THE ECOLOGY OF THE
Isle Royale Moose
WITH SPECIAL REFERENCE TO THE HABITAT

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RAL EXPERIMENT STATION
OF MINNESOTA

LEFT: This bull moose, feeding on upland vegetation in the summer, has antlers still in the velvet stage. (Photo is by D.R. Hakala, formerly of the National Park Service.) MIDDLE LEFT: This cow moose browses on basal sprouts of paper birch. (Photo is by Ernest Mulch, formerly of the Fish and Wildlife Service, USDI.) MIDDLE RIGHT: Here is ground hemlock, the most highly preferred moose food throughout the year. This luxuriant growth is within the exclosure at Windigo. BOTTOM LEFT: Deformed aspen are the result of severe moose browsing in the 1936 burn area. BOTTOM MIDDLE: This boat, named "Moose," was required to efficiently perform research on the large, rugged island. The 45-mile-long island has no roads but does have a system of foot paths. BOTTOM RIGHT: Paper birch is the most abundant tree species on the island.

ON THE COVER: Figure 1. This bull moose is feeding on aquatic plants in Washington Harbor. Moose can feed on pondweeds 8 feet deep or more. To do this, the moose completely submerge themselves. (Photo is by Maxham Photos, Duluth.)

ACKNOWLEDGMENTS

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Figure 2. This bull moose is standing in a clearing in the Windigo area of Isle Royale. Each year, thousands of visitors travel to Isle Royale to enjoy the scenery and to observe the moose. (Photo is by K.T. Gilbert, National Park Service.)

INTRODUCTION

The moose *(Alces alces andersoni)* occupies a prominent position in the fauna of Isle Royale National Park. Drastic die-offs from overpopulation in the early 1930's and late 1940's, together with the arrival of the timber wolf in the late 1940's, has focused worldwide attention to this island located in northwestern Lake Superior. At the request of the National Park Service, ecological study of the moose – with special reference to its habitat – was initiated by the U.S. Fish and Wildlife Service in 1944. Available funds and manpower limited research to include only winter range requirements. However, the importance of spring, summer, and fall ranges was recognized. Although the winter range regulates the upper limits of the population, the summer range determines the physical stature of the moose.

Moose exclosures were also established. These measured long term effects of winter browsing on survival and growth of trees and shrubs. Population trends were obtained from airplane counts in 1945 and 1947 and from pellet group counts in 1948, 1950, 1961, 1965, and 1970. Procedures and methods varied over the years, depending on the objectives of each phase of research. These procedures and methods are described under individual section headings. During this study, seven papers were published about Isle Royale: three on the moose (Aldous and Krefting, 1946; Krefting, 1951 and 1973); one on the birds of Isle Royale (Krefting et al., 1966); one on the history of the beaver (Krefting, 1963); one on the history of the coyote (Krefting, 1969); one on the forest of Isle Royale in relation to fire history and wildlife (Hansen et al., 1973); and a vegetation map of Isle Royale National Park (Krefting et al., 1970).

DESCRIPTION OF THE ISLAND

Isle Royale is the largest island on Lake Superior. It covers approximately 210 square miles and has about 200 small islands and rock outcrops. This wilderness archipelago – accessible only by boat or float plane – was set aside as a National Park in 1940. The park was dedicated in 1946. Interest in the island stems from its scenery and wilderness character as well as from its archeology, fauna, history, and geology. The main island – 45 miles long and 8 miles wide at its farthest reaching points – roughly parallels the north shore of Lake Superior. The closest point to Ontario, Canada, is 13 miles, and the distance to Minnesota is about 18 miles (figure 3). Because of its location in northwestern Lake Superior, the climate, vegetation, and animal life are associated more closely with Canada and Minnesota than with the south shore of Lake Superior (Hansen et al., 1973).

Since there are no roads, travel within the park is mostly on foot. The island has 120 miles of trails. Isle Royale's unique natural beauty, its prehistoric and early copper mining, and its commercial fishing have combined to create an interest which is lacking in more easily reached islands.

George Shiras III (1935) regarded Isle Royale as the most beautiful and most interesting island in the Great Lakes. Others have described it as the "Wonder Island of the North" and the "Enchanted Island" (Krefting, 1963). Gilchrist (1968) observed that "Isle Royale resembles a long piece of driftwood, half-worn to splinters; the toughest fibres standing out in ridges, some knotholes and gashes for lakes."

As early as 1640, rumors of copper on Isle Royale had reached France through explorers and Jesuit missionaries. The Indians showed these people pieces of copper, but the Indians were reluctant to talk about the metal. Copper was considered a gift from gods who lived beneath the waters of Lake Superior (Jackson, 1849; Gilchrist, 1968). Radio carbon-dating of wood recovered from prehistoric mines has shown that aboriginal mining of copper on Isle Royale was carried on at least 3,300 years ago (Drier, 1961). Copper mining was tried intermittently in the last half of the 19th century, but it proved economically unfeasible. Explorations were abandoned by 1900. The first attempts at mining flourished from 1844-55. Later attempts were from 1871-83; and the last explorations were made from 1889-99.

Commercial fishing has had the longest continuous history of economic activity on Isle Royale (Rakestraw, 1968). Rakestraw has reviewed this enterprise for the period 1800-1967. Although commercial fishing probably started before 1800, historic records show it was initiated by the American Fur Company in 1837 (Nute, 1926). Fishing posts were maintained at four locations on the island before operations ceased in 1841. During a 3-year period (1837-1839), 12,000 barrels of salt fish were shipped from the island (Rakestraw, 1968). The three kinds of fish sought were lake trout *(Cristivomer namaycush*)*, whitefish *(Coregonus clupeaformis)*, and lake herring *(Leucichtheys artedi)*. Fishing continued after the American Fur Company closed its operations. By the 1880's, there was a boom in fishing (Rakestraw, 1968). Each year, from 20 to 60 crews came from the mainland in June and left in November. The passage of time and the arrival of the sea lamprey *(Petromyzon marinus)* in Lake Superior and around Isle Royale have resulted in a drastic reduction in commercial fishing.

Isle Royale was subjected to the action of ice sheets of the Pleistocene Age. These ice sheets ground the rocky surfaces smooth and gouged out basins that are present day lakes. Now there are 38 named lakes and about as many unnamed ponds. The largest and deepest is Siskiwit which is about 7 miles long and 140 feet deep. Drainage is poor within the valleys, although there are four important streams: Big Siskiwit River; Washington Creek; Little Siskiwit River; and Tobin Creek. The south shore and the two ends of the main island have sheltered coves and deep fiordlike harbors. These offer good weather protection for boats. In contrast, the north side of the island has few protective harbors.

The island has been of special interest to geologists for at least 125 years.

*Scientific names follow Hubbs, C.L., and K.F. Lagler (1949), Fishes of Isle Royale Lake Superior, Michigan. Papers of the Mich. Acad. Sci., Arts, and Letters 33:73-133.

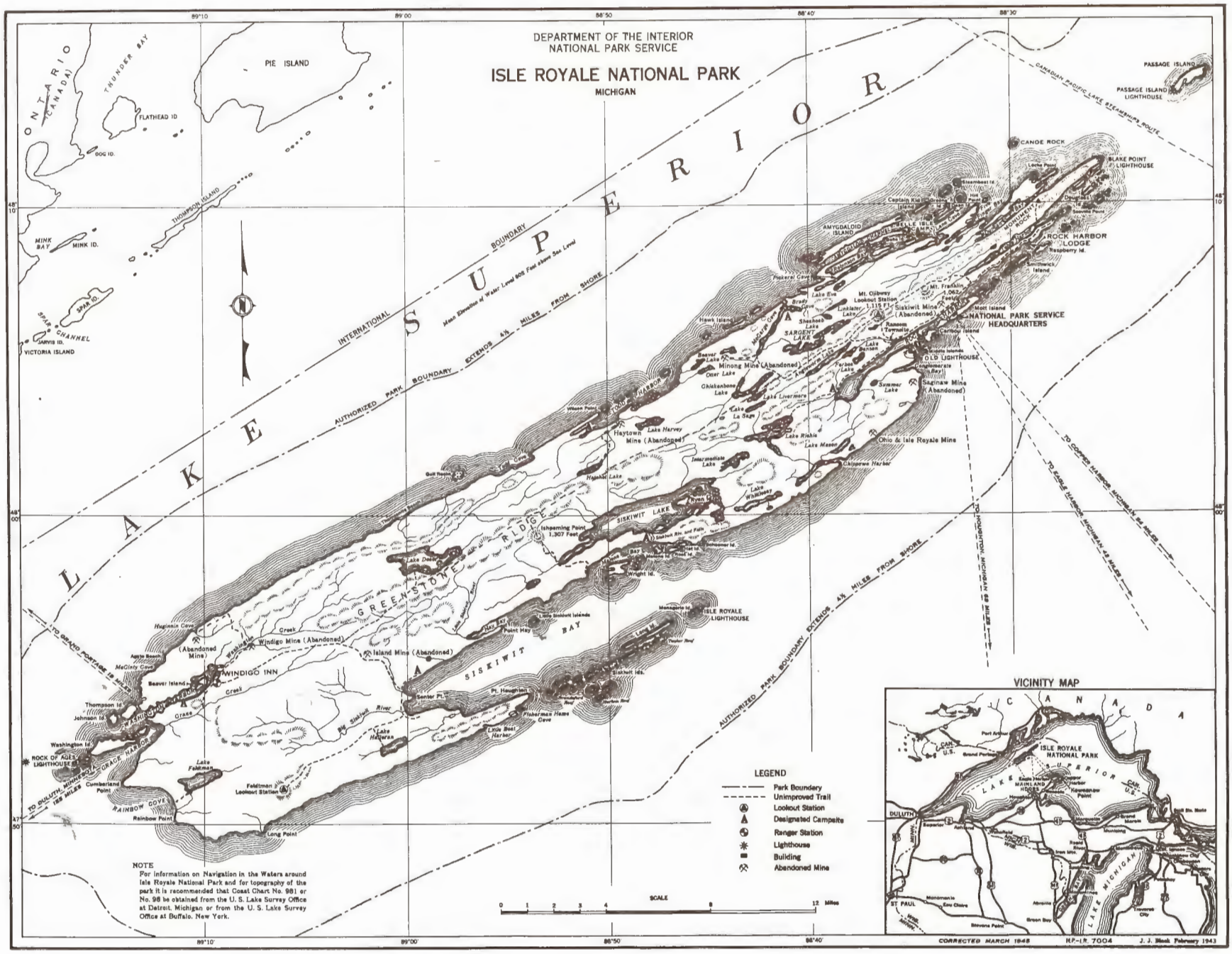


Figure 3. Isle Royale National Park is an island 210 square miles in size. It is 45 miles long and 8 miles wide at its widest point.

