animals that it could support without damage to the vegetation. While surplus animals in such places as Yellowstone Park could still be trapped, there was almost no place left to put them.

Still another way of dealing with animal loss from starvation was to increase the carrying capacity of the native range by forage improvement. Investigations were made of increasing production of native forage species by use of herbicides (Krefting, *et al.*, 1956), planting preferred forage species (Holmgren and Basile, 1959), manipulating the plant composition through the use of fire or machinery (Biswell, *et al.*, 1952), or even fertilization. It has generally been found, however that so long as an overpopulation of animals remains on a range, attempts to balance animals and forage by improving the range are fruitless, since every forage gain is quickly met by a population increase, and the situation remains as unbalanced as before.

At length it became widely accepted, among the men responsible for conserving game and its habitat, that a balance between population and food could only be achieved by reducing the population and keeping it under control. Since it was also desirable to furnish the maximum amount of sport and recreation for the hunting public, it was assumed that the sport hunter should now not only hunt males, but females as well. Herd control was to be accomplished by sport hunting,

and methods for adjusting hunting pressure to harvest needs were developed. At the moment of writing there is abundant evidence that while sport hunting has successfully controlled game numbers in some cases, there is a far greater number of cases in which it has failed to do this. Among the reasons for this failure are: (1) reluctance or inability on the part of the hunter to shift his concept of a trophy from antlered to antlerless animals; (2) public fear that game stocks would be unduly reduced or eliminated, with resulting pressure for more restrictive legislation; (3) administrative mistakes leading to local overcrowding of hunters, deterioration of sportsmanship, or excessive game kill; (4) failure to solve technical problems of game census, especially in mountainous or forested range, making it difficult for the wildlife biologist to demonstrate the substantial game populations that actually survive the hunting season; (5) an increasing tendency on the part of the hunters to hunt along roads and in readily accessible areas and to avoid regions more difficult to get into; (6) the difficulty of obtaining sufficient public access to big game populations on private land or on land which is only accessible by crossing private land.

As a consequence of the difficulties involved in achieving an adequate harvest of many cervid populations, severe overpopulations still occur, with the accompanying deterioration of plants and soil. In spite of this, private and governmental agencies responsible for land management still tend to rely on public hunting to control big game populations. Although governmental land management agencies are authorized to carry out direct reductions of big game populations in the interest of plant and soil protection, such action is almost never taken. There are, however, some exceptions. In the National Parks of both countries public hunting is not allowed and the necessary control of big game populations is often carried out by park officials. Generally, however, herds are not controlled and in many areas over-use of the forage and damage to the watershed continue unchecked on both public and private lands.

SPECIES ACCOUNTS

WAPITI

In aboriginal times the wapiti (or elk, as it is more commonly called) was widely distributed across temperate North America in many different types of habitat - a reflection of the ability of this animal to adapt to a variety of ecological situations (see Fig. 2). Its range included much of the temperate humid deciduous forest, the northern and western temperate humid coniferous forest, the cordilleran forest, and the central and northern grasslands. It was not found to any great extent in the southwestern deserts or the hot humid, southern portion of what is now the United States, nor in the boreal forest (Murie, 1958).

THE WAPITI IN THE TEMPERATE HUMID DECIDUOUS FOREST AND HUMID GRASSLAND:

The temperate humid deciduous forest, in its original state, was made up largely of broad-leaved deciduous hardwood trees. The soils supporting such forest are also generally capable of supporting agriculture, and rainfall is well distributed through the growing season. Consequently, this type of forest has been extensively cleared for cultivation. While the original forest of North America has been reduced by only about seven per cent, the reduction, amounting to almost three hundred thousand square miles, has taken place largely within this forest type. Temperate humid deciduous forest remnants exist along streams, as isolated woodlots, and on mountains, but agriculture prevails as a major land use over most of this forest's original extent.

The former tall-grass prairie occupying the zone just west of the deciduous forest is also extremely fertile, with ample well-distributed rainfall. Consequently, it too is under intensive cultivation.

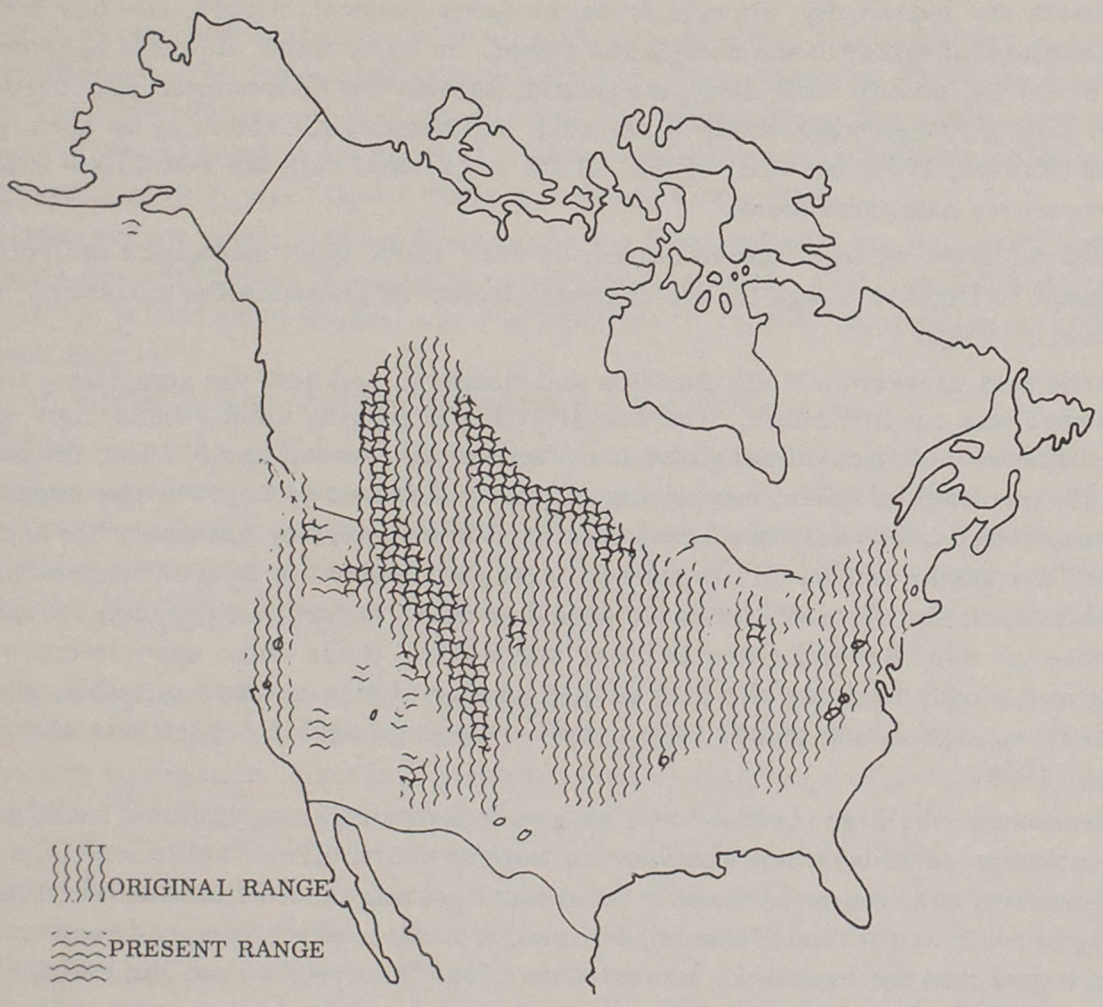

Figure 2. Original and present range of the wapiti *(Cervus canadensis)* in America north of Mexico (based on Seton, 1927 and Longhurst, 1957).

Agriculture rendered these areas unfit as wapiti habitat, not because these animals could no longer exist in the modified habitat, but because of conflicts with farming. Seeking its food principally in the fields (for it is a grazing animal by choice), wide ranging, strong, and adaptable, the wapiti is too much of a threat to agricultural values to be tolerated in farming regions. Even in the forested mountains of the eastern United States, where wapiti once lived, it seems probable that their tendency to move downslope with the onset of winter would bring them onto farmland. All things considered, it is unlikely that wapiti can ever be restored in substantial numbers where farming is a principal land use.

THE WAPITI IN THE CORDILLERAN FOREST:

The cordilleran forest occupies the mountains of the temperate part of western North America, exclusive of the heavy rainfall areas along the northwest Pacific Coast and the well watered western slopes of the northern Sierra Nevada and Rocky Mountains (see Fig. 1). The lower slopes of these mountains are usually without much summer precipitation. Typical lower elevation forest species are ponderosa pine *(Pinus ponderosa)* and Douglas-fir *(Pseudotsuga menziesii)*. The higher slopes are cooler, and receive more summer precipitation. Common forest trees are lodgepole pine *(Pinus contorta)*, Engelmann spruce *(Picea engelmanni)*, white fir *(Abies concolor)*, grand fir *(A. grandis)*, and alpine fir *(A. lasiocarpa)*.

Because summers are usually dry, especially on the lower mountain slopes, fire has always been an important ecological factor in the cordilleran forest. In early times, frequent fires caused by lightning or set by Indians crept along the ground, burning the accumulated pine needles and dry branches, killing low-growing woody vegetation, and keeping the forest in an open, park-like condition (Weaver, 1959; Biswell, 1959). In the occasional very dry years fires killed most of the trees over extensive areas.

