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THE ECOLOGY AND MANAGEMENT OF MOOSE IN NORTH AMERICA

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Concepts of the status, productivity and management of North American moose (*Alces alces*) have changed greatly during the past decade. The rapidity of the change is illustrated by the published record. TUFTS (1951) questioned, « Is the moose headed for extinction ? » and discussed the then current belief that moose populations had seriously declined across much of the continent. Five years later, PETERSON (1955:217) stated, « It appears almost inevitable that the days of unlimited hunting for moose must soon pass from most of North America. » He also suggested (1955 : 216) that a kill of 12 to 25 per cent of the adult population is the highest that would permit the maintenance of the breeding population. Four years later, I showed (PIMLOTT, 1959a) that moose in Newfoundland could sustain a kill of twice the magnitude suggested by Peterson. I also suggested (PIMLOTT, 1959b) that the North American moose kill could be very greatly increased—in spite of progressive liberalization of hunting regulations over much of Canada and a marked increase in annual kill.

It is not realistic to assume that the status of the species has changed, within the decade, from threatened extinction to annual harvests of approximately 40,000 and potential harvests of two to three times that number. Although moose populations have increased in some areas since 1950, there is little doubt that the changed thinking about moose management is more the result of the increase in knowledge than of any other factor.

I wish to acknowledge the assistance that I received in the preparation of this paper. Several state and provincial Wildlife Departments, of the United States and Canada, respectively, provided me with background information on moose, much of which was unpublished. I am



F. Bourlière



F. Bourlière

Moose in Yellowstone

also grateful for the critical comments of a number of my colleagues.

Populations

Previous Numbers and Fluctuations. — Estimates of North American moose numbers, their trends and fluctuations, have not been based on quantitative information. Either they have been guesses (SETON, 1929) or, at best, have been based on information of a subjective nature, such as trappers' estimates, or on roughly calculated annual kills. PETERSON (1955 : 209-213), in discussing population fluctuations in four provinces based on kill data, stated (1955 : 209), « Since so many variable factors may be influencing these data they must be considered as only rough indications of trends. » I suggest that the variables and biases present are so great that their use in discussing population trends is not warranted. For example, the kill data for Nova Scotia show a peak in numbers in 1931 and a decline between then and 1937 (the decline was particularly marked in 1935 and 1936); however, the annual reports (Nova Scotia, 1936, 1937) did not suggest that the decline in kill indicated a declining population. One of the important variables was the length of the hunting season which was successively shortened from a month, 1928 to 1932, to 20 days, 1933 and 1934, to 10 days, 1935 to 1937.

I studied the annual reports of the province of New Brunswick for the period extending from 1918 to 1937. I concluded that even greater biases and variables are present in these data than in those from Nova Scotia. For example, declines in the reported kill (from 1,381 in 1926 to 842 in 1927, and from 1,066 in 1930 to 447 in 1931) appear to be largely the result of changes in the hunting regulations since they occurred in those years when regulations were changed. In addition, many comments in the reports indicate that the kill data were uncritically compiled.

I conclude that it is impossible to obtain any clear impressions of past trends in continental moose populations from available information. The population data reported by SETON (1929), HOSLEY (1949), PETERSON (1955) and LONGHURST (1957) cannot be compared one to the other or to quantitative estimates presently being made from aerial survey data.

Censusing Moose from Aircraft. — In 1945, ALDOUS and KREFTING (1946) made the first estimate of moose numbers based on an aerial survey. They flew transect

lines on Isle Royale, Michigan, and calculated the population on the basis of the percentage of the total range sampled. Similar studies have since been reported for British Columbia (EDWARDS, 1952; MARTIN, 1952), Ontario (DE VOS and ARMSTRONG, 1954; PETERSON, 1955), and Alaska (SPENCER and CHATELAIN, 1953). Aircraft have also been used to secure population trends (BOWMAN, 1955; NIELSON, 1957). Attempts to appraise results obtained by the transect method were reported by EDWARDS (1952) in British Columbia, and by TROTTER (1958) and FOWLE and LUMSDEN (1958) in Ontario. The latter indicated that the results of transect surveys on the relatively close forest cover of Ontario range were too variable to be of value. As a result, the use of transect surveys has been discontinued in Ontario and a system has been adopted of intensive search of 25 square mile (65 sq. km.) plots. Experimentation and testing of the intensive-search procedures are continuing, for, even with this method, it appears that only about 75 per cent of the moose can actually be seen.