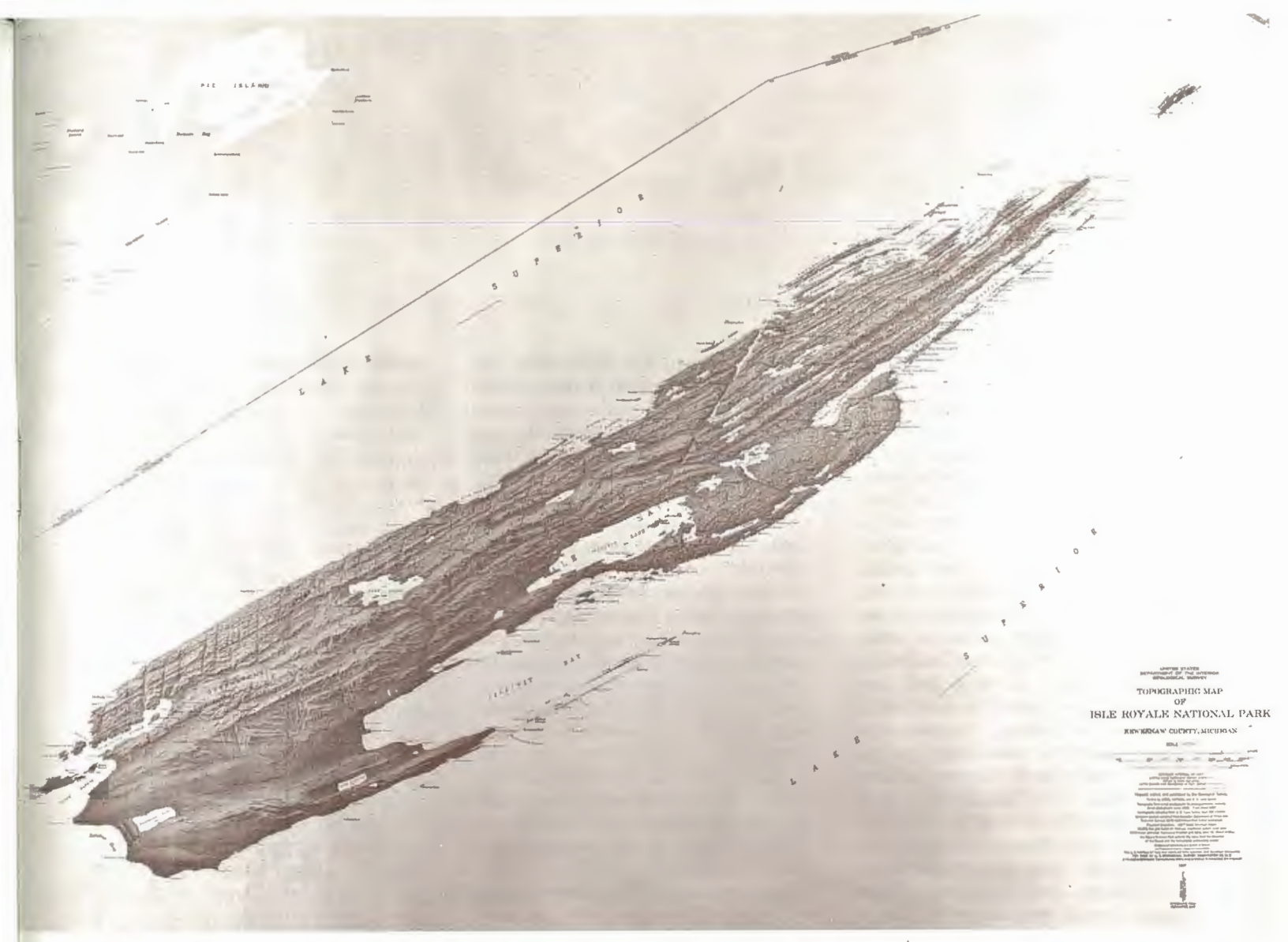


Figure 4. This topographic map of Isle Royale National Park shows Greenstone Ridge, which runs the full length of the island.

Foster and Whitney (1850, 1851) reported on the first survey by the federal government. Bedrock geology was later described by Lane (1898). Huber (1973) made the most comprehensive study which has provided the basis for the following descriptions. Thin rock-mantled soils – formed mostly from till, talus, and some glacial debris – cover most of the island. These soils are deepest in the southwest section. Ancient beaches and wave-cut terraces at various levels document the postglacial lake levels in successive stages. The island emerged after the glacial ice was removed from the earth's crust.

The topography is mostly rough and rocky. It has numerous ridges of varying lengths, and heights are oriented northeast and southwest (figure 4). These landform features were formed in preglacial times by the differential erosion of the softer and harder strata in the outcrops of the Keweenawn lava flows. These lava flows contained narrow bands of interbedded sediments. Only the southwestern section of the island consists mainly of sediments, sandstones, and conglomerates (Lane, 1898). The most resistant flows formed the Greenstone Ridge which is the backbone of the island; less prominent ridges are the Minong and Red Oak. The southeastern slopes are quite gentle and correspond to the structural dip of the rock formations. In contrast, the northwestern faces are more precipitous. Mount Desor in the southwestern area – the highest point on the island – has an elevation of 792 feet above Lake Superior.

Pollen samples – collected from nine bogs at different levels above present day Lake Superior – have made vegetative chronology possible (Potzger, 1954). Pollen samples from lower elevations record the decline of the fir-spruce dominance. They reveal the span of the xerothermic climatic period when *Acer, Quercus,* and *Pinus* pollen predominated. In later research, Linn (1957) noted . . . "bogs at the lowest elevations record only the recent spruce-fir climatic climax; a fact which supports the theory that the island has emerged from Lake Superior waters in successive stages since glaciation."

CLIMATE

Isle Royale's climate is typical of the Great Lakes region. The island's rather cool summers and sometimes severe winters are somewhat modified by Lake Superior. Some years, ice bridges form between the island's northwestern shore and the Canadian mainland. Records show solid bridges formed in 1961, 1962, and 1963. Weather records are incomplete since the Park Service has complete records only for spring, summer, and fall and only for a 6-week period in winter starting in 1958. To better understand the Isle Royale climate, data were gathered from lakeshore stations in Michigan, Minnesota, and Wisconsin (table 1). These were based on the data of Stromme (1969), on climatological data of the U.S. Department of Commerce (1941 – 1972), and on a summary by Hansen et al., 1973. Comparative data show the high and low temperature extremes and the mean annual temperature at Grand Marais, Minn., are much like Isle Royale. An exception is the first fall freeze; it usually occurs 2 to 3 weeks later on the island, indicating the strong moderating influence of Lake Superior.

The summer rainfall is well-distributed. It ranges from a minimum monthly mean of 2.1 inches in October to a maximum monthly mean of 3.4 inches in September (Hansen et al., 1973). The earliest snowfall usually occurs in late October. Some years, patches may be found in protected areas in May. Snow accumulation is light or moderate most years when 18 to 24 inches occur except for drifts on the northwestern faces of ridges. There, snow seldom exceeds 36 inches. Mech (1966) noted that depths did not exceed 26 inches in wind-protected areas in 1959, 1960, and 1961. From 1962 to 1972, snow depths exceeded 36 inches only for short periods in 1966, 1969, and 1972 (Park Service, Houghton, Mich.). Winter temperature records (late January to about March 15) from 1962 to 1972 showed that temperatures were 20 degrees below 0°F. seven times. The lowest temperature was -28°F. in 1966. In the fall, frosts sometimes occur as early as mid-September.

Since climate is generally the ultimate factor determining broad aspects of vegetation, the island vegetation is more closely related to the nearby mainland of Ontario and Minnesota. Linn (1957) found microclimatic relationships within the island. He said that the Lake Superior effect moderated temperatures and increased air moisture in shoreline areas. He found warmer and drier conditions on the southeastern slopes compared to the northwestern exposures. These differences had a direct effect on the species composition and type distribution patterns of vegetation.

Table 1. Comparative weather summary on Isle Royale and vicinity.*

	Grand Marais, Minn.	Bayfield, Wis.	Ontonagon, Mich.	Mott Island,[1] Isle Royale
Highest temperature (F) and median date	82° (July 17)	94° (July 30)	93° (July 18)	89° (July 20)
Lowest temperature (F) and median date	-33° (Jan. 22)	-33° (Jan. 25)	-36° (Feb. 5)	-29° (Feb. 13)
Median date last spring frost	May 15	May 16	May 22	May 17
Median date first fall frost	Sept. 24	Sept. 28	Sept. 17	Oct. 15
Mean annual temperature (F)	39.0°	43.0°	46.6°	38.1°
Total annual precipitation (inches)	24.72	26.68	28.56	30.44

*U.S. Weather Bureau and Isle Royale National Park records.

[1] May through October data available since 1941. Because of some gaps in records, especially for November and April, Isle Royale data are not strictly comparable to other stations.

VEGETATION

Early accounts – 1840 to 1900

The earliest reference to the island vegetation was from an 1840 Indian Service report. It said, "Indeed a barren rock island of about 8 to 15 miles from the mainland, covered with small scrubby timber, destitute of game, with the exception of a solitary herd of reindeer, and almost of soil, it is incapable of supporting even an Indian population" (U.S. Indian Service Annual Report for the Fiscal year 1840, p. 354).

Some basic information about the island's vegetation was obtained from the Ives' linear survey notes and the notations he made on the survey plats. These notes discussed the island's vegetation, soils, and forest fires (Ives, 1848). From tabulations of 1,578 witness trees at section corners, the following species distribution (percent) was found: balsam fir *(Abies balsamea*)*, 40; northern white cedar *(Thuja accidentalis)*, 22; spruce *(Picea glauca* and *Picea mariana)*, 16; paper birch *(Betula papyrifera)*, 8; yellow birch *(Betula alleghaniensis)*, 6; tamarack *(Larix laricina)*, 5; sugar maple *(Acer saccharum)*, 2; and aspen *(Populus tremuloides)*, 1.

Balsam poplar *(Populus balsamifera)* and white pine *(Pinus strobus)* made up less than 1 percent of the distribution (Hosley, 1949). Selection of these species as witness trees probably approximated their distribution in the forest types, with the possible exception of short-lived aspen. For the shrubs, written descriptions of the 72 surveyed sections revealed this distribution (percentages): ground hemlock *(Taxus canadensis)*, 56; mountain maple *(Acer spicatum)*, 60; beaked hazelnut *(Corylus cornuta)*, 46; and speckled alder *(Alnus rugosa)*, 18.

*Botannical nomenclature of tree species follow Little (1953); that of shrubs and herbs, Fernald (1950).

A forest cover-type map was also reconstructed, based on Ives' (1848) data about the Washington Harbor area (Pietela, 1965). The map showed that white cedar, tamarack, and white pine were apparently more common in 1848 than they were in 1965. Linn (1957) found yellow birch was more widely distributed than was sugar maple in 1848.

Jackson (1849) also described the island's vegetation. He said the upland was a mixture of maple, birch, spruce-fir, and pine trees. The lowlands were mostly thick evergreen swamps of white cedar. Foster and Whitney (1850) reported the shores were lined with dense, but dwarfed, forests of cedar. These trees had drooping festoons of moss on their branches.

Although from about 1844 to 1900, interest in the island was pretty much centered on copper mining, Isle Royale gradually attracted plant collectors. After 1900, interest in the island's flora continued rapidly. Adams (1906 and 1909), Cooper (1911, 1912, 1913, 1914, and 1928), McMurray (ca., 1933), and Brown (ca., 1935) gave it special attention.

Ecological Studies – 1900 to 1973

In connection with a 1905 ecological survey of northern Michigan, A.G. Ruthven visited Isle Royale from Aug. 13 to Sept. 15 (Adams, 1906). His party collected 91 plant species. Ruthven noted there was a preponderance of boreal plant societies in addition to certain plants and animals usually associated with western ranges. Adams (1909) established field stations to collect flora and fauna and to describe the habitats. He reported on the ecological succession of birds (p. 121-154), and Max M. Peet prepared an annotated list of these birds. W.P. Holt collected plants and made plant society studies. H.A. Gleason described habitats and their lines of development leading to the climax forest.

W.P. Holt (p. 224 in Adams, 1909) said balsam fir was the most common conifer and was superseding spruce and tamarack. He added that aspen and birch dominated burns and clearings. These aspen and birch had understories of bush honeysuckle, thimbleberry, flowering dogwood, and blueberry. He reported the presence of ground hemlock to be: "Everywhere abundant in the upland forest of the island. On account of its low, spreading growth, it forms one of the greatest impediments in penetrating the island's forests. The rankest growth was noted in the lower forest region around Washington Harbor where it attains a height of four or five feet" (Holt, p. 236 in Adams, 1909). That area still has scattered sprigs of ground hemlock.