The white settlers in the western United States, up until about 1900, sometimes deliberately burned this forest to improve forage for the domestic livestock grazed in the mountains in summer and fall (Biswell, 1959)

With early settlement of western North America and mining in and near the mountains, the more accessible timber was cut for lumber. The accumulation of logging slash (limbs, tops, etc.) increased the intensity of fire and permitted it to "crown" and sweep upslope into the moister forest types above. Lack of roads, manpower, and tools hampered attempts at fire suppression, and during exceptionally dry years the forest continued to be swept by extremely hot and wide-spread fires. To a lesser extent, this is still so. Areas so burned are frequently dominated by seral shrub association for a considerable period of time. On dry (south-facing) slopes, especially those reburned several times in close succession, these shrub associations advance toward forest very slowly because of a lack of tree seed, and also because of rather poor growing conditions. Such shrub ranges have come to support sizeable populations of wapiti (Mohler, *et al.*, 1958).

Wapiti often summer at the higher elevations, on government-administered forest land, and winter on lower elevation grasslands, where the snow is more shallow. These lower regions are frequently in private ownership, and managed primarily for summer grazing for beef cattle. There is thus a direct conflict between wapiti and livestock for food, a conflict which becomes even more critical when wapiti raid the haystacks (stored winter food for livestock) on the valley floors in winter (Morris, 1956)

These conflicts have been overcome to some extent by protecting haystacks with wapiti-proof panels, by herding the wapiti up away from the valley floor and lower slopes through winter hunting pressure, and by state and federal acquisition of important winter range areas (Morse, 1958). Regarding the last point, however, there is growing political opposition in the Rocky Mountain area of the United States, where most of the remaining wapiti are located, to the increase of publicly-owned land. It is believed there that public land ownership weakens the social fabric and economic basis of rural communities.

TABLE 1. Approximate area of range, population and harvest of cervids in America north of Mexico (based on Longhurst, 1957)

Species	Area of habitat (square miles)	Population	Annual Harvest	Increase in Kill Needed to Stabilize Population (a)
Wapiti	482,956	336,869	64,850	5%
Mule deer	1,437,664	6,242,050	1,031,000	80%
White-tailed deer	1,473,415	7,146,730	908,000	200%
Moose	1,507,523	236,871	16,815	180%
Caribou	823,375	726,235	(b)	

(a) Present author's opinion, based on known reproductive rates.

(b) Not known with any certainty because of heavy kill by natives.

Another aspect of land use in these semi-arid mountains affecting wapiti locally is the construction of dams. The impounded waters flood the lower slopes on which the animals spend the winter. The winter range, while relatively small in proportion to the whole seasonal range of the herd, is of course vital to its survival. Since dam sites are found principally in mountains, this conflict is found most often in the western montane forest type.

Other conflicts between wapiti and land use in the cordilleran forest are not great, and so it seems probable that this type will continue to support most of the wapiti in North America. The wapiti is a highly prized game animal, and it is possible to control populations fairly well through hunting (see Table 1).

THE WAPITI IN THE TEMPERATE HUMID CONIFEROUS FORESTS:

The designation temperate humid coniferous forest includes three distinct forest regions: the southeast evergreen forest, the hemlock-hardwood forest of the Great Lakes area and the Pacific forest of the west coast of North America (forest region terms from Oosting, 1956) (see Fig. 1.). These forested regions have in common the facts that they are largely in private ownership and that they are managed primarily for softwood timber production, with other uses being secondary.

In each of these regions, there has been a past history of heavy logging in the early days of white settlement, followed by widespread uncontrolled fires. Now fire is almost entirely under control. Present management aims at creating a forest of rapidly growing softwoods of preferred species, usually some species of pine, but with much aspen in the Great Lakes area and Douglas-fir in the Pacific Northwest. Broad-leaved trees, conifers of less economic value, malformed and diseased trees, etc. are eliminated from these intensively managed forests. Trees are harvested as soon as they reach economic size - as early as 30 years of age in pulpwood stands, or at 80–100 years of age in timber stands. Mature forests of slow growth increment are becoming a thing of the past in these regions.

Because well-adapted tree species of the temperate humid coniferous forest grow quite rapidly, these regions tend generally to be under intensive forest management. Whether the forest is managed for pulpwood or timber the objectives are much the same: to obtain the maximum growth possible per unit area, with the greatest possible proportion of this growth concentrated in the stem, or bole - the harvested part of the tree. In addition, it is generally desirable to have the harvest consist of a single species; the harvesting on one area can then be done at one time with one method and with a single avenue of disposal for the harvested material.

The forest management plan reconciles these objectives as well as the situation allows. Where the forest land is productive, this plan endeavors to harvest mature trees soon after their period of rapid growth is past; to achieve rapid regeneration with preferred species following the harvest, and wherever possible to discourage non-commercial and encourage commercially desirable species.

The humid forest intensively managed for wood production in accordance with these objectives tends to be closely stocked, with little light reaching the forest floor. The forest understory is therefore inhibited and less food for wapiti or other ungulates is produced. Even the surge of shrubs and other low-growing plants that follows timber harvest is short-lived, since every effort is made to effect speedy regeneration. In addition, the hardwoods that provide forage are often non-commercial species and are therefore eliminated from the forest.

The temperate humid coniferous forest of the southeastern United States apparently never supported many wapiti, and that of the Great Lakes region no longer supports many. The original race of wapiti around the Great Lakes was killed out during the sweep of settlement across that area in the 19th century, and although the animal can adapt to the present Great Lakes habitat of intensively managed forest and farmland, its return has not been encouraged.

Essentially a forest-edge or grassland animal, it does not remain in the forest (especially where forage is low) but seeks open ground in which to feed. In the closely interspersed forest and cropland of the Great Lakes region, conflicts inevitably follow, and because of this it cannot be expected that the wapiti will occupy this habitat in any significant numbers as long as the present land management practices prevail.

In contrast, in the western temperate humid coniferous forest, specifically the coastal forest of northern California, Oregon, Washington, and southern British Columbia, there is a forest-dwelling wapiti subspecies the Roosevelt elk *(C.c. roosevelti).* Here, in a sector of North America containing more rough land and fewer people, this wapiti survived the heavy reduction period of the last century. Since then, populations have been encouraged both by regulation and also by opening of the forest through logging. In this area, intensive forest management with its clear-cut blocks springing up with young timber, herbs, and shrubs, has apparently provided an acceptable habitat for the Roosevelt elk, especially where forest restocking is slow. Populations are dense and reproduction is high (Graf, 1955). There is definitely some damage by wapiti to timber reproduction, and forest managers attempt to alleviate this by encouraging heavy hunting pressure on the Roosevelt elk herds (Mace, 1956). The private timber companies owning much of this highly productive forest land actively solicit sportsmen, providing them with maps of road systems and information on wapiti concentrations.

As forest management in the Pacific Northwest becomes still more intensive the period between the timber harvest and the dense growth of timber regeneration will become shorter (as has occurred in the Great Lakes forest). This will mean less production of wapiti forage than is now the case and a consequent lower carrying capacity. However, the Roosevelt wapiti have not yet spread over all their possible range, and populations are now substantially below carrying capacity in much of the region. The animal may therefore become more widespread but at a lower density (Graf, 1955). All in all, it appears that the future of the wapiti along the coastal Pacific Northwest is reasonably well assured.

THE DECLINE OF THE DWARF WAPITI:

In aboriginal times the interior valleys of California were inhabited by a small wapiti, the dwarf or tule elk. Like other big game species of North America it was severely reduced by hunting during the early days of settlement (Evermann, 1915). In contrast to other cervids. however, its habitat was also destroyed. The overflow lands along the rivers, supporting the tule *(Scirpus acutus)* beds that provided cover for the dwarf wapiti, were dyked and drained and converted to agricultural land. The drier areas were cultivated or heavily grazed by domestic livestock. The original perennial flora was widely replaced by annual flora of Mediterranean origin. Practically all of the original range of this animal is now in private hands and has been strongly modified. Small populations exist on privately owned ranges and a very small population exists under fence on a small government-administered range managed primarily for the preservation of the species.

SUMMARY OF WAPITI SITUATION:

One may summarize the situation with regard to wapiti and land-use in North America by saying that the original range has been greatly reduced but that substantial populations remain in the arid and humid forests of the West, with good future prospects. The most pressing conservation need is for a better understanding of the relations between wapiti ecology and land-use practices. The dwarf wapiti, in contrast, has not been provided with the habitat which would permit more than its bare survival as a species.

MULE DEER

The mule deer was, and is, an animal of the temperate western portion of North America, especially the mountainous parts of this region. Its present distribution is much the same, in general, as it was aboriginally, but local land-use patterns have had profound effects on the species (see Fig. 3).