Population and Density. — In the winters of 1957-58 and 1958-59, Ontario conducted aerial surveys of moose over large areas using intensive-search methods. During the second winter, all of the range open to licensed hunting, 180,000 square miles (468,000 sq. km.), was included. The range was divided into four moose-management regions based on the characteristics of the forest type. On 276 plots in the four regions, 2,733 moose were actually observed and 967 others were considered to be present, on the basis of the presence of tracks. It was estimated that the total population of the four regions was approximately 107,000 moose. The population density varied from approximately 1 moose per 6 square miles (15.6 sq. km.) in the southern region where tolerant hardwoods make up the characteristic forest type, to approximately 1 moose per 1.5 square miles (3.9 sq. km.) in the other mixed- or coniferous-forest regions (LUMSDEN, 1959). It is of interest that these population estimates are approximately four times as great as the estimates based on trappers' reports, reported by Reynolds (1953) for the period 1949 to 1953.

A survey based on the Ontario intensive-search method was conducted in Minnesota during the winter of 1960. The survey covered two areas together comprising over 8,000 square miles (20,800 sq. km.). The results indicated a total population of 3,026 moose; density varied from approximately 1 moose per 2 square miles (5.2 sq. km.) to 1 moose per 3.5 square miles

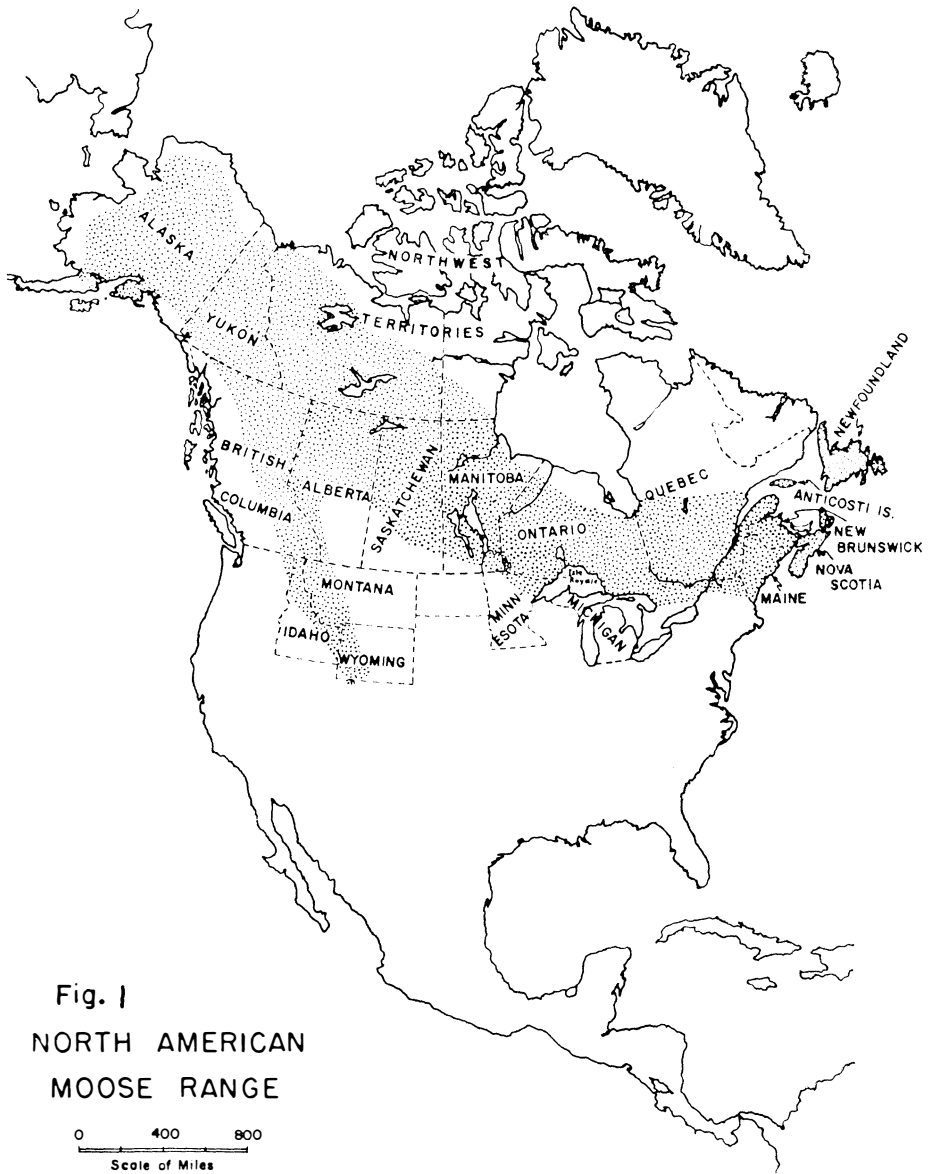


Fig. 1
 NORTH AMERICAN
 MOOSE RANGE

(9.1 sq. km.). The estimates were considered to be minimal for the areas (LEDIN, *in litt.*), since no estimate was made of animals not observed. These estimates indicate that average moose densities in eastern North America may be considerably higher than the 1 moose per 5 square miles (13 sq. km.) suggested by PETERSON (1955 : 202).

In British Columbia, EDWARDS (1952) estimated that there were between 2,000 and 2,500 moose wintering in Wells Gray Park, an area of approximately 2,000 square miles (5,200 sq. km.). HATTER, *et al.* (1956) estimated a winter population of between 4,000 and 6,000 moose in a 1,500 square mile (3,900 sq. km.) area. These authors did not state the area of the range over which these animals disperse in the summer.

Reproduction and Productivity

Generally, moose have been considered to have a low rate of reproduction. The term « barren cow », meaning a cow that has not produced a calf or that has lost her calf, has long been common among northern woodsmen and sportsmen. The concept arose because so many cows were seen without calves at heel. Observational evidence obtained by research programs (PIMLOTT, 1953; PETERSON, 1955; WRIGHT, 1956) confirmed that lone cows are indeed a common phenomenon. However, many facts challenged the belief that moose reproduce slowly.

Two studies were inaugurated, one in British Columbia (EDWARDS and RITCEY, 1958) and one in Newfoundland (PIMLOTT, 1959a) to obtain age-specific data on reproduction. The data for these studies were obtained from the uteri and mandibles of moose shot during the fall and winter period. (In the following discussion, these two studies will be intensively quoted without specific reference to the authors; other works cited will receive specific reference.)