This ground hemlock is such highly preferred moose food that the moose browses the area all year. The species is now thriving within an exclosure established in 1948 in the Windigo area. Holt (p. 226 in Adams, 1909) also noted: "The succession of the burnings and clearings due to the early copper prospectors to clear the land, as well as the results of later forest fires, presents an interesting problem; also, the peculiar distribution of hard maple and white pine on the island." Gleason (p. 77, 78 in Adams, 1909) reported three lines of plant succession: through the tamarack and peat bog; through the gravel beach and arbor vitae swamp; and through the rock beach and *Cladonia* clearings.

In a classic publication, Cooper (1913) described: "The Climax Forest of Isle Royale, Lake Superior, and its Development." He described the climax as general boreal association (fir – spruce – paper birch) with three species: balsam fir; white spruce; and paper birch. Of these species, balsam fir was the most common. In the

southwestern area of Isle Royale, the maple-birch climax forest contained sugar maple and yellow birch.

Cooper also noted that all fires tended to return the forest to xerophytic conditions. Where the shade was not too dense beneath the conifer overstory, ground hemlock thrived together with green alder *(Alnus crispa),* highbush cranberry *(Viburnum trilobum),* red-berried elder *(Sambucus pubens),* and bush honeysuckle. Ground hemlock was the most important understory plant. Again, this observation is significant because the moose arrived at about 1912. Since then, the moose have been gradually eliminating the species. A revisit to his study area on Smithwick Island 17 years later showed a rapid secondary succession change had occurred on the area that had burned in 1903 or 1904 (Cooper, 1928).

During following two summers (1929 and 1930) and in the fall of 1931, a University of Michigan geographical survey determined the important components of the major forest associations, including ground cover in relation to the moose herd (McMurray ca., 1933). Based on the 1930 aerial photographs and ground checks of vegetation types, four associations were determined: birch-poplar and birch-poplar-balsam; balsam-spruce-white birch (climax forest); hardwood and hardwood conifer; and the swamp forest.

Brown (ca., 1935) prepared an annotated list of "The Ferns and Flowering Plants of Isle Royale, Michigan." This list included a description of the location and physiography, climate, history, and general description of the vegetation. He cited changes in vegetation due to various factors such as insects, mammal damage, fire, and natural changes.

The spruce-fir-maple-yellow birch forest was studied in detail to determine the nature and causal factors of the transition in southwestern Isle Royale (Linn, 1957). Linn found soil moisture was the most important factor affecting the location of each species in the forest types. At the highest moisture level, spruce-fir dominated; at the lowest level, the northern hardwoods dominated. In the transition zone, sugar maple is dominant on the xeric sites; balsam fir, white spruce, and sugar maple are dominant on the mesic sites. At the lower elevations near Lake Superior, boreal conifers form the spruce-fir-birch climax forest.

Figure 5. This is the paper birch—aspen—balsam fir—white spruce type on Isle Royale. In this stand, aspen predominates in the overstory.

In 1970, an Isle Royale map was prepared which delineated the locations of the broad vegetational types as interpreted from 1957 U.S. Geological Survey aerial photographs (Krefting et al., 1970). The vegetation is mostly typed as "forest cover." These types are considered relatively homogeneous assemblages of species distinguished from adjacent types by differences in species, age (size), or development (figures 5, 6, and 7). The vegetation types have been described in detail by Hansen et al., 1973.

Maycock and Curtis (1960) studied the phytosociology of the boreal conifer-hardwood forests of the Great Lakes Region. Although Isle Royale was not included, the study described and explained the nature of the forest belt which is transitional between the boreal conifer forest to the north and the deciduous forest to the south. Also, the Society of American Foresters (1967) forest cover-type classification for eastern North America recognized three broad regions: the Boreal; Great Lakes-St. Lawrence; and Acadian-Appalachian. Isle Royale would be included within the Great Lakes-St. Lawrence Region and not the Boreal Region. This is because of the widespread distribution of northern hardwoods; such species are not found within the Boreal Region.

Figure 6. Here is paper birch—balsam fir—white spruce climax forest on Isle Royale. At the right on the photo, the browse line on the overstory balsam fir is 10 to 12 feet high. Unbrowsed white spruce is on the left. Mountain ash, willow, and beaked hazelnut are sparse because of browsing by moose.

Figure 7. This is sugar maple—yellow birch climax forest on Isle Royale. This virgin stand of sugar maple and yellow birch has trees up to 28 inches in diameter and over 220 years of age. Sugar maple reproduction predominates, but it is browsed very little by moose in winter.

HISTORY OF THE MOOSE HERD

Time and method of arrival

Both the method of migration and the time of arrival of the moose on Isle Royale are unknown. Hickie (ca., 1943) reported . . . "it seems probable that a few moose came to Isle Royale from the north shore of Lake Superior, either by swimming or walking on the ice, sometime around 1905. This corresponds with a marked decrease of caribou on the island and the neighboring mainland, and an increase of moose in the same area. The difficulties involved in either type of crossing would make it an unusual rather than commonplace event. Although some moose may have crossed over in 1912-13, it seems doubtful that these were the first to reach the island."

Murie (1934) noted . . . "J. Abner Sherman, of Dearborn, Mich., states in a recent communication that when he visited Isle Royale in 1880 moose were very scarce. Sometime prior to 1880 he visited the island and had seen four or five moose out on the ice." Murie also reported: "According to persons long familiar with Isle Royale, the last influx of moose occurred during the winter of 1912-13. That winter was so cold that the water between the island and the mainland to the north froze over. The presence of moose on the island the following summer is correlated with conditions of the previous winter, and it is presumed that a few moose crossed over on the ice. Since 1913, the moose has increased in numbers until now it is very abundant."

Moose were present along the north shore of Lake Superior in 1870 (Shiras III, 1935); by 1890, they were increasing (Swanson et al., 1945). And in the Thunder Bay Region of Ontario (Blake Township), they were common in 1899 (Denis, 1959). Scott (1925) lived in the Windigo area of Isle Royale from 1890 to 1892, but he saw no moose. And in 1904 and 1905, an ecological survey team (Adams, 1909) spent much time on the island, but did not include moose on the list of mammals there. If moose had been present, it seems likely they would have been seen or that other evidence of their presence would have been noted. One clue is a report by Max Peet, a member of the 1905 team. He observed broken and browsed maples which he attributed to caribou. Murie (1934) later concluded it was the type of feeding done by moose, not caribou.

The moose could have reached Isle Royale via the ice bridge. However, they are strong swimmers (figure 8). A moose was reported swimming in Lake Superior near Little Marais, Minn., about 15 miles from shore (personal communication, R.K. Semel, 1969). A bull moose was observed swimming in Lake Superior about halfway between the northeastern tip of Isle Royale and Sibley Peninsula, Ontario (Mech, 1966, p. 21). In Scandinavia, the writer obtained additional information on the ability of the moose to swim long distances. A moose was reported swimming in the Oslo Fjord near Arendal, Norway, about 30 kilometers (19 miles) from shore (personal communication, O. Akersveen, June 27, 1968). Helmuth Strandgaard of

Figure 8. This cow moose and her two calves are swimming in Rock Harbor. Moose enjoy swimming. (Photo is by William Dunmire, National Park Service.)

Denmark also reported two instances of moose swimming long distances (personal communication, Nov. 8, 1963). One moose swam from the Äland Islands near Stockholm, Sweden, to Mariehamn, Sweden. This is 32 kilometers (20 miles). Another moose swam across the Öresund Strait from Sweden to Denmark, a distance of 16 kilometers (10 miles).

Although evidence suggests that the moose may have reached Isle Royale by swimming, the possibility that they reached the island via the ice bridge should not be ruled out. In British Columbia (Fraser River), tracks were repeatedly found on the ice (McCabe and McCabe, 1928). Newsom (1937) also made observations in northern Quebec, reporting: "It has, I believe, been said by at least one authority that moose do not like to travel over ice. Naturally, they will not go on glare ice where they cannot stand up, but my understanding is that they were said to be afraid of ice even when covered with snow. We met two moose at different times at least one half mile from the shores of lakes. Also, we repeatedly saw tracks where moose had crossed lakes. On two occasions I found tracks crossing bays where it would have been easy for the moose, and but little out of their way, to have followed the shore around the edge of the bay. In these two cases the moose chose the snow-covered ice in preference to following the shore."

Population fluctuation

By 1915, moose were well-established on the island. With good forage available, the moose increased rapidly. Two hundred animals were estimated at that time, about 1 per square mile (Hickie, 1936). Later estimates were: 250-300 in 1915-16; 300 in 1917-18; 300 in 1919-20; 1,000 in 1921-22; no estimate in 1923-24; and 2,000 in 1925-26 (Hickie ca., 1943). In 1928, the estimate was 1,000-5,000 (Hickie, 1936).

Hickie (ca., 1943) summarized the estimates: "After 1926, estimates were omitted from the biennial reports of the Department (Michigan), but guessing went on. Summer residents, boy scouts, tourists, conservation officers, fishermen, wildlife investigators, and game experts offered opinions. The "estimated" population varied from 500 to 5,000 moose – 2 to 20 per square mile – for any year between 1926 and 1930. Although individual estimates varied, everyone agreed moose were plentiful."

And in 1929, Hickie (ca., 1943) reported 60 moose were seen in one day at the east end of Lake Ritchie. In the summer of 1930, Murie (1934) noted: "Without an organized count of some sort, it would be impossible to know the moose population. From general observations, I should estimate that in 1930 there were at least 1,000 moose on Isle Royale, and I think that a count would give a figure far above the estimated minimum. As a rule, wild populations are greatly underestimated so it would not be surprising if the actual number of moose in 1930 proved to be two or three thousand."

With reference to overbrowsing, Murie noted: "On Isle Royale all of the important winter foods as well as several species eaten only in summer are overbrowsed – if the population is not reduced, the rate at which the vegetation is destroyed will rapidly increase, and, in the future, the moose will begin to be eliminated by disease and starvation." He listed: the exhaustion of ground hemlock; the severe overbrowsing on poplar, birch, mountain ash, and most shrubs; and the disappearance of pondweeds and water lilies. Fortunately, biologists of

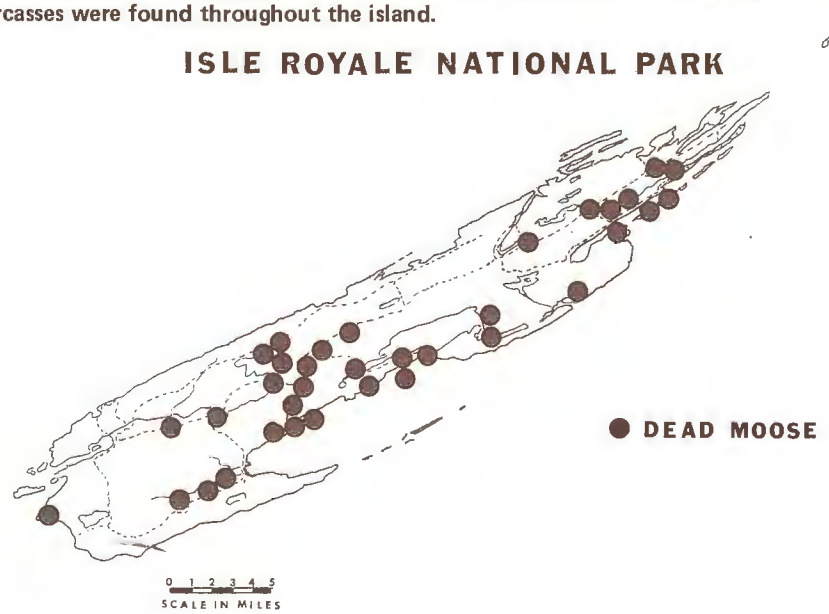
the Michigan State Game Division also visited the island and photographed the severe browsing on balsam fir (figure 9).