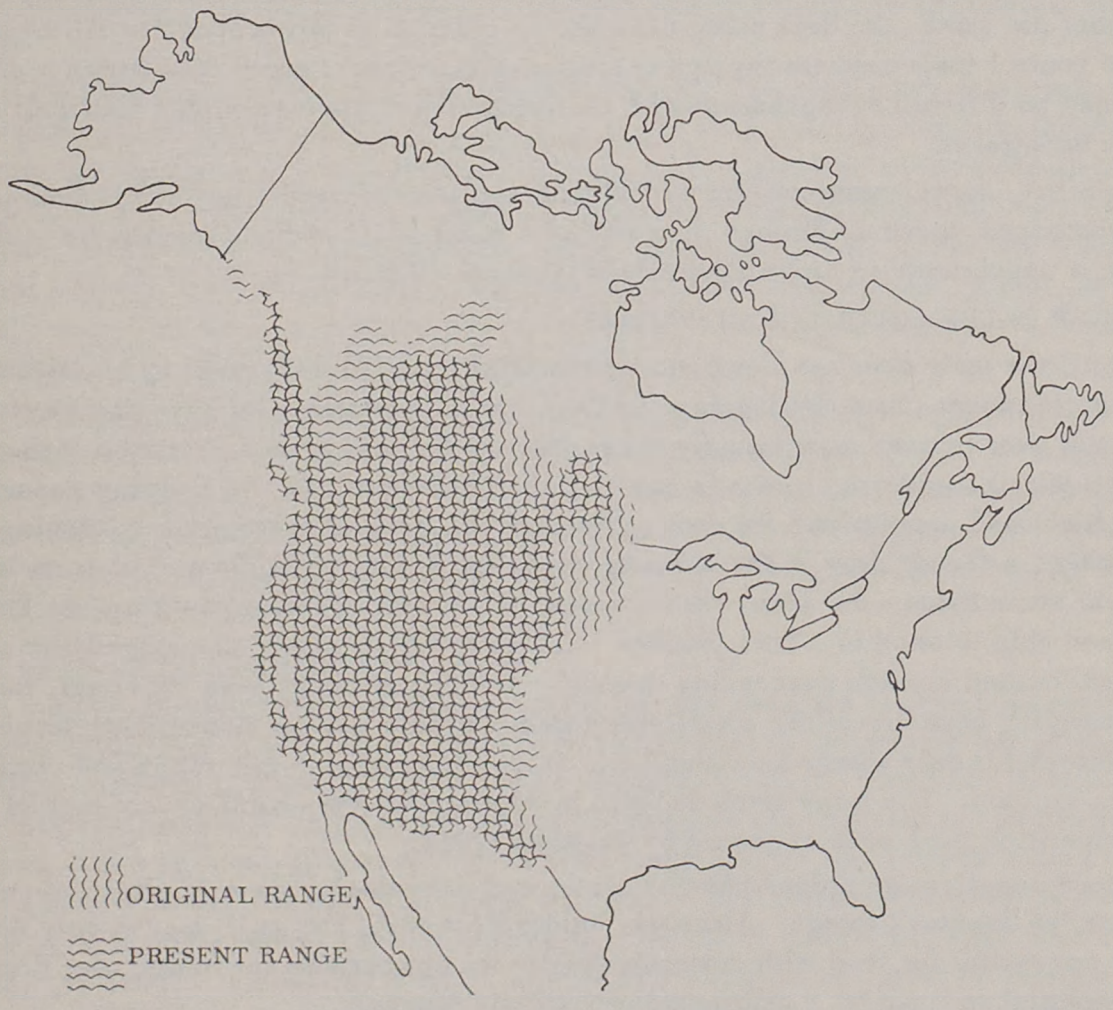

Figure 3. Original and present range of the mule deer *(Odocoileus hemionus)* in America north of Mexico (based on Seton, 1927 and Longhurst, 1957).

THE MULE DEER IN THE TEMPERATE HUMID CONIFEROUS FOREST:

The only sort of temperate humid forest occupied by this species is that of the Pacific Northwest. Here the two subspecies, Columbian and Sitka black-tailed deer *(O.h. columbianus* and *O.h. sitkensis)*, were originally found in low population densities in the deep shade of the full-canopy virgin forest, much like the Roosevelt elk, although with a more extensive range both north and south.

The opening of this forest by logging and fire caused a heavy production of shrubs - the principal food of the deer - and consequent increase in population density. Current land-use in this forest-type, with protection from extensive fires and speedy forest regeneration following cutting, will result in a carrying capacity higher than that of the virgin forest but lower than that of areas heavily burned by uncontrolled fires (Brown, 1961). A conflict exists between the deer

and the forest-manager in that the deer find some forest timber species, notably western redcedar *(Thuja plicata)*, Port Orford cedar *(Chamaecyparis lawsoniana)*, and black poplar *(Populus trichocarpa)*, highly palatable (Taber, 1961). However, the important timber species in this region, Douglas-fir, is only moderately palatable (Hines and Smith, 1962).

The problem of protecting the regenerating forest from excessive damage by deer may be met to some extent by modifying forest management practices. The principal tool for reduction of deer density, and hence damage, is the application of heavy hunting pressure. But where harvested blocks of timber are small, the deer using them are so close to escape-cover that it is virtually impossible to control their numbers through recreational hunting. Larger cuts permit a greater harvest, but may be difficult to regenerate with preferred timber species unless artificial seeding or planting is undertaken.

Another possibility, not yet perfected for widespread application, is the use of systemic repellents. These are substances drawn up through the roots of a plant which, when they appear in the foliage, make it unpalatable to browsing animals (Spencer, 1958).

THE MULE DEER IN THE CORDILLERAN FOREST:

Like the wapiti, the mule deer has been encouraged in the cordilleran forest by widespread heavy fires and, in more recent times, by logging. In fact, since it subsists largely upon browse in the winter, the mule deer is even more heavily dependent on the subclimax forest than is the wapiti. Since so much of the cordilleran forest is now in subclimax condition, its carrying capacity for mule deer is high, and populations are consequently high. Several factors are combining, however, to cause a steady drop in the carrying capacity of this forest type. The most important is simply plant succession - the slow, steady return of the climax forest wherever the forest trees have been able to seed in. This process is aided by increasingly successful fire control - fewer acres are burned in each succeeding decade. Another, although less important, factor in the lowered carrying capacity of the cordilleran forest for mule deer is competition between deer and livestock for deer winter food supplies. In late summer and fall sheep and cattle may turn to shrubs for food. The many methods used in determining the extent of this type of deer-livestock competition have been reviewed by Julander (1958).

Deer winter food supplies are reduced by livestock, and conversely, there is often competition from mule deer for livestock forage. Although, unlike the wapiti, the mule deer is only occasionally a significant competitor for food with domestic cattle, its competition for forage with domestic sheep is substantial and can be a year-round problem for ranchers.

Mule deer have sustained considerable range loss in the cordilleran forest regions, a large proportion of their winter range in the lower mountain slopes and valleys having been pre-empted by agriculture (Yeager, 1961). Generally, the increase in deer numbers combined with loss of range and decline in available forage has often resulted in a serious over-use of winter food plants by the deer.

Cordilleran forest land tends to be rather low in productivity. Its economic value is therefore not great, and management intensity is light. This may ultimately prove to be an advantage for deer, since on public lands small areas may be set aside and managed for the production of natural deer winter food. At present, however, the necessary technical knowledge for accomplishing this economically is still imperfect. Even when information on range improvement is sufficient, it will still be necessary to control mule deer numbers. Control through recreational hunting has only rarely and locally been accomplished in North America (Longhurst, 1957). Direct control by personnel of land-management agencies, such as that used for wapiti by National Parks authorities in both Canada and the United States, might well be applied to mule deer on both public and private lands to alleviate damage to plants and soils of the deer range.

THE MULE DEER IN GRAZING LANDS:

There has been a heavy increase in shrubs on arid grasslands and semi-deserts in North America, essentially due to grazing. Heavy grazing by domestic livestock concentrates on herbaceous plants, reducing plant cover and causing soil disturbance on which woody plants can seed in. The reduced herbaceous component does not effectively compete with the seedling shrubs for moisture. In addition, lack of grass for fuel and the policy of fire suppression reduce the frequency and extent of grassland fires and allow the woody vegetation to maintain its dominance.

Shrubs are a principal food source of mule deer in the seasons when fresh grass and succulent herbaceous plants are not available. The animals make use of shrubs along drainages to penetrate far out into grasslands, and have been reported as far east as Iowa (Sanderson, 1956; Kline, 1959). In such habitat the deer can also forage on wheat, alfalfa, and other cultivated plants (Egan, 1960), these being particularly useful food supplements in the late summer season of deer food scarcity on the western parts of the prairie. In a few regions, notably in California, local mule deer populations are dependent on agricultural crops for a substantial portion of their food and are a cause of conflict with farmers.

A counter-tendency to the decrease in grazing land fires through better suppression and less fuel, as described above, has been the wide invasion of cheatgrass *(Bromus tectorum)* into the western United States in recent years. This introduced annual grass becomes extremely dry and inflammable in summer, and accidental fires carried by it often kill out woody plants, especially when burning is repeated. The potential result of the cheatgrass invasion can be a decrease in shrubs for deer forage.

SUMMARY OF MULE DEER SITUATION:

One might sum up the general situation with regard to mule deer and land-use by saying that in most regions where this deer is found it has been encouraged by the ecological changes accompanying land use to increase to the limits imposed by the environment. This increase has been aided by protective legislation. It seems probable that populations in the near future will decline, due to an increasing intensity of forest management and a deterioration of habitat caused by the deer itself, but that even these diminished populations will be large and widespread. In general, only partial success has been achieved in controlling mule deer numbers by hunting. As Table 1 indicates, it would require something in the order of an eighty per cent increase in kill to achieve herd stability. Chronic overpopulations continue to cause starvation losses and range deterioration through over-use. It seems obvious that more effective methods of population control are needed.

WHITE-TAILED DEER

The original range of this deer covered most of the southern and central latitudes of North America. Since white settlement it has extended this range northward and into some newly irrigated lands in the arid West (see Fig. 4). The white-tailed deer is the most abundant big game animal in North America, with an estimated population of over seven million. The annual kill necessary to hold such a population at a stable level would be about 2,860,000 (Chase and Jenkins, 1962), and in many places the population should not only be held stable, but reduced. The actual estimated kill of 908,000 (Table 1) is thus about one third or less of what the annual white-tailed deer harvest should be and is an extreme example of the chronic under-harvest of some of the big game species in North America.