The British Columbia and Newfoundland studies suggest that factors of the environment and/or of the population density, can be just as critical for moose as for domestic or laboratory animals. It seems evident that the reproductive rate of moose living under optimum conditions could conceivably be twice as high as that of moose living under submarginal conditions.

The two studies have given new insight on three aspects of moose reproduction that are basic determinants of the productivity of the species, i. e., breeding

and pregnancy rates of yearlings, pregnancy rates of adults, and the occurrence of twin births. All three of these aspects may vary from area to area. It appears, however, that the breeding of yearlings and the occurrence of twins are particularly indicative of environmental conditions.

In the British Columbia study, the uteri of 15 yearling moose were examined; none was pregnant. This and other evidence leads the authors to conclude « ...that yearling females can be disregarded as a productive age class. » The situation is quite different in Newfoundland, where examination of 107 uteri from yearling moose proved 37 per cent were pregnant. Of the 78 yearlings collected in December or later, 46 per cent were pregnant. The percentage varied from 29, in an area of high moose density, to 67, in an area of lower population density. The occurrence of corpora lutea showed similar variation and suggested that 60 per cent of all yearlings in the areas studied had ovulated.

Marked differences were also evident in the occurrence of twins in the uteri of adult moose. In British Columbia there were 10 per cent twins in a sample of 196. Marked variation existed in the samples collected from year to year. The herd that was studied was migratory, and, basing their conclusion on the fact that twins occurred in years of early migration, the authors suggested that the animals carrying twins were those that summered at higher altitudes. In Newfoundland there were 14 per cent twins in a sample of 182 adult animals. In the section of the island where the occurrence of pregnant yearlings was lowest, only 3 per cent of the adult females were carrying twins, while in the section where the percentage of pregnant yearlings was highest, 41 per cent of the adult breeding resulted in the conception of twins. The incidence of pregnancy among adult moose followed the same trend as the incidence of twinning and of pregnancy among yearlings. The differences were not statistically significant at the .05 confidence level, although the similarity of trend suggests a biological relationship.

In discussing Newfoundland, British Columbia and Swedish data in terms of harvestable rates and rates of population increase, I defined « productivity » as the percentage that can be removed yearly without diminishing the population. I also defined the terms « potential », « gross » and « net » productivity. The gross productivity of Newfoundland moose was of the order of 25 per cent and the net productivity was approxima-

tely 22 per cent, based on the percentage of calves in the fall population. Gross productivity for British Columbia and Sweden was computed at 26 per cent. The data suggested gross rates of increase for the Newfoundland, British Columbia and Swedish data at 33, 36 and 37 per cent, respectively.