By 1932, the number of moose far exceeded the carrying capacity of the island. Titus (1941) reported the herd decreased from 3,000 to 500 in 1934. Hickie (ca., 1943) noted the die-off began in 1933. In the spring of 1934, he found about 40 dead moose on about 10 percent of the island. He reported . . . "the few carcasses were emaciated." Another 20 were found in the spring of 1935.

Although Hickie's estimate (1936) was 400 to 500 moose in 1936, later research by Aldous and Krefting (1946) suggested that . . . "the number perhaps did not exceed 200 by 1935." From a low of an estimated 200 animals, the herd began a slow but steady increase. This increase was enhanced by abundant food following a fire in 1936 which covered about 26,000 acres (19 percent of the island). The herd increased to an estimated 510 animals (airplane strip count) by 1945 (Aldous and Krefting, 1946). A second airplane strip count in February 1947 placed the herd at an estimated 600 animals (Krefting, 1947a & b). The 1948 spring browse survey (Krefting and Lee, 1948) showed the range was severely overbrowsed and the moose were abundant (75 moose were seen).

Figure 9. Severe moose browsing is shown on these balsam fir in 1935. The browse line is 10 to 12 feet high. (Photo is by the Michigan Department of Natural Resources.)

Figure 10. Thirty-five dead moose were found on Isle Royale in 1949 and 1950. Carcasses were found throughout the island.



Based on the airplane estimate in 1947 and the browse and sight records in the spring of 1948, the herd was estimated at 800 in the fall of 1948 (Krefting, 1951). A second die-off followed in the 1948-1949 (Krefting, 1949) winter; it continued through the 1949-50 winter. A minor search of the island both springs (1949 and 1950) produced a total of 35 yearling and adult moose (figures 10 and 11). Krefting (1951) noted: "It appears that the herd decreased by approximately one third, which would place the 1950 spring estimate around 500. These estimates are open to question but without doubt they show the rise and fall of the moose herd."

Mech (1966) estimated there were 600 moose in 1960 (about three per square mile). His estimates were based on counts on strips paralleling the length of the island.

To determine moose population trends, pellet "group" counts were made in 1948 in representative forest cover types. The counts reflected moose use from leaf fall in mid-October to mid-May when the counts were made. A pellet "group" consisted of a definite pile of fecal droppings, generally with several hundred pellets. The tallies were made on transects of varying lengths in various parts of the island. The plots, 1/100-acre in size, were taken at 10 chain (660 ft.) intervals in 1948, 1950, 1961, 1965, and 1970 (figure 12). From 1948 to 1950, the tally for the main island showed that the count decreased significantly ($P < .01$), reflecting the known die-off of the herd.

A significant population trend increase followed from 1950 to 1970 ($P < .01$). This increase occurred in spite of the timber wolf known to be present since 1949. However, Jordan et al., 1971, reported the population – based on quadrat airplane counts – remained stable at about 1,000 moose from 1959 to 1969. The diagrammatic sketch (figure 13) illustrates the fluctuations in the Isle Royale moose herd based on estimates from the literature, from airplane strip counts, from airplane quadrat counts, and from pellet group counts from the early 1900's to 1970.

Figure 11. This dead bull moose was found on Isle Royale in 1949. The population was estimated to have decreased from 800 to 500 from the year 1948 to 1950.

Figure 12. This was the trend in the Isle Royale moose population from 1948 to 1970, based on pellet group counts for the northeastern, central, and southwestern areas as well as for the main island.

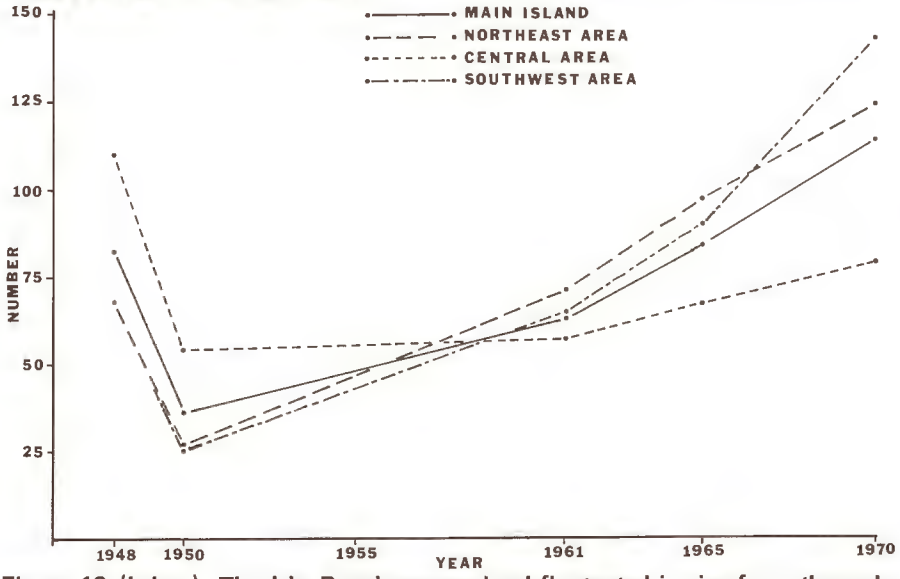
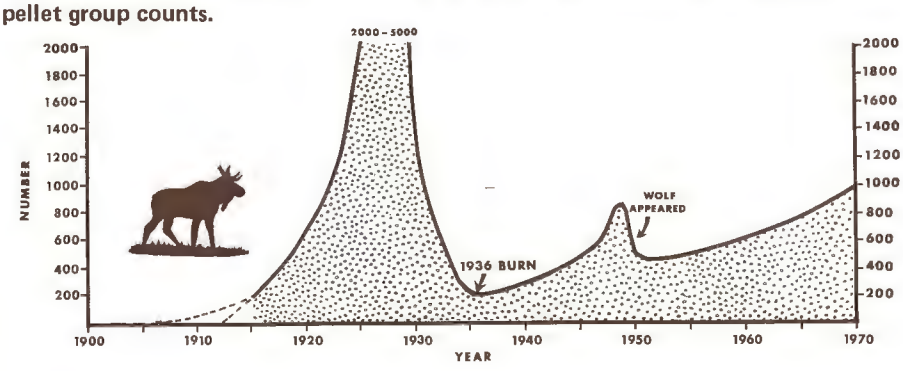


Figure 13 (below). The Isle Royale moose herd fluctuated in size from the early 1900's to 1970. The probable fluctuations to 1945 are based on estimates from the literature. Fluctuations from 1945 to 1970 are based on airplane counts and pellet group counts.



WINTER FOOD HABITS OF THE MOOSE IN NORTH AMERICA

"The feeding habits and plants used by moose for food should be ascertained to fully understand the interspecific, intraspecific, and environmental relationships of the species" (Peek, 1973). Peek's review of moose food habit studies in North America included: six studies from Alaska; 13 from the intermountain west; and 22 from Canada, Isle Royale, Maine, and Minnesota.

The moose is a browsing species, especially during the winter months. Its food habits are quite different in eastern and western North America where significant differences exist in the availability of browse species. Most investigators agree that willows are the main source of winter browse in the west (Murie, 1944). And in the east, balsam fir, aspen, and paper birch are the major species (Pimlott, 1961).

Eastern North America

In Newfoundland, paper birch and balsam fir are the leading winter browse species (Pimlott, 1953). Species next in importance are shadbush, sweetgale *(Myrica gale),* mountain alder, willow, aspen, ground hemlock, mountain ash, mountain maple, and fire cherry. Pimlott reported no browsing on black spruce, white spruce, tamarack, and white pine. When ground hemlock was lightly or moderately browsed, he noted the range was usually below carrying capacity. Whenever balsam fir was severely browsed, ground hemlock was killed by browsing. Ground hemlock was not only highly palatable, but also intolerant to browse use.

Later research in Newfoundland by Pimlott (1963) showed paper birch made up one-half to three-fourths of the winter diet. Balsam fir exceeded paper birch in the diet, especially in high density moose areas and where mature timber predominated. A comparison of the 1953 and 1963 species importance list showed the later study included three additional species: sweet pear *(Amelanchier sp.);* wild

raisin *(Viburnum cassinoides);* and mountain holly *(Neomopanthus micronata).*

Other Newfoundland studies noted the diet of paper birch and balsam fir adequately maintained a healthy moose herd (Bergerud and Manuel, 1968). Dodds (1960) reported 35 browsed species were in high density moose areas dominated by balsam fir. Browse use in these areas was 47 percent balsam fir, 20 percent paper birch, and 13 percent raspberry. In uncut balsam fir and white spruce stands, having lower moose densities, the diet was 44 percent balsam fir, 22 percent willow, and 11 percent alder. On cutover high density moose areas, the diet was 29 percent fire cherry, 25 percent paper birch, 15 percent balsam fir, and 10 percent aspen.

Winter range studies in Nova Scotia showed the five most highly preferred species were Canadian honeysuckle, speckled alder, *Rubus alleghaniensis,* sugar maple, and yellow birch (Telfer, 1967). Lower preference species in descending order were beaked hazelnut, mountain maple, balsam fir, and raspberry.

In Lauerentides Park, Quebec, the moose diet in a 10-acre yard was 86 percent balsam fir and 14 percent paper birch (des Mueles, 1962). Since spruces were the only other available woody species in the yard, des Mueles felt that the habitat was able to support one moose for 200 days of winter.

Analysis of 26 stomachs (24 Ontario, 1 Manitoba, and 1 Quebec) collected from October 19 to May 5 showed balsam fir present in 21 of 23 stomachs where balsam occurred (Peterson, 1953). Other species occurred in the stomachs as follows: willows, 16; paper birch, 11; beaked hazelnut, 10; aspen, 9; white cedar, 4; redosier dogwood, 2; juneberry, 1; and maple, 1. In Ontario's St. Ignace Island, Lake Superior, the winter diet was: (percentages) balsam fir, 27; paper birch, 12; mountain maple, 9; redosier dogwood, 9; and highbush cranberry, 5 (Peterson, 1953). Peterson also observed that, from spring to fall, the conifers were not browsed. Barking occurred on aspen and mountain maple.

In Baxter State Park, Maine, studies showed the five most important browse species were balsam fir, fire cherry, mountain ash, mountain maple, and paper birch (Dyer, 1948). Near the mountain tops where snow depths of 8 to 10 feet occurred, there was only limited browsing to reproduction of this height. In these high altitude yards, balsam fir was stripped of lateral branches up to 1/2 inch in diameter. Seven species made up the diet in the low altitude yards. Balsam fir accounted for 54 percent, mountain maple 23 percent, and the rest in order of importance were mountain ash, paper birch, moose wood *(Acer pennsylvanicum),* fire cherry, and aspen.

Feeding site examination studies in northeastern Minnesota showed that willows were most important (Peek, 1971) on a yearlong basis. Peek concluded that Bebbs and pussy willows were most important. Other species in order of importance were aspen, paper birch, and beaked hazelnut. Balsam fir was the most important species in late winter.

Peek (1973) summarized the important moose browse species for eastern North America, based on 10 separate surveys in six areas (table 2). Balsam fir, mountain ash, mountain maple, and paper birch were the important species in four of the five areas. In four areas, balsam fir, mountain maple, and willows were important. Balsam fir and paper birch are the major forage species in eastern North America, with the exception of areas where these species are poorly distributed.

Table 2. Important moose browse species in eastern North America.