THE WHITE-TAILED DEER IN THE TEMPERATE HUMID DECIDUOUS FOREST:

Like the mule deer, the white-tailed deer is essentially a feeder on browse and, when available, fresh green grass and succulent herbaceous plants. In the virgin temperate humid deciduous forest of early times, where little light reached the forest floor and low-growing vegetation was

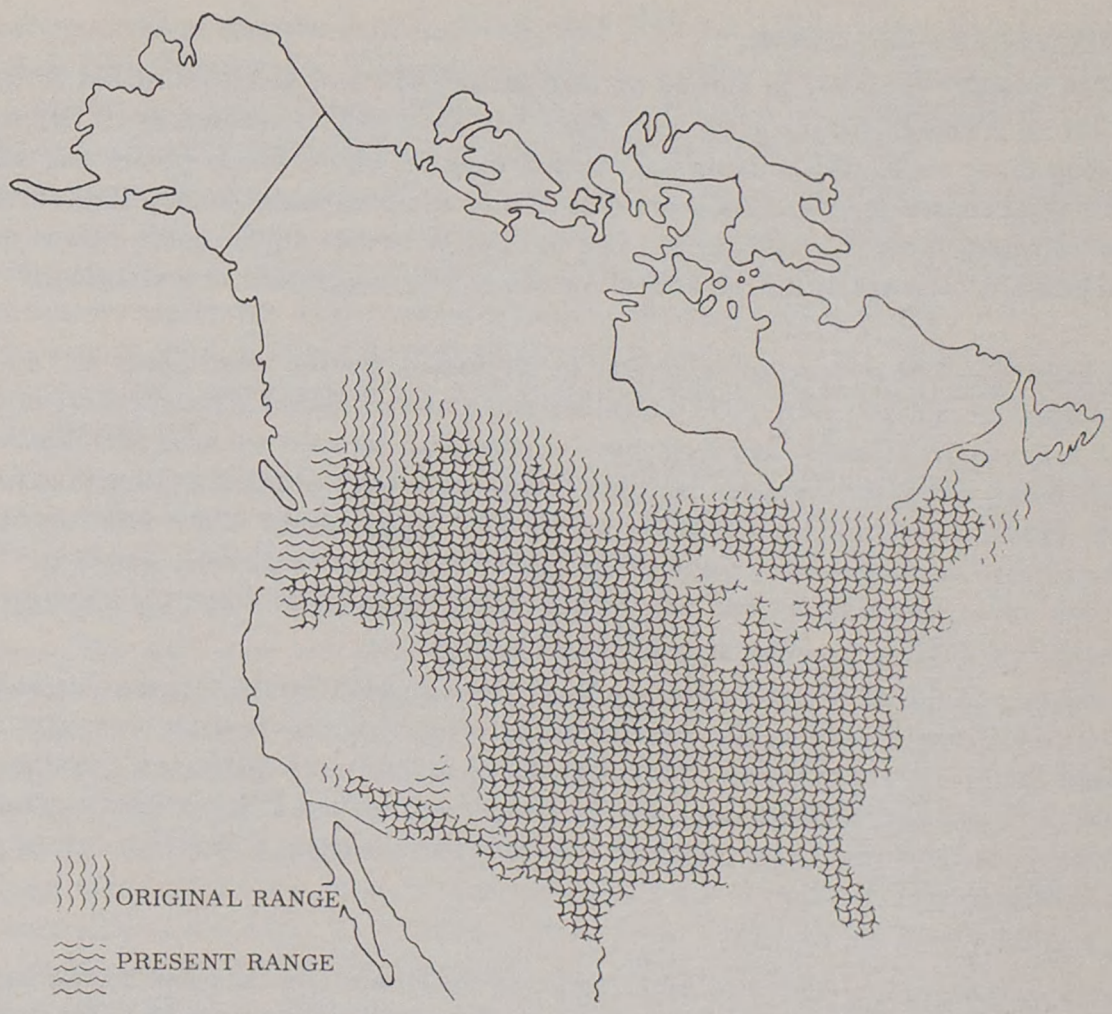

Figure 4. Original and present range of the white-tailed deer *(Odocoileus virginianus)* in America north of Mexico (based on Seton, 1927 and Longhurst, 1957).

consequently not abundant, there were few white-tailed deer. But where there was a forest opening (as at a lake) or where fire or hurricane had levelled the trees, the understory vegetation grew thickly and provided good white-tailed deer habitat. Toward the western edge of this great aboriginal hardwood forest, stringers of prairies ran back into the woods, or isolated prairie groves were found. Here, the carrying capacity of the country for white-tailed deer was high, and deer were abundant. Acorns from the various species of oak in this forest were an important item in the deer's diet.

The massive invasion of agriculture into the temperate humid deciduous forest did not result in the elimination of white-tailed deer from these regions. Areas not suitable for cultivation, such as swamps, have provided a habitat for the species over much of its original range. Able to conceal itself well in even small patches of vegetation, this deer has adapted to the close proximity to man, often venturing forth to feed in cultivated land at night.

Agricultural damage by white-tailed deer can on occasion, be substantial. In such cases, the deer population must be held to a level well below the environmental carrying capacity by heavy hunting. In most farming regions the cover is in relatively small blocks and carefully

regulated hunting pressure can be used successfully to control the deer population, if the public will accept the need for such control. It appears that white-tailed deer will continue to flourish in the remnants of the temperate humid deciduous forest on farming lands so long as adequate bits of cover remain.

The former temperate humid deciduous forest has not all been converted to agriculture. In addition to the woody cover remaining along streams and in farm woodlots, forest prevails in mountainous areas. Many attempts to farm lands which were actually too steep or rocky for agriculture have now been abandoned, and on these areas secondary plant succession has provided good deer habitat. As these areas proceed toward a full-density forest the carrying capacity for deer declines (Severinghaus, 1962). In general, as the temperate humid deciduous forests come under more intensive management, there will be some habitat for deer, but the quality of that habitat will depend upon the concessions made to the needs of the deer in the forest management plan. In the mature hardwood forest deer can exist at naturally low levels without damage to the habitat (Webb, King and Patric, 1956). But after logging, deer often do damage to forest reproduction when populations are too high (Curtis and Rushmore, 1958; Forbes, 1959). Some foresters recommend deer densities of not over about 16 deer per square mile (Bennet, 1958). Local densities are often several times this. In addition, recommendations for successful integration of deer conservation and forest management include such things as logging in winter so that deer may browse on the tops (Alkon, 1961), the piling of logging debris (slash) so as to protect tree seedlings (Grisez, 1960), and the leaving of 5–10 acorn-bearing trees per acre after logging (DeGarmo and Gill, 1958). All of these help to raise carrying capacity for deer, but herd control remains the primary necessity for rational forest management wherever, as in the United States and Canada, labor costs discourage such standard European measures as fencing out game to obtain forest reproduction.

THE WHITE-TAILED DEER IN THE TEMPERATE HUMID CONIFEROUS FOREST:

In the Great Lakes area deer typically summer in the upland forest and winter in swamps dominated by northern white cedar *(Thuja occidentalis)* or ash-maple *(Fraxinus nigra* and *Acer rubrum)* (Christensen, 1962). In aboriginal times the deer probably had adequate winter range; where the upland was in climax the summer carrying capacity was probably low (Christensen, 1959) and where disturbance by fire, windthrow, etc. had caused secondary plant succession, summer carrying capacity was probably high (Habeck and Curtis, 1959).

Scarcely any climax upland forest remains in this region; the present forest is intensively managed for rapidly-growing subclimax trees such as pine and aspen. Drainage has greatly reduced the swamps, and both here and on the uplands a chronic over-abundance of deer causes damage to forage and timber species (Christensen, 1959).

The quality of upland forest as deer habitat depends largely on an admixture of broad-leafed trees and shrubs. However, these are generally 'weed' species to the forester, and therefore deer range quality declines with the forester's successful efforts to grow pulpwood. This sort of forestry does not eliminate deer but it reduces the carrying capacity for them.

Forest succession as such in the subclimax jackpine *(Pinus banksiana)*- scrub oak *(Quercus ellipsoidalis)* forests of central Wisconsin appears to increase rather than decrease deer forage (Habeck, 1959) - natural succession in this area tending to bring in the broad-leafed plants. However, nothing is yet known concerning changes in quality of deer forage that may occur with forest succession. Quality may well decline under increased shading. Herbicides are frequently used to 'weed' out the broad-leafed trees in jackpine plantations. This results in the removal of broad-leafed species from further succession, but also stimulates basal sprouting of these species and so provides deer forage (Krefting and Hanson, 1958; Krefting, *et al.*, 1960). Deer food is also produced by winter logging of broad-leafed trees (Stoeckler, *et al.*, 1958; Gill, 1957) and cedar (Verme, 1959). However, stable long-term production of

winter forage by logging requires a level of management continuity and control that is still rare in North America. A more practical approach is to arrange the pattern of logging so that the deer still have access to what natural forage remains (Gill, 1958; Stenlund, 1958).

Deer densities compatible with temperate humid coniferous forest management vary widely with the local ecological situation (Graham, 1958). In one natural forest a population of 110 deer per square mile practically eliminated forest regeneration; when the population was held at 20 per square mile the forest recovered (Bartlett, 1958). In another study 35–54 deer per square mile were found to be a serious hindrance to forest management (Stoeckeler, *et al.*, 1957). For forest regeneration deer populations should be held low and then be allowed to increase to the moderate levels that the intensively-managed forest can support without undue damage, but this requires a level of population control (presumably through hunting) as yet almost unknown in North America.

In the pinelands of the southern and southeastern United States the general pattern is similar to that in the Great Lakes area, although, since there are no winter snows in the South, special swamp wintering habitat is not necessary. Here again, pines - subclimax upland plants - are the preferred timber trees, and forest management has as a prime objective the control of hardwood 'weeds' that naturally increase in the course of forest succession. The attempt to maintain pine forests for lumber and pulp has been largely successful, and therefore, in such forests, winter is a time of low forage quality for deer. Management practices to raise carrying capacity for deer include plantings of green winter food, fertilization or removal of competition from desirable food species, prescribed burning, timber harvest, encouragement of oaks for acorn production, cessation of grazing by domestic swine and cattle, and plantings of palatable evergreen shrubs (Lay, 1957). Timber harvest permits an increase in the growth of understory vegetation, including deer food plants (Blair, 1960). Of the other measures listed above, the one best fitted to current forestry practices is prescribed burning, a standard procedure in pine silviculture for preparation of a seedbed. Burning benefits deer by releasing nutrients from the soil and so raising the quality of both herbaceous and woody forage. In addition, it provides browse by causing basal sprouting of some hardwood trees (Goodrum and Reid, 1958).