Food and Cover

The summer and winter feeding habits of moose have been extensively reviewed by HOSLEY (1949) and PETERSON (1955) for both eastern and western ranges. HARRY (1957) gave a detailed account of moose food habits in winter in the Jackson Hole area in Wyoming. The utilization of browse species for several areas in Newfoundland was studied in detail (PIMLOTT, 1955).

The availability of food in winter is the key to the carrying capacity of any moose area. There are important differences in the winter foods of moose on eastern and western ranges. In the east the key browse species are trees : balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). *Abies* is prominent in the climax forest, while *Betula* and *Populus* occur in the seral stages resulting from fire or logging. On Ste. Ignace Island, in Lake Superior, PETERSON (1953) found that *Abies* comprised 27 per cent of the total winter diet and that it occurred in 100 per cent of the 211 samples of feces that were analyzed. In Newfoundland where *Betula* and *Abies* are the key species, I found that in cut-over or burnt-over areas with moderate to low moose populations, *Betula* often provides 50 to 75 per cent of the total winter diet. As the density of the moose population rises, the utilization of *Abies* increases greatly, and in areas of high moose density it becomes the most important food. It is also the most important food in areas where mature forests predominate (PIMLOTT, 1955).

In the western part of the continent (Alaska, British Columbia, and Wyoming, specifically), a marked difference exists, with shrubs, principally *Salix*, comprising a high percentage of the winter diet. In Wyoming, HARRY (1957) estimated that *Salix* comprised 75 per cent of the winter food. According to MARTIN (1952) and SPENCER and CHATELAIN (1953), *Salix* is also a key species in British Columbia and Alaska.

There is also a marked difference in the winter distribution of moose on eastern and western ranges. In the East the animals tend to be rather uniformly distri-

buted, most commonly in association with immature forests of *Abies*, *Betula*, *Populus* and *Picea*. In the West there is a much greater tendency for them to concentrate, usually in river bottoms or in areas recently burned over (EDWARDS, 1952; HARRY, 1957), where there is frequently little coniferous cover.

Limiting Factors

The reported occurrence of disease and parasites in moose was reviewed by PETERSON (1955), and the subjects of timber wolf (*Canis lupus*) predation, starvation, and competition with white-tailed deer (*Odocoileus virginianus*) and other species were discussed. I will not undertake a similar review of these topics but will attempt, through specific examples, to give additional perspective to the role of some of these factors in limiting moose populations in North America.

It is popularly believed that timber wolves and winter ticks (*Dermacentor albipictus*) are serious limiting factors to moose populations (CALLISON, 1948; COLLIER, 1954, 1955). The hypotheses that interspecific competition with white-tailed deer, or climatic change operating through environmental factors, may be limiting moose populations have been advanced by PETERSON (1955) and by BENSON (1958), respectively.

Moose in Areas of Optimum Range. — Moose were unknown in central British Columbia prior to 1900 (HATTER, 1947, 1948), when they began to populate the area in the wake of forest fires that destroyed vast areas of mature coniferous forests. The population built up very rapidly and had reached peak numbers in some areas by the early 1930's, when heavy winter mortality was first reported. Heavy winter mortality also occurred in the late 1940's and in the early 1950's. HATTER (1949) reported that between 100 and 200 dead moose were found on a relatively small portion of range. Such mortality was probably common in a large section of the central interior, since HATTER (1952) stated that during the years 1945-48 a large part of the calf crop died during the winter.

Timber wolves and the winter tick are indigenous to British Columbia. However, they exercised no apparent effect in slowing the rapid build-up of the population. HATTER (1948) stated that it was not until « ...after a large moose population built up and area after area became overbrowsed by moose that heavy wolf predation

became apparent. » It was at the same stage that infestations of winter ticks became most noticeable. A number of mild winters succeeded the hard winter of 1951-52 with an apparent increase in numbers of moose. HATTER, *et al.* (1956) stated, « A further increase in numbers is virtually impossible, for in spite of the open winters moose ranges are considered at their carrying capacity. »

This evidence indicates that depleted range is the primary factor limiting moose in central British Columbia. The death of moose is often the result of the interaction of a low nutritional plane and a heavy infestation of winter ticks. COWAN (1954) gave a lucid discourse on the possible interaction of these factors.