Reference	Date	Area	Five most important browse species in order of importance	Remarks
Peek	1971	Northeast Minnesota	Willows, aspen, white birch, beaked hazel, fire cherry	Moderately high moose population; feeding site examination technique
Aldous and Krefting	1946	Isle Royale, Mich.	Aspen, white birch, balsam fir, mountain ash, willows	High moose population (1945); browse survey technique
Krefting	1951	Isle Royale, Mich.	Balsam fir, white birch, mountain ash, aspen, willows	1948 higher moose population than in 1945
Krefting	1951	Isle Royale, Mich.	White birch, aspen, redosier, willows, mountain ash	1950 lower moose population than in 1945
Peterson	1953	St. Ignace Island, Ont.	Balsam fir, white birch, mountain ash, redosier, mountain maple	1947-48 most important species rather than most palatable
Dyer	1948	Maine	Balsam fir, mountain maple, mountain ash, white birch, fire cherry	1940's; browse survey technique
Telfer	1967	Nova Scotia	Mountain maple, yellow birch, sugar maple, red maple, Canada honeysuckle	1968 light browsing pressure; stem counts in spring
Pimlott	1953	Newfoundland	White birch, balsam fir, mountain maple, mountain ash, fire cherry	Stem count method; heavy browsing pressure
Dodds	1960	Newfoundland	Balsam fir, white birch, raspberry, elderberry, juneberries	High moose density; cutover area 1953, 56, 57
Dodds	1960	Newfoundland	Balsam fir, willows, alders, mountain maple, rhododendron	Low moose density, stem count method

FOOD HABITS OF THE MOOSE IN ISLE ROYALE NATIONAL PARK

Method and procedures

Isle Royale is an unique area for determining the food habits of moose. Since the moose is the only ungulate present, there is no problem confusing its feeding activity with other browsers. However, since the range was already badly overbrowsed in 1945 when the first range survey was made, browse species preferences have been altered. Good interspersion of cover types on the island provides the kinds of winter habitat needed by the moose.

Winter browsing on woody plants was sampled using the Aldous system of measuring availability and utilization (Aldous, 1944; Aldous and Krefting, 1946; and Krefting, 1951). The technique was designed originally for deer browse surveys; therefore, it was necessary to extend the height of the browsing zone from 7 to 10 feet for moose. Vegetation tallies were made on circular plots 1/100 acre in size (11. 8 foot radius). The cover percent (density) of each browse species on the plot was estimated and recorded in one of three broad percent cover groups. For coverage up to 10 percent, an average of 5 was used. Thirty was used to represent cover percentages from 10 to 50. From 50 to 100 cover percent, the figure 70 was used to represent the midpoint. Utilization or degree of browsing was the percentage of the annual growth eaten from each stem during the winter months. Sometimes, more than the annual growth was removed by moose browsing. An average figure for each browse species was estimated and recorded using the same percentage groups used for cover percent. For use in summer and fall browse surveys, as described earlier, the technique was modified slightly. The degree of browsing was estimated from the percentages of the leaves and tips of branches eaten on each plot.

Transects were established in various parts of the main island and on

Figure 14. Browse and pellet count transects were located in the northeastern, central, and southwestern areas of Isle Royale.

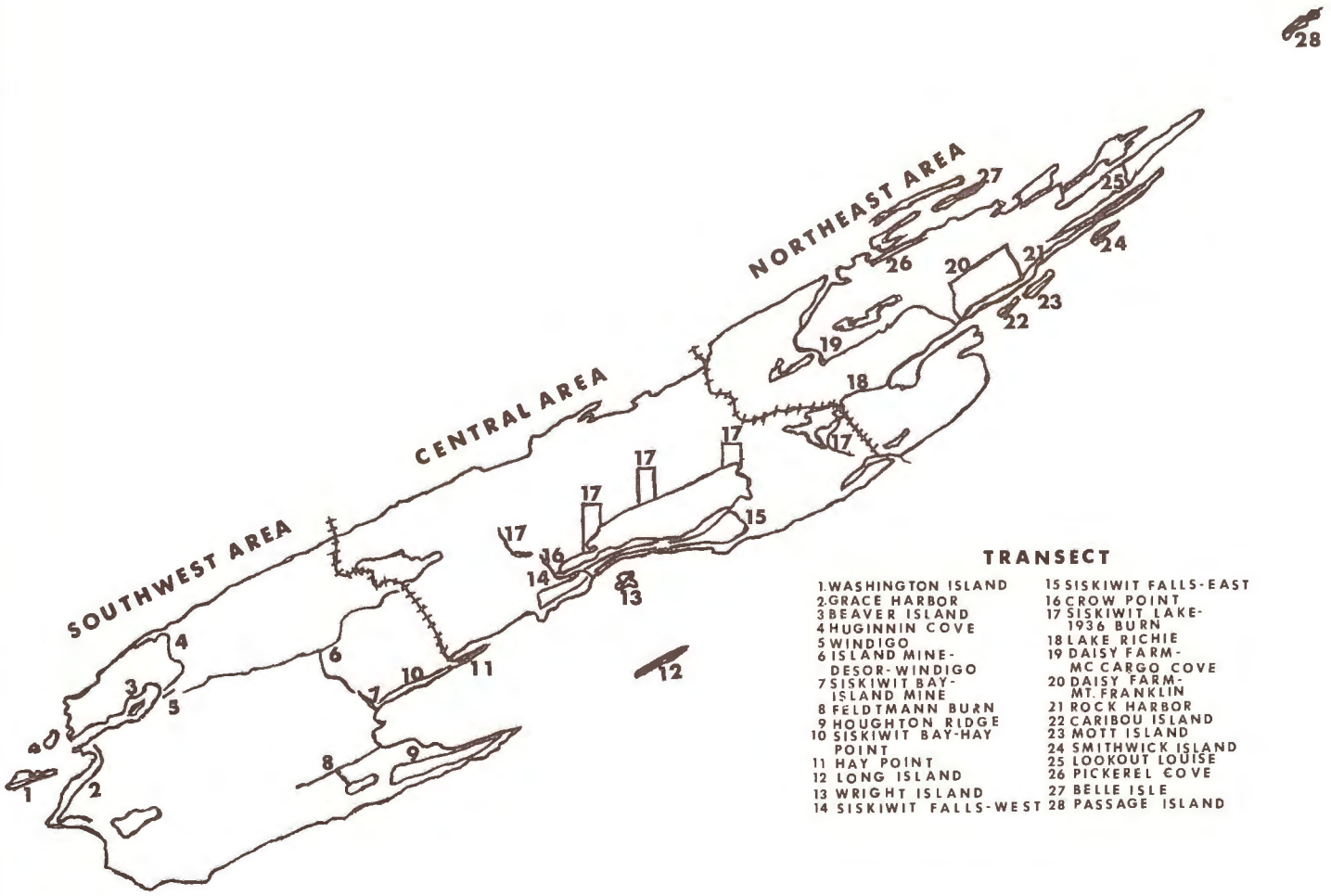


Table 3. Number of 1/100-acre plots sampled on Isle Royale from 1945 to 1970.

Year	Main islands	Nearby islands			Total
		Northeast	Central	Southwest	
1945	592	49*	40	22	703
1948	844	129*	63**	40	1,076
1950	844	102	63	40	1,049
1961	844	102	40	40	1,026
1965	844	88***	40	40	1,012
1970	844	88***	—	40	972

*27 plots on Passage Island in 1945 and 1948.
**23 plots on Long Island in 1948.
***No plots on Belle Isle in 1965 and 1970.

Table 4. Isle Royale summer browse survey in the sugar maple–yellow birch climax type and the birch–fir–spruce type in 1946.[1]

Species	Percentage of each species in the diet
Sugar maple	18.4
Mountain maple	15.5
Mountain ash	12.5
Paper birch	11.8
Trembling aspen	9.1
Willow sp.	7.5
Redosier dogwood	3.9
Pin cherry	3.8
Yellow birch	2.7
Black ash	2.4
Beaked hazelnut	2.3
Juneberry sp.	2.1
Red-berried elder	1.9
Speckled alder	1.9
Roundleaf dogwood	1.7
Canadian honeysuckle	0.5
Balsam poplar	0.5
Bush honeysuckle	0.3
Mountain alder	0.2

[1] Based on 206 1/100-acre plots, September 1946.

Table 5. Isle Royale fall browse survey in the sugar maple–yellow birch climax type and the 1936 burn area in 1948.[1]

Species	Percentage of each species in the diet
Mountain ash	27.0
Paper birch	20.5
Sugar maple	13.1
Mountain maple	9.9
Willow sp.	9.9
Yellow birch	6.3
Trembling aspen	4.0
Redosier dogwood	3.0
Beaked hazelnut	2.2
Pin cherry	1.9
Red-berried elder	1.6
Juneberry sp.	0.6
Balsam fir	0.1

[1] Based on 108 1/100-acre plots, October 1948.

most of the surrounding islands (figure 14). Browse surveys and pellet group counts were repeated on each transect each time a survey was made. The plot interval was 10 chains (660 feet) on the mainland transects. On the smaller islands, the interval was 5 chains (330 feet). Where trails were followed for access, the plots were offset one chain to avoid the excessive browsing that is characteristic along trails. Surveys for browse were made in 1945, 1948, 1950, 1961, 1965, and 1970. Pellet group counts were made on the same plots starting in 1948. The number of groups found on each plot was recorded.

A total of 703 plots was tallied in 1945; 592 of them were on the main island, and 111 were on nearby islands (table 3). In 1948, the number tallied was increased to 844 on the main island and remained the same through 1970. The total number in 1948, including the nearby islands, was 1,076. The number decreased each time to 972 in 1970. Spring storms on Lake Superior were the main reason tallies were not made regularly on the nearby islands. The number of plots on the main island was increased from 592 in 1945 to 844. This allowed better samples of the island in proportion to the acreages occupied by the various forest cover types.

For the 1945, 1948, and 1950 surveys (Aldous and Krefting, 1946; and Krefting, 1951), the browsing values for each species for each transect (5, 30, and 70) were totalled. To determine the average degree of browsing, the totals were divided by the number of plots where each species was found on the transect. This computation resulted in an unweighted average degree of browsing figure. However, Cringan (1957) used the Aldous method on woodland caribou studies in Ontario. He determined that a weighted average degree of browsing gave more representative findings. Percentages of cover for each species were multiplied by their respective browsing values. The results were totalled and divided by the sum of the cover percentages. Cringan used the weighted average method since he observed that "The greater the variety of browse available at a location, the more likely is intensive feeding there; but the greater variety, the lesser the density (cover percent) attainable by each species."

Summer and fall food habits

Upland woody vegetation

Moose browsing observations were made on upland woody vegetation in the summers of 1929 and 1930. This was when the population was at its highest peak and before the crash decline in population (Murie, 1934). Murie noted summer browse was principally the leaves of woody plants, although the tips of the twigs were sometimes eaten. Almost all of the deciduous trees and shrubs fed on in summer were also eaten in winter. The major species were aspen, paper birch, beaked hazelnut, redosier dogwood, mountain alder, mountain ash, pin cherry (*Prunus pennsylvanica*), hard maple, and willow. Of special interest was the browsing on the bursting buds of thimbleberry (*Rubus parviflorus*). Plants browsed less frequently included round-leaved dogwood (*Cornus rugosa*), prickly rose (*Rosa acicularis*), staghorn sumac (*Rhus typhina*), huckleberry, red-berried elder, highbush cranberry, bush honeysuckle, and Canadian honeysuckle (*Lonicera canadensis*).

In September 1946, field tallies were made in the island's southwestern area, within the sugar maple-yellow birch and the spruce-fir-birch climax types (Krefting, 1946). Sugar maple, mountain maple, mountain ash, paper birch, willow, redosier dogwood, fire cherry, yellow birch, black ash, beaked hazelnut, and juneberry made up 98 percent of the diet (table 4). The first six species listed made up three-fourths of the diet.

Vegetation tallies were also taken in October 1948 in the southwestern area of the island (Krefting, 1948). Mountain ash, paper birch, sugar maple, mountain maple, willow, yellow birch, aspen, and redosier dogwood formed 94 percent of the food eaten in the sugar maple-yellow birch type (table 5). In the 1936 burn area, the percentages of food eaten were: paper birch, 40; willow, 24; aspen, 9; pin cherry, 9; red-berried elder, 7; and mountain ash, 2.