On public lands, where wildlife production is one of the aims of management, detailed recommendations have been made for improving wildlife habitat in various forest types (Fisher and Thomas, 1959). The lower moister areas in the southeastern pine region support commercial stands of mixed hardwoods and are good deer habitat without special management measures, but they can be improved by favoring mast-production species and maintaining a variety of age-classes (Fisher and Thomas, 1959).

A consideration of the temperate humid coniferous forests of the Great Lakes region and the Southeast, as sketched above, leads the author to believe that as forest management on private lands becomes ever more intensive deer carrying capacity will decline. At present, deer bring little or no financial return to the landowner, whereas the timber crop brings a great return. Unless the financial return from game increases, the forest manager will have no economic reason to modify his forest management plan to increase deer carrying capacity, and every reason to pursue forest management policies that will lower deer carrying capacity. On the other hand, since white-tailed deer tend to be grossly under-harvested in these regions, it is apparent that far fewer deer could support the hunting and harvest that now prevail.

In this discussion of the white-tailed deer in the humid temperate coniferous forest no mention has been made of this type of forest in the Pacific Northwest, due to the fact that the white-tailed deer does not occupy this forest to any appreciable extent; its niche is occupied by the Columbian black-tailed deer, a subspecies of the mule deer previously discussed. In the cordilleran forest of the northern Rocky Mountains the white-tailed deer responds to land-use patterns in much the same way as the mule deer, although preferring heavier plant cover for shelter.

THE WHITE-TAILED DEER IN THE GRASSLANDS:

The early abundance of this deer in the prairie-forest margin has been mentioned. All through the central part of North America, wherever sufficient woody cover for shelter exists, white-tailed deer are found. Such cover is often confined largely to streambanks, thus imposing a dendritic pattern of deer distribution (Taylor and Elder, 1959). Some of the largest, healthiest, and most productive white-tailed deer in North America are found in the intensively-farmed state of Iowa, demonstrating that deer and intensive land-use can be biologically compatible (Haugen, Pers. Comm.). In general, the ease with which deer populations can be controlled (assuming public consent) is inversely proportional to the amount of heavy cover; for this reason, it is possible to attain the level of population control necessary to avoid excessive crop damage in highly productive farmland. The principal problem in such regions is the distribution of hunting pressure to avoid killing out local populations (Allen, 1958).

In the more arid grasslands, where livestock grazing constitutes a primary land use, the increase of shrubs described under the section on mule deer has also encouraged the white-tailed deer. Livestock use of this deer habitat affects deer in two principal ways: competition between domestic animals and deer for food, and the effect on deer of livestock range improvement practices.

While it is widely accepted that cows eat grass and deer eat herbs and shrubs, there is still enough overlap in the Southwest to make dual stocking a matter of concern. The competition between sheep and goats, raised in great numbers in the Southwest, and deer is even greater. Therefore, when deer share the range with domestic stock, population levels of both must be taken into account in balancing forage use to forage production (Grelen and Thomas, 1957).

For example, one study in Texas recommended that six adult deer be equated, in forage consumption, with six adult sheep or goats or one mature cow (Merrill, *et al.*, 1957).

It is interesting to note that in Texas, where there is virtually no public land, hunters ordinarily pay for the privelege of hunting deer. Quite often the economic return to the landowner equals or even exceeds his income from livestock (Booker, 1957; Carroll, 1957).

The previously mentioned spread of shrubs in arid grasslands under heavy grazing and fire control has increased carrying capacity for white-tailed deer. On the other hand, where shrubs are being killed with herbicides, burned, or grubbed out mechanically, deer cover is destroyed and carrying capacity drops. It is difficult to forsee just what will happen in years to come with regard to the reconversion of shrub-covered land to grassland. More efficient methods of brush eradication are continually being developed. Simultaneously, better methods of economic appraisal may cause a shift from the widespread attack on shrubs to concentration on the better grass-producing or agricultural sites.

SUMMARY OF WHITE-TAILED DEER SITUATION:

In summing up the situation with regard to white-tailed deer it is apparent that this species fits in well with many kinds of land use, that in practically all habitats its numbers must be controlled to avoid conflict with other land uses, and that at present control of numbers has been successfully maintained in only a few regions - most notably around rich agricultural lands where cover is limited. It is probable that this species, in common with other big game animals, will diminish in number, though not be eliminated, as forest management intensifies. At present, however, need for advances in herd control are obvious. Indeed, the attainment of such control is a primary objective of wildlife authorities.

MOOSE

The original range of the moose (Fig. 5) included parts of the boreal forest, the temperate humid coniferous forest of the Great Lakes region and the northeastern United States, and the cordilleran forest of the northern Rocky Mountains. At present, the moose is flourishing in the

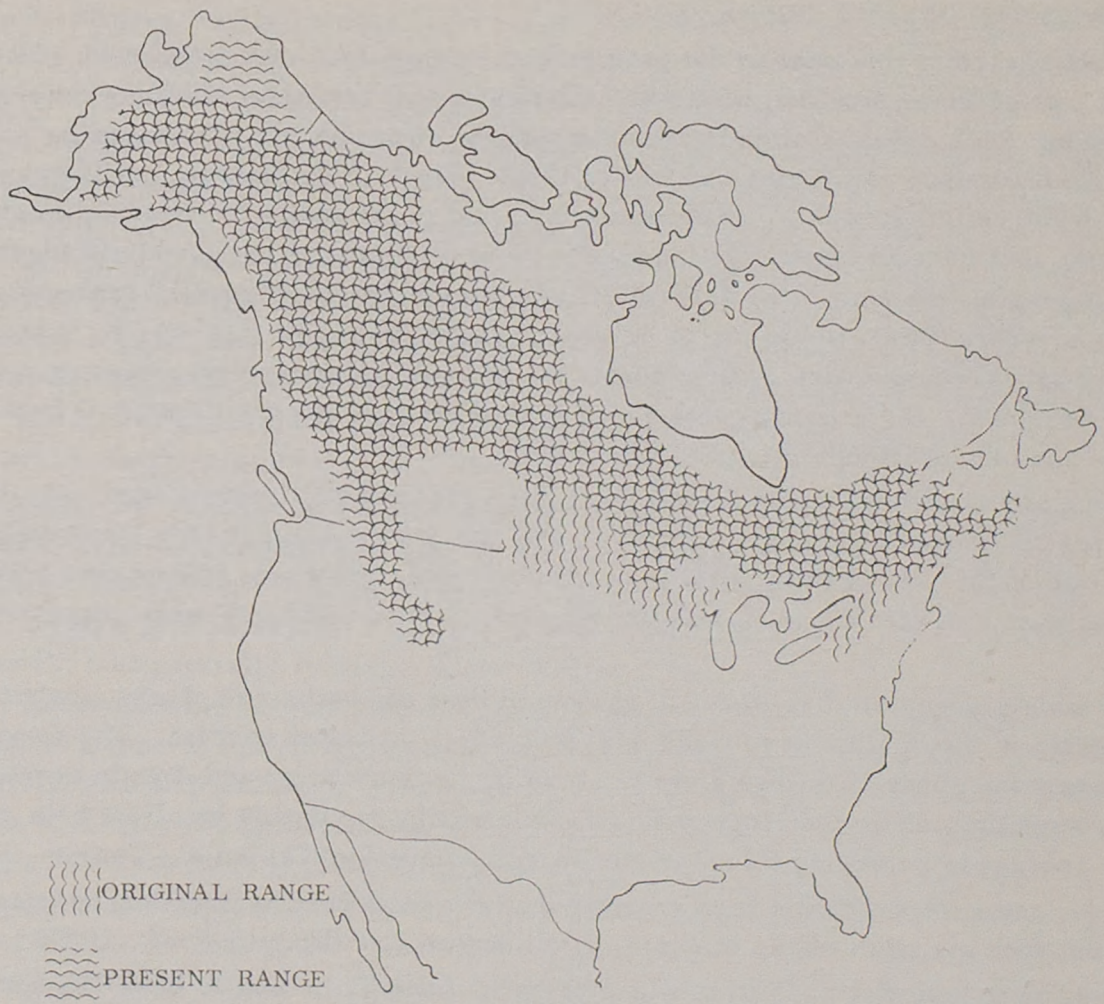

Figure 5. Original and present range of the moose *(Alces alces)* in America north of Mexico (based on Seton, 1927 and Longhurst, 1957).

boreal and northern Rocky Mountain forests, but are rare or absent along the southeastern borders of its original range. Here, in the northern temperate humid coniferous forest, moose were eliminated by over-hunting during the eighteenth and nineteenth centuries (Peterson, 1955). They have remained absent from most of their previous range in this forest type. Peterson (1955) presents evidence to support the hypothesis that the principal reason for low moose populations in what we have called the temperate humid coniferous forest is competition with white-tailed deer for food. He speculates that the various moose populations may be still expanding northward as a consequence of the last major glacial retreat, but also points out that fire and logging have had major recent effects on habitat.

THE MOOSE IN THE BOREAL FOREST:

The boreal forest comprises some three million square miles in North America. The climax is generally dominated by white spruce *(Picea glauca)* except in very wet areas, where black spruce *(Picea mariana)* predominates. It is a relatively open forest, characterised by low precipitation, long hours of sunshine during the summer period when remarkably high air temperatures occur, trees of low stature often heavily bearded with lichens, and a heavy, inflammable ground cover of mosses, lichens, and small shrubs (Lutz, 1955).