The history of moose in Ontario has a number of parallels to the one just related for British Columbia. The main build-up of the population is believed to have started at a later date, occurring mostly during the past 25 years. In many areas the population is probably still below the carrying capacity of the range. The important point is that here also the build-up has occurred in the presence of timber wolves and winter ticks. It now appears that, unless hunting pressure can be greatly increased, the limiting factor on moose in many parts of this province will be the limit of the carrying capacity of the range.

Insular Moose Populations. — Moose occur in three insular situations where timber wolves are absent, or were absent during the periods that I will consider. Moose were introduced into Anticosti Island (NEWSOM, 1937) and into Newfoundland (PIMLOTT, 1953) around the turn of the century. At about the same time they reached Isle Royale, in Lake Superior, apparently having crossed over on the ice from Ontario (MURIE, 1934). The areas of the three islands are 4,000, 42,000 and 210 square miles (10,400, 109,200, and 550 sq. km.) respectively. Moose increased very rapidly on Isle Royale, and by 1930 had reached an estimated density of between 5 and 15 per square mile (2.6 sq. km.) (MURIE, 1934). Very severe mortality from starvation occurred shortly after, and the population declined abruptly. The population has since increased again as a result of a fire that burned more than one-fourth of the island in 1936 (ALDOUS and KREFTING, 1946; KREFTING, 1951).

White-tailed deer and moose were introduced into Anticosti Island at approximately the same time (NEWSOM, 1937). The deer increased very rapidly, and heavy mortality was reported in 1934. I visited Anticosti in

1953 and found the deer to be very numerous. Moose have persisted on the island but they have established themselves in only one area. I observed that all of the browse species palatable to moose were intensively utilized by the deer, and that the winter feces of moose were always associated with those of deer. The deer browsing on balsam fir and white birch is so severe that it is virtually impossible to find an unbrowsed seedling or sapling in an unprotected location. In such locations I was unable to find any balsam fir originating as a seedling since 1930 that had grown beyond 6 feet in height.

Six moose were introduced into Newfoundland, two in 1878 and four in 1904 (PIMLOTT, 1953; PIMLOTT and CARBERRY, 1958). It appears that the colonization of the island resulted largely from the second introduction. The moose spread rapidly across Newfoundland during the first 30 years and then began to increase in density. By 1950, when a research program was started, it was evident that overpopulations existed in a number of areas, although no winter mortality had occurred. A considerable portion of the good range is centered on the trans-island railroad, and is at least moderately accessible through roads built and maintained by newsprint-manufacturing companies. By 1958 it was estimated (PIMLOTT, 1959b) that 60,000 moose had been harvested by the people of the island since the moose were introduced. In most areas that are accessible to moose hunters, the intensive kill appears to be maintaining the herd at a healthy level. Parts of the interior are inaccessible to hunters and in these areas hunting pressure is too low to act as a limiting factor. The browse species are intensively utilized, and it appears that the population in these areas is being, or will be, limited by a lowered productivity rate, and possibly by winter mortality as a result of a limited food supply.

The history of moose in these three insular areas suggests that interspecific competition with white-tailed deer may be the primary factor limiting moose on Anticosti Island.

Moose at the Southern Limit of their Range. — In eastern North America, Nova Scotia, New Brunswick and Maine were popular moose-hunting areas during the first third of the present century. Hunting seasons have been closed in the three areas since the late 1930's, due to the reported decline of the moose population. There is little or no factual evidence to support the contention that the populations had, in fact, declined in Nova Scotia

and New Brunswick prior to the closing of the hunting seasons. The one generalization that can be made—a conclusion drawn from studying the literature (New Brunswick, 1940-58; Nova Scotia, 1940-58; Wright, 1956; BENSON, 1958)—is that the closed seasons have not resulted in population increases such as those that have occurred in British Columbia, Newfoundland, Isle Royale, and parts of Ontario. BENSON (1958), in fact, stated that the moose population in Nova Scotia decreased rapidly between 1940 and 1955. The factors that are believed to be most important in limiting moose populations in these areas are interspecific competition with white-tailed deer (PETERSON, 1955), and moose « disease » or « sickness » resulting from climatic changes (BENSON, 1958).

There is a very broad overlap in the food and cover requirements of white-tailed deer and moose (PIMLOTT, 1954; PETERSON, 1955), and, as PETERSON (1955 : 169) stated, « In areas where either moose or white-tailed deer become abundant, there is little doubt that direct competition for the available food takes place, especially during the winter months. » He concluded that in the Canadian Biotic Province, as described by DICE (1943), deer have been an important factor in preventing moose from increasing, but that in the Hudsonian Province there was no evidence that this happened. I examined this hypothesis (PIMLOTT, 1954) and found that the areas of Nova Scotia and New Brunswick where moose were reported to be most numerous were the higher mountainous regions of each province. I concluded that these regions are probably outposts of the Hudsonian Biotic Province.