In August 1971, vegetation tallies in the spruce-fir-birch and sugar maple-yellow birch types in the southwestern area showed 7 species made up 95 percent of the diet: mountain ash, 57; mountain maple, 23; paper birch, 9; beaked hazelnut, 3; sugar maple, 2; and yellow birch and aspen together, 1 (Krefting, 1971) (table 6).

In the northeastern area, vegetation tallies were made on five transects in August 1972 (Krefting, 1972) (table

Table 6. Isle Royale summer browse survey in the sugar maple–yellow birch climax type and the birch–fir–spruce type in 1971.[1]

Species	Percentage of each species in the diet[2]
Mountain ash	57.4
Mountain maple	22.6
Paper birch	9.1
Bush honeysuckle	4.0
Beaked hazelnut	2.7
Sugar maple	1.8
Trembling aspen	0.9
Juneberry sp.	0.6
Cherry sp.	0.4
Yellow birch	0.4

[1] Based on 118 1/100-acre plots, August 1971.

[2] Canadian honeysuckle, speckled alder, red maple, black ash, and rose made up less than 0.1 percent of the food eaten.

Table 7. Summer moose browse survey in the northeastern area of Isle Royale in 1972.

Species	Birch–aspen spruce (1936 burn area)[a]	Birch–aspen fir–spruce (Lake Ritchie)[b]	Birch–aspen fir–spruce (Moskey Basin)[c]	Birch–aspen fir–spruce (Mt. Ojibway)[d]	Birch–aspen fir–spruce (Rock Harbor)[e]	All Areas[f]
	Percentage of each species in the diet					
Trembling aspen	48.2	48.4	13.6	12.2	12.8	25.1
Balsam poplar	3.7					2.7
Cherry sp.	2.9	1.8		3.8		1.8
Highbush cranberry		1.7	0.1		2.3	0.7
Juneberry sp.	0.3	5.3	26.6	27.0	7.6	16.5
Mountain ash	0.2	3.7	1.1	****	29.6	4.7
Paper birch	30.8	5.1	1.5		4.9	4.9
Redosier dogwood	2.3	2.3		0.1	0.7	1.1
Red maple				1.1		0.3
Sumac sp.		10.0				1.6
Willow sp.	11.1	5.6	0.1	0.9	1.9	2.8
Beaked hazelnut		14.4	0.1	34.4		13.7
Bush honeysuckle			0.1	2.1	1.5	0.8
Canadian honeysuckle		0.1		0.1		****
Mountain alder	0.2	1.3	56.4	17.9	38.3	22.8
Mountain maple		0.1	0.1			****
Rose sp.		0.1	0.1		0.3	****

Number of 1/100-acre plots: a, 21; b, 20; c, 24; d, 62; e, 64; and f, 191.

****Less than 0.1 percent.

7). In the 1936 burn area, aspen accounted for 48 percent, paper birch 31 percent, and willow 11 percent. In the aspen-birch-fir-spruce type, the percentages of major foods eaten were: aspen, 49; beaked hazelnut, 15; sumac, 10; and willow, 6. Along the shore of Rock Harbor, 56 percent of the diet was mountain alder, 27 percent was juneberry (*Amelanchier Bartramiana*), and 14 percent was aspen. Similar results were obtained on a second transect along Rock Harbor. Percentages of food eaten were: mountain alder, 38; mountain ash, 30; aspen, 13; and juneberry, 8.

On the Mount Ojibway transect in the aspen-birch-fir-spruce type, the percentages of major foods eaten were: beaked hazelnut, 34; juneberry, 27; mountain alder, 18 (figure 15); and pin cherry, 4.

These tallies show that almost all upland species are fed on in the summer and fall. Species availability in a particular area determines what is eaten. Along the Rock Harbor shore, mountain alder is apparently highly preferred and is also well-distributed. In the 1936 burn area, aspen, paper birch, and willow form the bulk of the diet because these species are readily available.

In northeastern Minnesota, 13 species were browsed in June. Aspen made up 70 percent of the use (all leaf stripping), and upland willows were next (Peek, 1971). Tallies in July and August suggested preferences for willow, fire cherry, white birch, aspen, and mountain maple. While leaf browsing predominated in July, both leaves and tips of twigs were used in August. In September, feeding on aspen decreased, but it increased on the upland willows. Over 70 percent of the September diet consisted of upland willows, fire cherry, and white birch. For the first time, green alder, redosier dogwood, and mountain ash were utilized appreciably. In October, the upland willows were utilized most, and redosier dogwood was second in use. Eighty-one percent of the use was confined to these species.

Stomach examinations

The stomach content of six moose killed on Isle Royale in the summers of 1929, 1930, and 1931 showed that these moose had been feeding mainly on aspen, willow, fire cherry, bush honeysuckle, mountain alder, beaked hazelnut, and thimbleberry (Murie, 1934). Grasses and sedges made up a small part of the diet. Aquatic plants appeared in only one of the stomachs. Also, the examination of four stomachs collected in 1949 revealed that two of them contained mostly balsam fir along with aspen leaves and twigs. The leaves and twigs of mountain maple made up the entire content of one stomach. The fourth stomach contained equal amounts of the leaves and twigs of aspen and mountain maple as well as a mixture of grasses and sedges.

Herbaceous plants

Herbaceous plants are consumed in varying amounts in summer (Murie, 1934). The species eaten most frequently were: bracken fern (*Pteridium aquilinum*); horsetail (*Equisetum fluviatile*); sedge (*Carex* sp.); rush (*Juncus* sp.); red clover (*Trifolium pratense*); fireweed (*Epilobium angustifolium*); jewel weed (*Impatiens biflora*); and large-leaved aster. Other Isle Royale observations (Krefting, 1946) showed feeding on false Solomon's seal (*Smilacina racemosa*), large-leaved aster, Jack-in-the-pulpit, jewel weed, and wild lettuce (*Lactuca canadensis*).

On Ontario's St. Ignace Island, Lake Superior, large-leaved aster was used (Peterson, 1953). In northeastern Minnesota, Peek (1971) noted herbaceous plants contributed very little to the food supply.

Aquatic plants

In summer, the moose become semiaquatic, feeding on a variety of aquatic plants. On Isle Royale, this kind of feeding usually begins in June. It reaches a peak in late July and tapers off in a striking manner by late August. In the early 1930's, Murie (1934) observed moose fed extensively on pondweeds (*Potamogeton* sp.) in several lakes. Murie also reported that large yellow pond-lily (*Nymphae advena*) and white pond-lily (*Castalia odorata*) – formerly abundant – were rare because of moose feeding. Also, sedges (*Carex* sp.) and rushes (*Juncus* sp.) were fed on extensively.

In the middle 1930's, Brown (ca., 1935) made observations on the use by moose of aquatic plants in summer. Brown noted water lilies were conspicuously absent. Adam's earlier (1909) photographs of aquatic vegetation in the same lakes showed water lilies were then abundant on the surface of the water, particularly on Moose and Sumner Lakes. However by the 1930's, lilies were sparse in these lakes. Also, moose destroyed sedge mats around the edges of the lakes. Cooper (1928) studied on Isle Royale in 1909 and 1910 and returned in 1926 to make observations. He noted that, in many bogs, the moose herd converted the sedge mat zone to mud wallows. Other plants moose utilized included: *Heracleum lanatum; Nymphaea americana; Najas flexilis; Elodia canadensis; Osmunda regalis;* and *Osmunda Claytonia*.

Aldous (1944) observed the use of aquatic plants by moose in September. He studied nine lakes and four streams. On Hidden Lake, water lily and smartweed (*Polygonum* sp.) were common, and the shoreline contained sedges. On Moose Lake, water lilies were plentiful even though the species had been almost eliminated in 1930 (Brown ca., 1935). On Sumner Lake, water lily, pondweed, and smartweed had been utilized excessively. Other important aquatic lakes in the northeastern section include Ojibway (figure 16), Forbes, and Wallace. In the southwestern section, the horsetail growing along the shore of Halloran Lake had been eaten only sparingly. At the head of Washington Harbor and Washington Creek, moose fed extensively on pondweed. Much of the feeding in Washington Creek is at depths of 2 to 4 feet (figure 16). In the harbor, moose feed at depths of 8 feet or more. The moose completely submerge to feed on the aquatics. In August 1971, the writer observed similar feeding on pondweeds in Washington Creek (figure 17). At the lower ends of Grace

LEFT: Figure 15. Here is evidence of summe browsing on mountain alder on Isle Royal Mountain alder is a medium preference specie that is browsed both summer and winte BOTTOM LEFT: Figure 16. This aquatic hab tat is in Ojibway Lake on Isle Royale. Moos concentrate in this lake in early spring. It wa formed by a beaver dam. RIGHT: Figure 17 This cow moose is feeding on aquatic plants i Washington Creek.

Creek and on Big and Little Siskiwit Rivers, the moose also fed on pond lilies and pondweeds.

Observations were made in the 1960's on the abundance of aquatic plants in Isle Royale's inland lakes, plus some wooded swamps, beaver ponds, and the rocky shores of Lake Superior (Cain, 1962). Cain observed moose may prefer water lilies and larger "potamogetons," but this material must be little more than "salad" and not the "entree." Only a small percentage of their total summer food is provided by aquatics. With the exception of their fondness for water lilies, he felt it unlikely that they select other plants. He concluded that the aquatic communities had improved in extent and density, compared to 1930 when they were reported to be greatly reduced because of moose.

In Ontario, the availability of large supplies of aquatic vegetation was the main reason moose frequented water during summer (de Vos, 1956). Moose distribution seemed to be governed by the abundance and distribution of aquatic plants. Feeding occurred at all times of the day and, at times, after sunset. The earliest feeding occurred in early June. It reached a peak from late June to early August. Feeding was also carried on until late October. In early June, the only plant eaten was horsetail. From late June through July, there was a steady increase in the consumption of eelgrass (*Vallisneria americana*), pondweed, yellow lily, and bullrush (*Scirpus* sp.). Of these species, eelgrass was the chief aquatic food.

On St. Ignace Island, the pondweed (*Potamogeton Richardsonii*) provided the bulk of aquatics (Peterson, 1953). The earliest feeding started June 4. It occurred to depths of 18 feet. And in Montana (McDowell and Moy, 1942), aquatic plants provided 2 to 5 percent of the summer diet. A study in northeastern Minnesota showed that the aquatic species moose preferred were yellow pond lily, wild rice (*Zizania aquatica*), and bur reed (*Sparganium* sp.) (Peek, 1971).

Although summer use of aquatic plants is apparently important to the moose, the importance of the aquatic environment is poorly understood. The meager information available from all studies suggests that, at best, aquatic plants make up only a small percentage of the summer diet. Also, the use of aquatic foods may vary considerably between years.

Winter food habits

Studies on Isle Royale in the early 1930's

Observations in the 1930's indicated balsam fir was the most important winter food (Murie, 1934); it was not only abundant, but also palatable. Murie noted ground hemlock was one of the most preferred foods both winter and summer and that it was fast disappearing. Other important species were: trembling aspen; paper birch; willow; beaked hazelnut; mountain ash; juneberry; fire cherry; redosier dogwood; staghorn sumac; sugar maple; prickly rose; Canadian honeysuckle; and red oak (*Quercus rubra*). Species browsed less severely were: white pine; mountain alder; mountain maple; red-berried elder; and huckleberry. Rarely-browsed plants included: juniper (*Juniperus communis*); white-cedar; black spruce; white spruce; speckled alder; and bush honeysuckle.

Winter feeding trials were also conducted on Isle Royale to learn the amounts of winter browse eaten. For these trials, captive moose were fed balsam fir, paper birch, poplar (trembling aspen), alfalfa hay, and a variety of grains (Hickie, 1936). Moose consumed an average of 25 pounds of mixed balsam fir and white birch browse per moose per day. The amount consumed increased with the size of the animal and the severity of the weather.