All the above listed factors are conducive to the occurrence and spread of fire - the most important modifying influence on the North American boreal forest and the cervids inhabiting it. The occurrence of fire in the boreal forest over time might be summed up in this way: without

man, fires caused by lightning, etc., are occasional; with settlement by primitive man, fire becomes more frequent; with the advent of western civilized man, fire becomes very frequent; with the development of an efficient custodial force by civilized man, fire declines. This last stage has been reached in only a few parts of the boreal forest; for the rest fire is widespread, recurrent, and largely uncontrolled, and the ecological consequences are profound.

Leopold and Darling (1953) summarize the findings of Lutz and other observers in concluding that four-fifths of the white spruce boreal forest of Alaska has burned at least once in the last century, and parts have burned repeatedly. They describe the ecological changes caused by fire as destruction (for possibly 50–100 years) of the lichens, including *Cladonia* and *Cetraria*, and the invasion of the burned area by subclimax shrubs, including willow, aspen, and birch.

Much the same situation prevails in the boreal forest of Canada, and it appears generally that fire will continue to be an important ecological factor in the boreal forest for some time to come, especially in the more remote northern areas where men are active in mineral exploration, etc., but fire control is extremely difficult.

The southern portion of the boreal forest is beginning to be extensively exploited, especially for pulpwood. One ecological effect of clear cutting is similar to that of fire - replacement of an open mossy forest with a rich growth of deciduous shrubs (Cowan *et al.*, 1950). The shrub stage will naturally be shortened in proportion to the foresters' success in obtaining regeneration of timber species.

Logging in the south and fires in the north have greatly augmented the carrying capacity of the boreal forest for moose, which have consequently increased in numbers and extended their range. The moose is now the most important big game animal of this forest (Peterson, 1955; Pimlott 1961).

Because of relatively poor conditions for plant growth in the boreal forest, plant succession is slow, so the moose range created by disturbance tends to be long-lived. In the southern parts of the boreal forest pulpwood logging is going on at an accelerating rate. This should ensure moose range indefinitely. It is probable, however, that sufficient hunting pressure to control moose populations can be applied only in the more accessible areas (Maliepaard, 1962).

The moose in the forests of eastern North America are not only influenced by timber harvest, but influence further timber harvest by browsing on subclimax vegetation. When a white spruce-balsam fir climax is logged (or burned), white birch *(Betula papifera)* and trembling aspen *(Populus tremuloides)*, or in Newfoundland white birch and balsam fir, come in (Pimlott, 1961). White birch is heavily used by moose, and balsam fir is moderately used. High moose populations can suppress these species, allowing spruce to make up a higher proportion of the climax vegetation (Pimlott, 1961). Since white birch is an economically valuable forest tree, maintenance of a high moose population can mean economic losses.

THE MOOSE IN THE CORDILLERAN FOREST:

The mountain valleys of the northern Rocky Mountains typically support an abundance of willows. These constitute an important food for moose in winter (Knowlton, 1960; Smith, 1962) and are often used at other seasons as well. Winter range is not being increased and may well be decreased by herbicide spraying. Also, the flooding of bottomlands by dam construction often destroys moose winter range (Edwards, 1957).

Moose populations in these regions are relatively small in comparison to populations of such other big game as deer, pronghorn antelope *(Antilocapra americana)*, or even wapiti, and are especially attractive to sportsmen. In addition, the observation of moose is an important aesthetic experience for fisherman, campers, naturalists, etc. The animal does not come in conflict with man's economic interests to any appreciable extent and therefore the main management problem is a population reduction sufficient to avoid range damage.

MOOSE HARVEST IN NORTH AMERICA:

Both in the boreal forest and in the cordilleran forest the moose tend at present to be underharvested. Whereas studies of moose reproduction in various habitats indicate a rate of production much like that of the species in Sweden, the North American Harvest is much lower than Sweden's (Pimlott, 1959 , and 1961; Skuncke, 1949). In North America, the moose is apparently about as grossly underharvested as the white-tailed deer (see Table 1). So far, there have been only localized reports of starvation losses, probably because many moose occupy newly created habitat of high carrying capacity. Also, since moose are not found in large concentrations, such animals as do die are not readily noticed. However, if continued, the present trends of harvest and habitat in much of North America's moose range can have only one outcome - range deterioration and starvation.

CARIBOU

The caribou is the only cervid species in North America of vital importance to human beings as a food source. Native Eskimo and Indian communities of the northern boreal forest and the tundra have depended heavily on this species for many centuries. Local caribou declines have caused great suffering and even starvation. Solution of caribou management problems is therefore a matter of pressing concern.

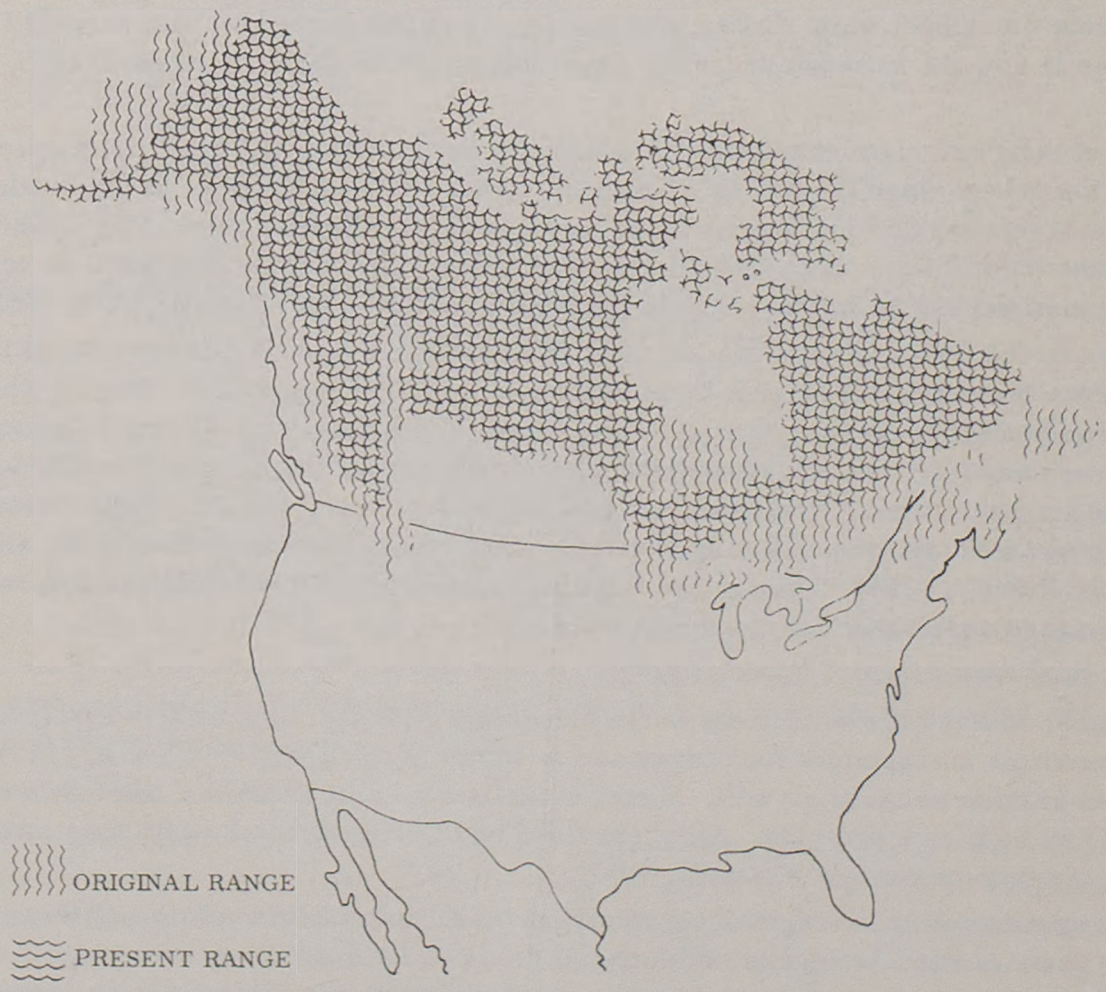

Figure 6. Original and present range of the caribou *(Rangifer tarandus)* in America north of Mexico (based on Seton, 1927 and Longhurst, 1957).

However, qualified observers believe that predation by the wolf may be important in helping to prevent the development of excessive moose populations (Pimlott, pers. comm.). If this is true, then reduction of wolf populations should be undertaken only where there is sufficient hunting pressure to achieve a full moose harvest.

...outhward ...orth- ...almost all ...ls, ...lra and ...t to winter ...g on trunks ...to reach ...od - ...boreal ...destroying arboreal and terrestrial lichens. It may take a century for plant succession following fire to advance to the point where lichens are once more abundant, and before the century has passed fire will probably have swept the site again. Over 30 per cent of caribou range in Saskatchewan alone has recently been burned over (Banfield, 1954), and fire is generally the most important known factor in caribou decline.

In addition to frequent fires, regular timber harvest in the forests where caribou originally wintered will also lower carrying capacity for caribou. The prime objectives of management should be to discover, long before this stage is reached, the areas most important for caribou winter range and to manage these areas in such a way as to maintain caribou populations. The information necessary for successful prosecution of such a plan has, however, been obtained only locally.

Loss of winter range from fire or logging is not the only factor limiting caribou increase. Great numbers are killed each year by Indians and Eskimos. Wolves kill others. And it has recently been shown (Harper, 1963) that great concentrations of radioactive fallout accumulate on lichens and so in caribou bodies. This may well have a detrimental effect on the physiology of the animals and on the human beings who eat them.

CARIBOU IN THE CORDILLERAN FOREST:

As mentioned earlier, the caribou of the mountains summer on alpine plateaus and winter in the adjacent subalpine forest (Edwards, 1958). They feed in winter largely on arboreal lichens, which are most abundant on old trees. Fire in the subalpine forest, as in the boreal forest, destroys caribou winter food (Edwards, 1954). This may account for the fact that the originally abundant caribou populations in present-day Idaho and Montana have not recovered (Flinn, 1959).