White-tailed deer reached Nova Scotia in the 1890's with the first hunting season in 1916 when 154 were killed. This species increased very rapidly; and in 1951 over 42,000 were killed (BENSON, 1954). The kill has since declined and in 1958 was approximately 31,000 (Nova Scotia, 1959). The history of the white-tailed deer population in New Brunswick is similar, although the annual kill has not reached the magnitude of the kill in Nova Scotia. The kill in 1958 was just over 20,000 animals (New Brunswick, 1959).

The winter tick and moose « disease » or « sickness » have always been prominent in the discussions of moose population decline in the eastern section of the continent. The occurrence of « moose disease » was first investigated in Minnesota (FENSTERMACHER and JELLISON, 1933; FENSTERMACHER, 1934, 1937; FENSTERMACHER and OLSEN,

1942), later in Maine (LAMSON, 1941), and in considerable detail in Nova Scotia (BENSON, 1958). BENSON (1958) concluded that the « disease » as described for the three areas « ...is a single entity... although no organism or pathogen has been isolated. » He concluded, « Climatic changes, operating through environmental changes and resultant nutritional problems are believed to constitute a primary cause of the decrease in the moose population during the past 25 years. » The possible influence of climatic change was discussed in an earlier paper (HAWBOLDT and BENSON, 1953). The authors stated that during the preceding 25 years (1928-1953) average daily temperatures had increased by almost 2 degrees, and that summer temperatures in New Brunswick had increased steadily since 1870, and since 1905 in Nova Scotia.

It appears that Benson does not accept the hypothesis of white-tailed deer dominance advanced by PETERSON (1955), for he does not refer to it in his paper (BENSON, 1958). The possible effect of interspecific competition with white-tailed deer cannot be disregarded. It is obvious from the kill records that Nova Scotia has been, and still is, supporting a high-density white-tailed deer population. This deer population could also have caused, or at least interacted with other factors to bring about, the environmental changes and nutritional problems which BENSON (1958) believes are responsible for the decline of the moose population.

Problems in the Management of Moose

The most pressing problem in the management of moose in North America is an inadequate harvest. Because very little information is available on moose throughout much of the northern part of their range where hunting is, to a large extent, done by Indians, the preceding statement and the following discussion apply to the moose range that is open to licensed hunting. In Ontario, for example, this consists of approximately 180,000 square miles (468,000 sq. km.), or about one-half the area of the province.

The problem of an inadequate harvest is complex and is usually the result of the interaction of a number of factors. Some of these factors are : (1) lack of detailed information on the status and ecology of moose, resulting in fears that the population will be decimated by more intensive kills; (2) inaccessibility of large areas, because of lack of roads or the refusal of forest industries to

permit hunters to traverse private roads; (3) public pressure against liberalizing hunting seasons and against the killing of calves and females; (4) lack of inclination and/or ability of most hunters to penetrate into a hunting area more than a mile (1.6 km.) from an established road. This last factor is common to most areas of North America.

Both the United States and Canada have federal systems of government and the jurisdiction of big game is vested in the individual states and provinces. Big-game hunting regulations may be established by direct action of the legislature (a common practice in the United States), by action of the Cabinet, or by action of the Cabinet Minister who heads the agency that administers the wildlife resources. (The two latter practices are most common in Canada). The large number of controlling agencies and the variety of means of establishing regulations result in a complex pattern of hunting seasons and regulations.

North American moose range can be broken down into five principal classes where somewhat similar regulations exist for the protection and harvest of the moose population. These classes are areas where : (1) There are no moose-hunting seasons. (2) There is a restricted issue of hunting licenses and where both sexes are hunted. (3) Only the hunting of male moose is permitted. (4) Female moose are hunted for shorter periods than males. (5) The hunting of moose of any sex or age is permitted for seasons extending up to four months in duration. Areas where moose are rare or where populations cannot be considered to have hunting potential, e.g., Michigan, New Hampshire, will not be included in the discussion.

Much of the information on which this section is based was obtained from published hunting regulations and annual reports of state and provincial organizations. Statements that are not otherwise documented are based on information from these sources. A list of the annual reports is included in the bibliography.