Later feeding trials were also made by Hickie (unpublished data) from Jan. 15 to May 1, 1937. For these trials, the number of moose fed per day ranged from 2 to 23 for a total of 1,234 moose days for that period. An average of 34 pounds of food was eaten per day per moose. The percentages consumed were: balsam fir, 69; alfalfa hay, 11; aspen, 9; white cedar, 7; and paper birch, 4.

Also, a small-scale study was conducted to determine the amount of browse produced on 1 acre of forest (Hickie, 1936). A typical mixed stand of paper birch, aspen, and balsam fir was selected at Chippewa Harbor. All the trees were cut down, and their branches were trimmed and weighed. The fresh weight of the browse of all the species amounted to 4,000 pounds. It was estimated that this amount of browse would feed an average moose for about 75 days. On that basis, 53 pounds of branches would be available per day. However, probably only about one half of this weight could be eaten since branches exceeding 1/2 inch in diameter probably could not be consumed. Hickie reported that cutting calculations suggested that 1,000 moose could be maintained on the island on a 40-year cutting rotation.

Studies on Isle Royale, 1945-1970

To relate the browse survey and pellet group counts, the data were analyzed separately from three areas of the island: northeastern; central; and southwestern (figure 10). Data for each transect within each area were also analyzed separately in the following section of this report.

Northeastern area

Description of the area

This area covers approximately 44,000 acres – about one-third of the island (figure 10). The principal forest cover type is aspen-paper birch-balsam fir-white spruce. This cover type occupies about 90 percent of the area. Because of its fire origin, the type is characterized by extensive stands of aspen and paper birch, mostly 80 to 100 years of age. During the past 10 years, the area has had a marked increase in balsam fir reproduction in spite of browsing by moose. On the main island, the greatest increases of balsam are near the shores of Lake Superior. This increase probably reflects the earlier (1948-1950) reduction in the moose herd. The young balsams present now are probably 15 to 25 years of age. White pine, white-cedar, and red maple are sparsely distributed throughout the type. A few red oak are confined to Greenstone Ridge. Understory shrubs include a mixture of beaked hazelnut, juneberry, mountain alder, mountain ash, redosier dogwood, highbush cranberry, Canadian honeysuckle, bush honey-

suckle, and willow. Bracken fern and thimbleberry are very common. About 10 percent of the area is covered with the paper birch-balsam fir-white spruce climax type; and the nearby islands are mainly a mixed paper birch-balsam fir forest. A mixed jack pine-black spruce type occupies 436 acres in the Conglomerate Bay area of the island. Black spruce and tamarack swamps are mostly small and occupy an insignificant area. Numerous rock outcrop openings of varied sizes are also scattered throughout the area. These are of great benefit to the moose. Most of the openings are destitute of soil, largely because of past forest fire. Because the sites are poor for tree and shrub growth, the moose are able to keep the browse supply within reach.

Population fluctuation

In 1948, 1950, 1951, 1965, and 1970, pellet group counts were made on 205 1/100-acre plots on five transects in the northeastern area. On four nearby islands, counts were made on 102 plots each survey year except in 1965 and 1970 on Belle Isle. Then, spring storms made it impossible to reach the island (table 3). In this area, the pellet counts showed a significant downward trend in the population from 1948 to 1950 ($P < .01$), reflecting the known die-off of the moose. From 1950 to 1970, the counts indicated a significant upward trend in population ($P < .01$). The counts on each of the five transects in the area also showed significant decreases ($P < .01$) from 1948 to 1950 as well as significant increases from 1950 to 1970 ($P < .01$) (table 10). In 1970 in the area, the number of pellet groups per acre ranged from a low of 98 to a high of 165. Pellet densities per acre on three of the islands were: Smithwick, 55; Mott, 95; and Caribou, 126.

Percentage of each species in the diet

In 1945, browse surveys were made in the northeastern area on 142 1/100-acre plots. In 1948, 205 plots were tallied. These findings have been summarized by years (1945-1970) and by browse preference groups (high, medium, and low) in table 8. The 1945 survey showed that 12 high preference group species formed 92 percent of the diet. In 1970, these high preference species accounted for only 75 percent of the diet – a decrease of 15 percent (figure 18). High preference species that decreased significantly ($P < .01$) from 1945 to 1970 were: aspen; paper birch; willow; and juneberry. Balsam fir, a high preference species, increased in the diet during that period. The medium preference group species were: beaked hazelnut; bush honeysuckle; Canadian honeysuckle; jack pine; mountain alder; and mountain maple. This group formed 8 percent of the diet in 1945 and 25 percent in 1970 (table 18). Two-thirds of the increase can be attributed to beaked hazelnut. The two low preference group species,

Table 8. Percentage of each species in the diet in the northeastern area of Isle Royale.

Species* and preference	Year					
	1945	1948	1950	1961	1965	1970
High						
Aspen	22.2	12.3	11.7	13.6	13.2	11.3
Balsam fir	21.8	26.4	14.5	13.2	19.8	38.9
Balsam poplar		0.3	0.3			0.5
Cherry sp.	2.5	3.2	0.8	1.6	1.5	
Ground hemlock				0.5	0.3	
Highbush cranberry	3.0	4.5	2.8	4.4	5.0	3.6
Juneberry sp.	7.4	5.3	13.5	12.8	10.0	3.6
Mountain ash	4.6	4.0	4.2	8.0	7.9	3.9
Paper birch	12.6	8.7	14.6	7.9	5.9	3.8
Redosier dogwood	4.2	10.4	11.7	9.0	4.7	4.4
Red maple	0.6	0.9	2.2	2.2	2.0	1.4
Sumac sp.	2.0	0.1	0.1			0.2
White pine	0.1	0.3	0.1	0.2	0.6	0.6
Willow sp.	10.7	9.3	13.4	10.6	2.2	3.0
Medium						
Beaked hazelnut	1.8	5.7	5.6	10.8	15.4	16.4
Bush honeysuckle		0.3		1.1	2.4	0.7
Canadian honeysuckle		0.3		0.1		0.2
Jack pine	0.2					
Mountain alder	5.6	3.4	3.1	2.3	2.2	3.1
Mountain maple	0.1	2.4	1.3	0.7	1.1	4.3
Low						
Speckled alder				0.2	0.6	
White-cedar	0.1	0.3		0.3	0.1	0.1

*Species found but not tallied were: currant and gooseberry (*Ribes sp.*), ninebark (*Physocarpus opulifolius*), tamarack (*Larix laricina*), thimbleberry (*Rubus parviflorus*), and blueberry (*Vaccinium sp.*)

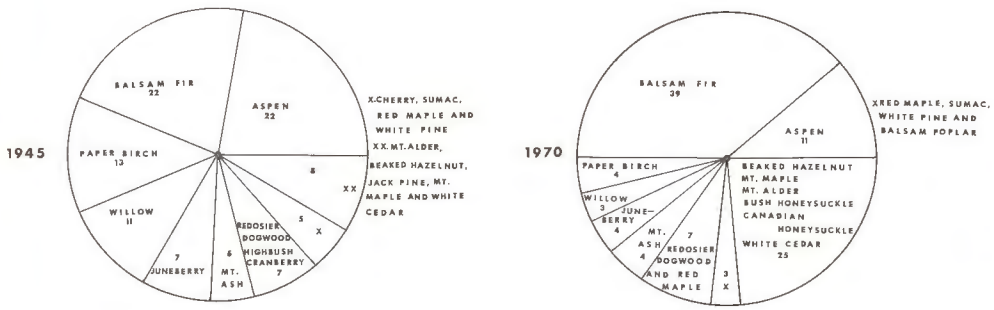
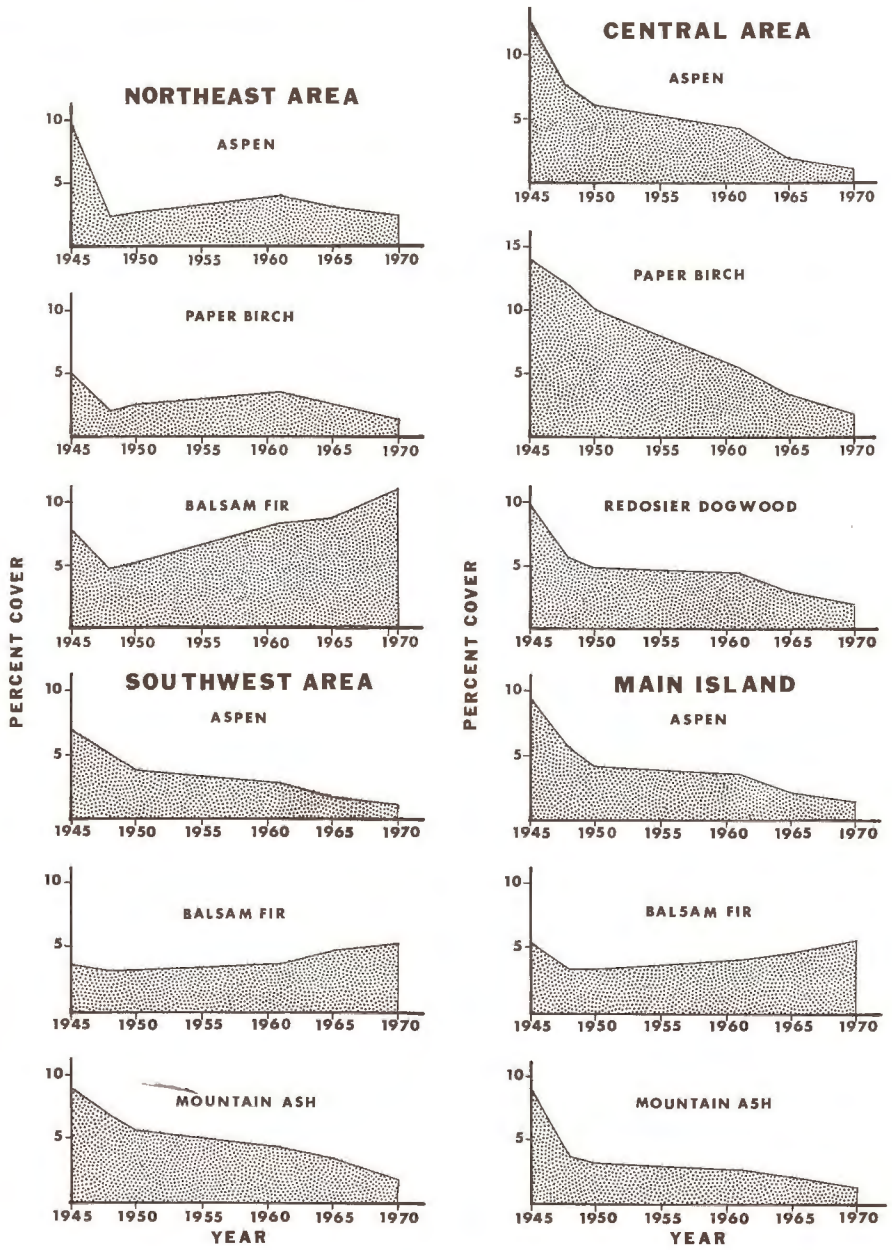


Figure 18. These are the percentages of each species in the diet in 1945 and 1970 in the northeastern area of Isle Royale.

Figure 19. Fluctuations are indicated here in the available browse supply of several species in the northeastern, central, and southwestern areas as well as in the mainland of Isle Royale.



speckled alder and white-cedar, were unimportant since they formed less than 1 percent of the diet each survey year.

Fluctuation in available browse

Key factors controlling the moose populations are the species and the amounts of highly preferred browse available in winter. On most winter ranges, the supply usually fluctuates from year to year. Factors responsible for these changes include the growing conditions, mortality factors, and severity of browsing in previous years. Changes in plant succession over the years also affect the browse supply. Less browse is available when the trees grow out of reach, suppressing the understory shrubs.