Control of fire is an accepted part of management in the cordilleran forest. But timber harvest is also a management objective, and logging in the subalpine forest destroys caribou winter range. Only if these winter ranges are protected and kept in climax or near-climax condition will they have a high carrying capacity for caribou. Such areas could well be kept in public ownership for caribou conservation (Edwards, 1956), but as yet little action has been taken in this direction.

OUTLOOK FOR CARIBOU

On the whole, it appears that although healthy caribou herds do exist, the prediction for caribou conservation in North America must be a gloomy one, if present trends are not reversed.

Caribou range originally covered the entire arctic region of North America, extending southward to the northern Rocky Mountains of Idaho and Montana, the Great Lakes, and into the northeastern corner of the United States. The present range shows a shrinking inward from almost all the original boundaries excepting those to the Canadian Far North (See Fig. 6).

Caribou populations in North America have been severely reduced from aboriginal levels, primarily because of habitat changes. Most of these animals summer on the arctic tundra and migrate south to winter within the boreal forest (Banfield, 1954). Similarly, the caribou summering in alpine regions of the western mountains descend into the subalpine forest to winter (Edwards and Ritcey, 1959). In either event, they feed in winter on the lichens growing on trunks and limbs of trees (Scotter, 1962; Edwards and Ritcey, 1960), or paw through the snow to reach those on the ground (Kelsall, 1957). Caribou are apparently able to detect palatable food - mostly lichens - beneath the snow if the snow is soft enough (Pruitt, 1959).

CARIBOU IN THE BOREAL FOREST:

The same widespread fires that have created so much new habitat for the moose in the boreal forest (see previous section) have reduced carrying capacity of caribou winter range by destroying arboreal and terrestrial lichens. It may take a century for plant succession following fire to advance to the point where lichens are once more abundant, and before the century has passed fire will probably have swept the site again. Over 30 per cent of caribou range in Saskatchewan alone has recently been burned over (Banfield, 1954), and fire is generally the most important known factor in caribou decline.

In addition to frequent fires, regular timber harvest in the forests where caribou originally wintered will also lower carrying capacity for caribou. The prime objectives of management should be to discover, long before this stage is reached, the areas most important for caribou winter range and to manage these areas in such a way as to maintain caribou populations. The information necessary for successful prosecution of such a plan has, however, been obtained only locally.

Loss of winter range from fire or logging is not the only factor limiting caribou increase. Great numbers are killed each year by Indians and Eskimos. Wolves kill others. And it has recently been shown (Harper, 1963) that great concentrations of radioactive fallout accumulate on lichens and so in caribou bodies. This may well have a detrimental effect on the physiology of the animals and on the human beings who eat them.

CARIBOU IN THE CORDILLERAN FOREST:

As mentioned earlier, the caribou of the mountains summer on alpine plateaus and winter in the adjacent subalpine forest (Edwards, 1958). They feed in winter largely on arboreal lichens, which are most abundant on old trees. Fire in the subalpine forest, as in the boreal forest, destroys caribou winter food (Edwards, 1954). This may account for the fact that the originally abundant caribou populations in present-day Idaho and Montana have not recovered (Flinn, 1959).

Control of fire is an accepted part of management in the cordilleran forest. But timber harvest is also a management objective, and logging in the subalpine forest destroys caribou winter range. Only if these winter ranges are protected and kept in climax or near-climax condition will they have a high carrying capacity for caribou. Such areas could well be kept in public ownership for caribou conservation (Edwards, 1956), but as yet little action has been taken in this direction.

OUTLOOK FOR CARIBOU

On the whole, it appears that although healthy caribou herds do exist, the prediction for caribou conservation in North America must be a gloomy one, if present trends are not reversed.

SUMMARY AND CONCLUSIONS

Extensive changes have taken place in land use in North America over the last three centuries and have profoundly influenced cervid populations. At present, all cervids are dependent at some season on some sort of wooded environment.

The wapiti, once widespread in temperate regions, survives in good populations mainly in the mountains of the west, because here the habitat is most suitable and conflict with agriculture is at a minimum. Past forest uses and changes have favoured the wapiti, and present and probable future forest management will still provide it with fair to good habitat. The future of the wapiti seems fairly well assured.

The dwarf wapiti, originally confined to the central valleys of California, has lost practically all of its habitat to agriculture and grazing of domestic stock. It survives only in small areas specially set aside, and its future is precarious.

The mule deer was originally found throughout the temperate West. Changes in forest and grazing land have favored it, and it continues to occupy most of its original geographic range. Deterioration of habitat by mule deer over-use continues to be a problem. Present and future land management will probably reduce the carrying capacity, but much habitat will remain.

The white-tailed deer was originally found mainly in the temperate humid eastern and arid southwestern parts of the present United States. Conversion of most of the heavy hardwood forest (temperate humid deciduous forest) to farm land has still left considerable habitat. Past changes in the temperate coniferous and southern portion of the boreal forests permitted population increases and a substantial northward expansion of range. Part of the original range along the Mississipi Valley, where the tall-grass prairie and the deciduous forest mingled, is now largely converted to agriculture, with a consequent reduction in deer population. In the Southwest the increase of shrubs in the grassland has increased carrying capacity. On the whole, the white-tailed deer continues to have acceptable habitat over much of its range, and therefore it will probably continue to be the most abundant North American cervid.

The moose is an animal principally of the boreal forest and adjacent regions. The quality of its habitat has been greatly augmented by fire and logging, permitting both population increase and range expansion. It appears that the moose will continue to have suitable habitat in the future.

The caribou occupies the tundra in summer and the boreal forest in winter. It has lost much winter range through increased fire and, to some extent, logging. Carrying capacity for caribou may still be on the decline. There is no present land-use reason why caribou habitat could not be restored, but this will require time and much better control of accidental fire. In the future, more intensive logging of the boreal forest could keep caribou carrying capacity down. While the caribou are not presently in danger of extinction, they are much reduced in population.

On the whole cervid populations in America north of Mexico are at substantial levels except for the dwarf wapiti and the caribou. However, there is a pressing need for the development of methods to attain control of populations, since local overpopulations of wapiti, deer, and moose are causing range damage. Once population control is achieved, methods of improving the carrying capacity of many environments could quite readily be put into practice. The continued or enhanced maintenance of cervid populations in America north of Mexico thus constitutes, at present, a social or political as well as a biological problem.

LITERATURE CITED

Alkon, Philip U. 1961. Nutritional and acceptability values of hardwood slash as winter deer browse. *J. Wildl. Mgmt. 25(1)* : 77–81

Allen, Jack. 1958. Indiana white-tails - their plight and progress. *Outdoor Ind. 2(5)* : 6–9

Banfield, A.W.F. 1954. Preliminary investigations of the barren ground caribou. *Can. Wildl. Serv., Wildl. Mgmt. Bul., Ser. 1, No. 10A.* 79 pp.

Banfield, A.W.F. 1961. A revision of the reindeer and caribou, genus *Rangifer*. *Nat'l Mus. Canada, Bul. No. 177. Biol. Ser. No. 66.* 137 pp.

Bartlett, Charles O. 1958. A study of some deer and forest relationships in Rondeau Provincial Park. *Ont. Dept. Lands and For., Tech. Bul., Wildl. Ser. No. 7.* 172 pp.

Bennett, A.L. 1958. Deer mismanagement - a threat to sustained yield forestry in Pennsylvania. *Proc. Soc. Am. For. Mtng. 1957* : 101–104.

Biswell, H.H. 1959. Man and fire in ponderosa pine in the Sierra Nevada of California. *Sierra Club Bulletin 44(7)* : 44–53.

Biswell, H.H., R.D. Taber, D.W. Hendrick, and A.M. Schultz. 1952. Management of chamise brushlands for game in the North Coast Region of California. *Calif. Fish and Game, 38(4)* : 453–484.

Blair. Robert M. 1960 Deer forage increased by thinning, Louisiana loblolly pine. *J. Wildl. Mgmt. 24(4)* : 401–405.

Booker, T.A. 1957. 3 R's of deer management. *Texas Game and Fish 15(10) : 5–7.*

Brown, Ellsworth Reade. 1961 The black-tailed deer of western Washington. *Wash. State Game Dept., Biol. Bul. No. 13.* 124 pp.

Burt, W.H. and R.P. Grossenheider. 1952. *A field guide to the mammals.* Houghton Mifflin Company, Boston. 200 pp.

Carrol, Theron D. 1957. Antlerless deer harvest (The first three years). *Texas Game and Fish Comm.*, Bul. *No. 37.* 26 pp.

Chase, Warren W., and David H. Jenkins. 1962. Productivity of the George Reserve deer herd. *Proc. First Nat'l White-tailed Deer Disease Symposium:* 78–88.

Christensen, Earl M. 1959. A historical view of the ranges of the white-tailed deer in Northern Wisconsin forests. *Am. Midl. Nat. 61(1)* : 230–238.

Christensen, Earl M. 1962. Classification of the winter habitats of the white-tailed deer in Northern Wisconsin based on forest ordination. *Ecology 43(1)* : 134–135

Cowan, I. McT., W.S. Hoar, and James Hatter. 1950. The effect of forest succession upon the quantity and upon the nutritive values of woody plants used as food by moose. *Can. J. Res., Sec. D, 28(5)* : 249–271.

Curtis, Robert O., and F.M. Rushmore. 1958. Some effects of stand density and deer browsing in reproduction in an Adirondack hardwood stand. *J. For. 52(2)* : 116–121.

DeGarmo, W.R., and John Gill. 1958. West Virginia white-tails. *Cons. Comm. W. Va., Div. Game Mgmt., Bul. No. 4.* 87pp.

Edwards. R.Y. 1954. Fire and the decline of a mountain caribou herd. *J. Wildl. Mgmt. 18(4)* : 521–526.