No Moose-hunting Seasons. Nova Scotia, New Brunswick, Maine, Minnesota. — The four areas that fall into this category are at the southern limit of moose range; closed seasons have been in effect there for periods varying from 23 to 38 years. They were all previously mentioned in the section on limiting factors.

The available information, including WRIGHT, 1956; K. W. HODGON, *in litt.*; Nova Scotia, 1957, suggests

that, although the moose populations are not high, some hunting could be permitted in Nova Scotia, New Brunswick and Maine. Some of the most pressing problems are the lack of detailed information on the status of the population, the high density of big-game hunters and the presence of white-tailed deer on the same range. When hunting seasons are opened it will be imperative to obtain detailed information on the kill from year to year, to determine the effect of the harvest on the moose populations of the three areas.

Restricted Issue of Hunting Licenses. Idaho, Montana and Wyoming. — These three states have the problem of attempting to maintain adequate, but not excessive, harvests of moose in the face of the complicating factors of small migratory moose populations that sometimes summer in one state and winter in another, a large number of big-game hunters, and the association of both elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) with moose on some sections of the range.

It appears that, in all three states, control of the kill is gradually being attained through the use of a system of restricting the issue of hunting licenses to a specified number of hunters. Both male and female moose are hunted in the three states (COLE, *in litt.*; BROWN, *in litt.*; NIELSON, 1957).

Hunting of Male Moose Only. Alaska and Quebec. — In these two areas, the situations that have resulted in restricting the hunting to male moose only, seem to be diametrically opposite. An intensive moose-research program is being conducted in central Alaska and some reports have been published (CHATELAIN, 1950; SPENCER and CHATELAIN, 1953). It is apparent from these reports and from annual reports of the Alaska Game Commission that there is no lack of information on the ecology and status of the species. It is also evident that a number of areas are being underharvested (LEOPOLD and DARLING, 1953 : 89-93). It is obvious that a considerable part of the underharvest of moose can be attributed to failure to legalize the hunting of both sexes and to adjust seasons so that adequate kills can be made.

The situation in Quebec appears to be one of a very incomplete knowledge of moose-population status and ecology, giving rise to fears of overharvest. The data provided LONGHURST (1957) by provincial authorities that suggested a static population of 12,000 moose in approximately 100,000 square miles (260,000 sq. km.) of moose range, reflect the lack of knowledge. It cannot be

considered a realistic statement of conditions, in view of the present status of moose elsewhere on the continent, and particularly in adjacent parts of Ontario.

Female Moose Hunted for Shorter Periods than Males. Alberta and British Columbia. — Although these two provinces both restrict the hunting of females to a portion of the regular season over all, or most, of their hunting zones, there is considerable variation between them. In 1959, for example, Alberta had a number of zones where only males could be hunted and in other zones permitted hunting of females and calves for only 4 days. The same year British Columbia had one zone where moose of any sex or age could be killed during the entire season, and a number of other zones where females and calves could be killed for periods up to a month in duration. In Alberta, the male hunting season was most commonly about 1 month's duration, while in British Columbia seasons of from 6 weeks to 10 weeks were common.

The trend toward liberalization of hunting regulations began in British Columbia in 1952, however, the first hunting of cows and calves was not permitted in Alberta until 1957.

The effect of the liberalization of regulations in British Columbia has been very pronounced as evidenced by an increase in kill from 5,220 in 1954 (Hatter, 1956) to approximately 11,500 in 1958 (British Columbia, 1959). In Alberta the estimated kill of moose was 5,540 in 1955 (Alberta, 1956) and approximately 5,000 in 1958 (Webb, 1959a). It is evident that high moose populations exist in a number of parts of Alberta and that winter mortality is occurring on some ranges (Webb, 1959a, 1959b; Alberta, 1959) as a result of underharvesting. This mortality and the short seasons for hunting female moose suggest that hunting regulations still tend to be too restrictive in this province.

Hunting of Moose of Any Sex or Age. Newfoundland, Ontario, Manitoba and Saskatchewan. — The first season open to the hunting of moose of any sex or age was held in 1953 in Newfoundland, Ontario and Saskatchewan and in Manitoba in 1959. In the case of Manitoba, the hunting of female moose over one year of age had begun in specified areas in 1953. The province still maintains the male-only regulations for the early season, September 21-October 17, in northern sections of the province.

The length of the hunting seasons is quite variable. In 1959 it extended over a 4-month period in Newfoundland, and was between 1 and 2 months in the other three provinces. The sale of hunting licenses and the annual kill increased markedly, co-incidental with the liberalization of hunting regulations. The most important remaining barrier to an adequate harvest of moose in these four provinces is inaccessibility of range.

The effect of Moose-browsing on the Forest. The extent to which moose have influenced, or are influencing, the development of plant associations in North America is not well known. The majority of studies (ALDOUS and KREFTING, 1946; KREFTING, 1951; PETERSON, 1953; SPENCER and CHATELAIN, 1953) have been specifically designed to provide data on palatability, availability and utilization of winter browse species rather than to show the effect of browsing on the flora. The exception to this is a study that I conducted in Newfoundland, the main objective of which was to obtain a quantitative appraisal of the effect of moose-browsing on commercial tree species (PIMLOTT, 1955).

I pointed out earlier that three species are more important in the diet of eastern than of western moose. This suggests that eastern moose probably exert greater influence in the development of the forest than do western moose. Because there is very little quantitative information published on moose-browsing on western range, and because I have had no personal experience in western areas, I will not attempt to discuss situations there.

In the boreal forest formation over wide areas of eastern North America, white spruce and balsam fir are the principal associates of the climax. White birch and trembling aspen are successional after disturbance by logging or fire and occur in pure or in mixed stands in the secondary succession. It is these young mixed stands that are most affected by moose-browsing.

In Newfoundland, removal of the mature forest by logging results in a secondary succession in which balsam fir is more numerous than the combined numbers of the other associates, including the shrub species. White birch is the most common deciduous species, and is very heavily utilized by the moose. In many areas browsing has been so heavy that reproduction of this species is being almost entirely limited. I concluded that the moose population would have to be reduced if white birch was not to lose its potential as a commercial tree species.

In the case of balsam fir, moose-browsing does not have serious economic implications until moose populations approach the carrying capacity of an area. I concluded that the intensity of browsing was of economic significance in three of the six areas that I studied.

I concluded that when heavy browsing pressure is maintained in an area, there is a resultant marked increase in the length of the rotation period, virtually complete elimination of white birch, and a higher percentage of spruce in the climax associations.

In the case of the shrub associates, ground hemlock (*Taxus canadensis*) is highly palatable to moose. It is the first species to show the effect of browsing as the moose population of an area builds up. It is often almost completely eliminated from areas where high moose populations exist. This trend has been well documented for Isle Royale (MURIE, 1934; ALDOUS and KREFTING, 1946) and was evident to me in many Newfoundland areas.

Summary

During the past decade, in North America, many concepts about moose have changed. Fears that they would be extirpated have been replaced with the knowledge that, when in good habitat, they can withstand heavy hunting pressure.

Many of the past estimates of moose numbers and population trends have been guesses, or have been based on information of a subjective nature. In general, very little is actually known about previous moose numbers and fluctuations.

Aircraft are now being used extensively to census moose. A transect-line survey method is widely used, however, in Ontario, the results obtained by this method are considered to be too variable to be of value. A system of intensive search of 25-square-mile (65-sq.-km.) plots has now been adopted for use in the province. Results of aerial surveys indicate that densities of 1 moose per 1 or 2 square miles (2.6 or 5.2 sq. km.) are not uncommon for large units of range.

The results of studies conducted in British Columbia and Newfoundland have shown that the reproductive rate of moose is quite variable. Three aspects of moose reproduction—breeding and pregnancy rates of yearlings, pregnancy rates of adults, and the occurrence of twins—were found to vary from area to area.

There are important differences in the winter food and cover of moose on eastern and western ranges. In the East the key browse species are trees, while in the West the most important species are shrubs (*Salix spp.*). Moose on eastern range tend to be rather uniformly distributed in winter, while on western range large concentrations are much more common.

The possible role of factors that limit moose populations is considered by the use of three examples : moose on optimum range, on islands, and at the southern limit of eastern range. Over most of the area of moose range, food shortage, interacting with winter tick infestations, appears to be the primary limiting factor. The inadequacy of the annual harvest is the most pressing problem in the management of moose. Hunting regulations across the continent vary from completely closed seasons to long open seasons for the hunting of animals of any sex or age.

Browsing by moose appears to have the greatest effect on the flora of the secondary succession of the white spruce-balsam fir-white birch associations of the boreal forest formation. White birch is highly palatable to moose at all times of year and under heavy browsing pressure it may be eliminated. Balsam fir is a winter food and is not seriously affected until the carrying capacity of the range is reached. Of the shrubs, *Taxus* is most heavily utilized and it virtually disappears when heavily browsed.

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