Edwards, R.Y. 1956. Snow depths and ungulate abundance in the mountains of Western Canada. *J. Wildl. Mgmt. 20(2)* : 159–168.

Edwards, R.Y. 1957. Dammed waters in a moose range. *Murrelet.* 38(1) : 1–3.

Edwards, R.Y. 1958. Land form and caribou distribution in British Columbia. *J. Mamm. 39(3)* : 408–412.

Edwards, R.Y. and Ralph W. Ritcey. 1959. Migrations of caribou in a mountainous area in Wells Gray Park, British Columbia. *Can. Field-Nat. 73(1)* : 21–25.

Edwards, R.Y. and Ralph W. Ritcey. 1960. Foods of caribou in Wells Gray Park, British Columbia. *Can. Field-Nat. 74(1)* : 3–7.

Egan, Joseph. 1960. Some relationships between mule deer and alfalfa production in Powder River County, Montana. *Proc. 40th An. Conf. W. Assoc. State Game and Fish Comm.*

Evermann, B.W. 1915. An attempt to save California elk. *Calif. Fish and Game 1(3)* : 1–11.

Fisher, W.H., and Leon R. Thomas. 1959. Guide to timber management and wildlife coordination, Region 8, U.S. Forest Service. Mimeo. 41 pp. plus appendix.

Flinn, Paul. 1959. The caribou of northern Idaho. *Idaho Wildl. Rev. 1115)* : 10–11.

Forbes, Stanley E. 1959. The Pennsylvania deer story - 1959 *Pa. Game News 30(11)* ; 13–17.

Gill, John D. 1957. Cutting Hardwoods to help deer. Maine Dept. Inland Fish and Game, Game Div. Leaflet. Ser. 1 (3) : 1–4.

Gill, John. D. 1958 Effects of pulpwood cutting practices on deer. *Proc. Assoc. Am. For. Mtng. 1957* : 137–140.

Goodrum, Phil O., and Vincent H. Reid. 1958. Deer browsing in the long leaf pine belt. *Proc. Soc. Am. For. Mtng.* 1958 : 139–143.

Graham. Aamvel A. 1958. Results of deer exclosure experiments in the Ottawa National Forest. (Michigan). TNAWC 23 : 478–490.

Grizez, Ted J. 1960. Slash helps protect seedlings from deer browsing. *J. For. 58(5)* : 385–387.

Grelen, Harold E. and Gerald W. Thomas. 1957. Livestock and deer activities on the Edwards Plateau of Texas. *J. Range. Mgmt. 10(1):* 34–37.

Grof, William. 1955. *The Roosevelt elk.* Port Angeles Evening News, Port Angeles, Wash. 105 p.

Habeck, James R. 1959. A vegetational study of the central Wisconsin winter deer range. *J. Wildl. Mgmt. 23(3)* : 273–278.

Habeck, James R. and J.T. Curtis. 1959. Forest cover and deer population densities in early northern Wisconsin *Trans. Wisc. Acad. Sci. 48* : 49–56.

Harper, Francis. 1963. Caribou and Eskimos. *I.U.C.N. Bulletin, N.S. No. 6,* Jan/March, 1963 : 6–7.

Hines, William W. and Carl W. Smith. 1962. An account of the relationship of black-tailed deer to the propogation of Douglas fir seedlings. *Oregon State Game Comm. Bul. 9(17)* : 3, 6, 8.

Holmgren, Ralph C. and Joseph V. Basile. 1959. Improving southern Idaho deer winter ranges by artificial revegetation. *State of Idaho, Dept. of Fish and Game, Wildlife Bul. No. 3.* 61 pp.

Julander, Odell. 1958. Techniques in studying competition between big game and livestock. *J. Range Mgmt. 11(1)* : 18–21.

Kelsall, John P. 1957. Continued barren-ground caribou studies. *Canadian Wildl. Serv., Wildl. Mgmt. Bul., Ser. 1, No. 12.* 148 pp.

Kline, Paul D. 1959. Additional Mule deer records for Iowa *J. Mamm. 40(1)* : 148–9.

Knowlton, Frederick F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. *J. Wildl. Mgmt. 24(2)* : 162–170.

Krefting, L.W. and H.L. Hansen. 1958. Comparison of winter and spring applications of 2, 4–D to induce regrowth of mountain maple for deer browse. *Minn. For. Notes. (U. Minn.). No. 66.*

Krefting, L.W., H.L. Hansen and R.W. Hunt. 1960. Improving the browse supply for deer with aerial applications of 2, 4–D. *Minn. For. Notes. No. 95.* 2 pp.

Krefting, L.W., H.L. Hansen and M.H. Stenlund. 1956. Stimulating regrowth of mountain maple for deer browse by herbicides, cutting and fire. *J. Wildl. Mgmt. 20(4)* : 434–441.

Lay, Daniel W. 1957. Some nutritional problems of deer in the southern pine type. *Proc. An. Conf. SE. Assoc. Game and Fish Comms., 10* : 53–58.

Leopold, Aldo, Lyle K. Sowls and David L. Spencer. 1947. A survey of over-populated deer ranges in the United States. *J. Wildl. Mgmt. 11(2)* : 162–177.

Leopold, A. Starker and F. Fraser Darling. 1953. *Wildlife in Alaska.* Ronald Press Company, New York. 115 pp.

Longhurst, W.M. 1957. The effectiveness of hunting in controlling big-game populations in North America. *TNAWC. 22* : 544–569.

Lutz, H.J. 1955. Ecological effects of forest fires in the interior of Alaska. *U.S. Dept. of Agriculture. Tech. Bul. No. 1133.* 121 pp.

Mace, Robert U. 1956. *Oregon's elk.* Ore. State Game Comm. 33 pp.

Maliepaard, Hugo S. 1962. Development of a moose harvest plan for the commercial forest zone, Saskatchewan. M.S. Thesis. Montana State Univ., Missoula. 130 pp.

Merrill, Leo B., Comm. Chrom. 1957. Livestock and deer ratios for Texas range lands. *Texas. Agr. Exp. Sta. (Coll. Sta.),* MP–221. 9 pp.

Mohler, Levi L., Paul D. Dalke, and Wesley M. Shaw. 1958. Elk and elk hunting in Idaho. *TNAWC. 23* : 491–500.

Morris, Melvin S. 1956. Elk and livestock competition. *J. Range Mgmt. 9(1)* : 11–14.

Morse, Wm. B. 1958. Sun River medicine. *Amer. Forests 64(4)* : 24–26.

Murie, Olaus. 1958. *The elk of North America.* Stackpole Co., Harrisburg, Pa. 376 pp.

Oosting, Henry J. 1956. *The study of plant communities.* W.H. Freeman and Company, San Francisco. 440 pp.

Peterson, Randolph L. 1952. Review of living representatives of the genus *Alces.* *Cont. of the Royal Ontario Museum of Zoology and Paleontology, No. 34,* Oct. 15. 1–30.

Peterson, Randolph L. 1955. *North American moose.* U. Toronto Press, Toronto. 280 pp.

Pimlott, Douglas H. 1959. Reproduction and productivity of Newfoundland moose. *J. Wildl. Mgmt. 23(4)* : 381–401.

Pimlott, Douglas H. 1961. The ecology and management of moose in North America. *La Terre et la Vie 1961* : 246–265.

Pruitt, William O., Jr. 1959. Snow as a factor in the winter ecology of the barren-ground caribou *(Rangifer arcticus).* *Arctic 12(3)* : 158–179.

Scotter, George W. 1962. Productivity of arboreal lichens and their possible importance to barren-ground caribou *(Rangifer articus).* *Arch. Soc. Zool. Bot. Fennicae 'Vanamo' 16(2)* : 155–161.

Sanderson, Glen C. 1956. Mule deer record for Iowa. *J. Mamm. 37(3)* : 457–458.

Seton, Ernest Thompson. 1927. *Lives of game animals. Vol. 3, Hoofed Animals.* Doubleday, Doran and Company, Inc., New York. 780 pp.

Severinghaus, C.W. 1962. The future for deer in New York. *N.Y. Conservationist 17(2)* : 2–4.

Skuncke, F. 1949. *Moose.* P.A. Norstedt and Sons, Stockholm. 399 pp.

Smith, Norman A. 1962. The fall and winter ecology of the Shiras moose *(Alces alces shirasi),* in the Rock Creek Drainage, Montana. M.S. Thesis. Montana State University, Missoula. 52 pp.

Spencer, D.A. 1958. Prevention of mammal damage in forest management. *Proc. Soc. Amer. For., 58* : 183–185.

Stenlund, Milton. 1958. A history of Itasca Co. deer. *Cons. Volunteer 21(125)* : 19–24.

Stoeckeler, J.H., R.O. Strothmann, and L.W. Krefting. 1957. Effects of deer browsing on reproduction in the northern hardwood-hemlock type in north-eastern Wisconsin. *J. Wildl. Mgmt. 21(1)* : 75–80.

Stoeckeler, J.H. John M. Keener, and R.O. Strothmann. 1958. Deer browse production from felled trees in the northern hardwood-hemlock forest type. *J. For. 56(6)* : 416–421.

Taber, Richard D. 1961. The black-tailed deer. A review of ecology and management. *La Terre et la Vie 2* : 221–245.

Taylor, Dale L. and James B. Elder. 1959. A preliminary survey of deer in Kansas. *Trans. Kans. Acad. Sci. 62(1)* : 67–79.

Verme, Louis J. 1959. Production of white-cedar browse by logging. *J. For. 59(8)* : 589–591.

Weaver, Harold. 1959. Ecological changes in the ponderosa pine forest of the Warm Springs Indian Reservation in Oregon. *J. For. 57(1)* : 15–20.

Printed in England for Her Majesty's Stationery Office by Spembly Publicity, Ltd., Chatham, 51 - 3058.