In the northeastern area, the average density (cover percent) in the high preference group decreased significantly from 1945 to 1950 ($P < .01$) (table 9). From 1945 to 1970, there was also a significant decrease ($P < .01$) in the browse supply in this group. Within the high preference group, aspen (figure 19), paper birch (figure 19), willow, and mountain ash decreased significantly from 1945 to 1970 ($P = .01$). Redosier dogwood showed no significant change from 1945 to 1970. Balsam fir decreased significantly ($P < .01$) from 1945 to 1948; it increased significantly ($P < .01$) from 1948 to 1970 (figure 19).

The medium preference species decreased significantly from 1945 to 1948 ($P < .01$), but there was no significant decrease from 1945 to 1970 (table 9). Among the medium preference species, beaked hazelnut decreased significantly from 1945 to 1948 and then increased significantly by 1970 ($P < .01$).

The low preference group (table 9) showed no significant differences in the browse supply from 1945 to 1970. Also, white-cedar showed no significant changes, but spruce (white and black) showed a significant increase from 1945 to 1970 ($P < .01$).

On Belle Isle, Caribou Island, Mott Island, and Smithwick Island, fluctuations in available browse supply varied a great deal. For Belle Isle, no significant differences occurred for the 1948-1961 period. Only aspen decreased significantly ($P < .01$) on Caribou Island, while balsam fir increased

significantly ($P < .01$). On Mott Island, ground hemlock, highbush cranberry, redosier dogwood, and mountain alder decreased significantly ($P < .01$). Mountain ash and paper birch also decreased significantly ($P = .02$ and $.05$) Where moose browsing has been more recent on Smithwick Island, significant decreases occurred in the browse supply of ground hemlock ($P = .02$) and mountain alder ($P = .05$).

Central area

Description of the area

This area covers about 40,000 acres (30 percent) of the island (figure 14). The major forest cover type is an aspen-paper birch mixture. It's the product of the 1936 burn that covered about 26,000 acres (about 20 percent) of the island (40 square miles). This burned-over area contains two separate parts: the 23,000 acre Siskiwit Lake burn in the central area; and 3,000 acres in the Feldtmann burn in the southwestern area. While white spruce and aspen occur groupwise, paper birch is the dominant tree species on large areas (Hansen et al., 1973). It is also the main reproducing species, averaging 1,600 stems per acre over 1 foot in height. Although it could be assumed that the trees are the same age because they date from 1936, this is not the case. Apparently, browsing by moose during the early development of these stands has accounted for the uneven ages of the trees.

The area also has an estimated 14,000 acres of the aspen-paper birch-balsam fir-white spruce type already described for the northeastern area. In addition, it has several thousand acres of the black spruce–white-cedar-type. The rock outcrop areas should also be mentioned, particularly those in the 1936 burn area. These rock outcrop areas are mostly south-facing. Because of this, the snow melts earlier in the spring in these areas than it does in the adjacent flats and swales. Like most rock outcrops, these areas are usually covered with heavily browsed and stunted aspen and paper birch. White-cedar, mountain ash, and white spruce are usually sparsely scattered. The most common shrub in the rock outcrop areas is willow.

Within the central area, typical understory shrubs are beaked hazel-

Table 9. Fluctuations in available browse in the northeastern area of Isle Royale.*

Species and preference	Year*					
	1945	1948	1950	1961	1965	1970
	Average cover percent					
High						
Aspen	9.5	2.4	2.5	4.1	3.1	2.5
Balsam fir	7.4	4.5	5.0	8.0	8.5	10.7
Balsam poplar		0.1	**	**	**	**
Black ash	0.1		**	0.3	0.2	**
Cherry sp.	1.5	0.8	0.4	0.5	0.6	0.1
Ground hemlock	0.2	0.8	0.7	0.6	0.6	0.3
Highbush cranberry	1.8	1.3	2.1	2.1	1.4	1.1
Juneberry sp.	3.9	1.2	2.7	3.2	3.4	2.9
Mountain ash	2.1	0.9	1.1	1.7	1.5	0.5
Paper birch	4.9	2.1	2.4	3.4	2.4	1.4
Redosier dogwood	2.2	1.8	1.8	2.0	1.3	1.1
Red maple	0.2	0.4	0.8	1.1	1.2	0.8
Sumac sp.	0.5	**	**			**
White pine	0.1	0.4	0.3	0.3	1.0	0.5
Willow sp.	3.4	1.9	1.8	2.3	1.0	0.7
Medium						
Beaked hazelnut	7.3	3.9	6.1	7.6	8.0	8.9
Bush honeysuckle	1.3	0.9	3.8	3.8	3.0	2.6
Canadian honeysuckle	5.7	1.2	0.8	0.4	1.1	0.6
Jack pine	**	0.2	0.2	1.9	0.1	**
Mountain alder	6.3	1.6	3.6	3.3	3.2	2.1
Mountain maple	0.8	0.8	0.8	0.7	1.0	1.5
Rose sp.		0.7	1.0	0.7	0.7	0.6
Sugar maple				0.1		
Low						
Juniper	0.4		0.7	3.2	0.7	1.9
Red-berried elder	0.2				**	
Speckled alder	0.6	1.2	0.9	1.6	1.0	0.1
Spruce sp.	1.4	1.8	1.7	2.5	3.4	4.5
White-cedar	0.5	0.5	0.7	0.9	0.3	0.8

*142 plots in 1945; 205 plots in 1948, 1950, 1961, 1965, and 1970.

**Less than 0.1 percent.

nut, fire cherry, juneberry, redosier dogwood, and willow. Fire cherry is the most widely distributed; mountain maple, speckled alder, beaked hazelnut, and bush honeysuckle are sparsely distributed.

Population fluctuation

Pellet group counts were made on 306 plots in the central area. They were made on six transects from 1948 to 1970 (figure 14).

Like the northeastern area, the central area counts showed a significant downward trend in population from 1948 to 1950 ($P < .01$). And from 1950 to 1970, the counts showed no significant upward trend in the population. Also, pellet group counts on all six transects indicated significant downward trends in the population from 1948 to 1950. The counts on five transects indicated significant upward trends in population from 1950 to 1970 ($P < .01$). Only the Siskiwit Lake-1936 burn counts indicated a significant downward population trend from 1950 to 1970 ($P < .01$).

Percentage of each species in the diet

Browse surveys in the central area were made on 184 1/100-acre plots in 1945 and 306 plots starting in 1948. The percentages of each winter food eaten in the area have been summarized by years (1945-1970) and by browse preference groups (high, medium, and low) (table 10). The 1945 survey showed that 12 high preference group species formed 94 percent of the diet. In 1970, the same group of species formed 86 percent of the diet. However during the 25 year period 1945-1970, the percentages of each species in the diet changed drastically (figure 20). High preference species that decreased in the diet by 1970 were aspen, paper birch, and willow. Medium preference species formed only 6 percent of the diet in 1945 and 12 percent in 1970. More than one-half the diet in 1970 was beaked hazelnut. Most years, low preference species made up less than 1 percent of the diet.

Fluctuation in available browse

In the central area, the available browse supply (average cover percentage) in the high preference group decreased significantly ($P < .01$) from 1945 to 1970 (table 11). Species that decreased significantly ($P < .01$) during the period were paper birch, redosier dogwood, and aspen (figure 19), and willow, balsam fir, and mountain ash. The medium preference group showed no significant change, although beaked hazelnut decreased significantly ($P < .01$). In contrast, the available browse supply in the low preference group increased significantly ($P < .01$). White-cedar and spruce in this group increased significantly ($P < .01$).

Southwestern area

Description of the area

The area covers about 50,000 acres (37 percent) of the island. It has many more forest cover types than do the central or northeastern areas. The largest cover type is the birch-fir-

Table 10. Percentage of each species in the diet in the central area of Isle Royale.

Species and preference	Year					
	1945	1948	1950	1961	1965	1970
High						
Aspen	22.2	15.1	15.5	11.9	11.8	9.0
Balsam fir	7.0	8.9	3.8	9.5	10.9	21.6
Balsam poplar	0.9	0.7	0.6	0.5	0.8	0.6
Black ash				0.5	0.2	
Cherry sp.	2.3	3.2	3.8	3.6	1.9	2.2
Ground hemlock		0.4		1.2		0.2
Highbush cranberry	0.8	0.9	1.1	0.9	2.6	1.9
Juneberry sp.	3.4	3.7	2.9	2.8	5.5	6.8
Mountain ash	5.0	5.6	4.6	12.5	9.2	11.8
Paper birch	21.4	21.4	31.6	16.7	10.4	6.6
Redosier dogwood	13.5	12.7	11.2	19.3	25.6	17.7
Red maple					0.1	
Sumac sp.	2.0	0.4	0.6	0.1	0.2	0.1
White pine	0.6	0.2	0.2		0.1	0.3
Willow sp.	14.6	14.6	13.8	10.1	9.8	7.3
Medium						
Beaked hazelnut	5.6	7.1	6.6	5.4	2.9	7.6
Bush honeysuckle				0.1		
Canadian honeysuckle		0.2	0.1			0.1
Mountain alder		3.0	1.2	1.5	5.1	2.2
Mountain maple		1.1	2.0	2.1	2.3	2.5
Rose sp.				0.1		
Low						
Red-berried elder						0.1
Speckled alder				0.2		0.1
White-cedar		0.5		0.6	0.1	1.0

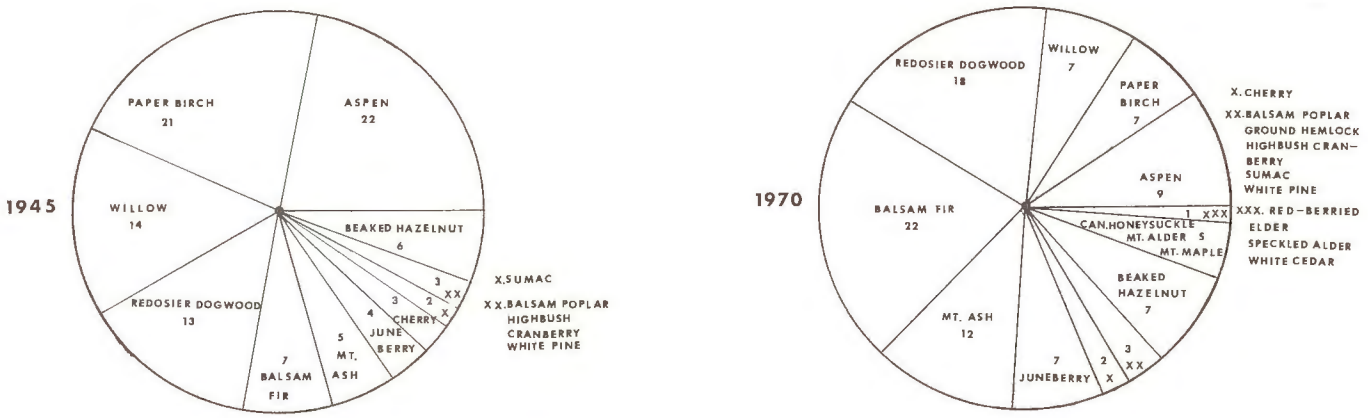


Figure 20. Percentages of each species in the diet in 1945 and 1970 in the central area of Isle Royale are indicated in this figure.

Table 11. Fluctuation in available browse in the central area of Isle Royale.*

Species and preference	Year					
	1945	1948	1950	1961	1965	1970
	Average cover percent					
High						
Aspen	12.3	7.6	6.1	4.3	1.9	1.1
Balsam fir	5.9	3.1	2.8	2.5	2.1	2.2
Balsam poplar	1.0	0.7	0.5	0.3	0.2	0.3
Black ash	0.4	0.3	0.2	0.3	0.3	0.1
Cherry sp.	3.0	2.1	1.8	1.4	0.8	0.5
Ground hemlock	1.9	0.9	0.7	0.5	0.4	0.3
Highbush cranberry	1.2	0.8	0.6	0.6	0.8	0.9
Juneberry sp.	3.6	2.2	1.6	1.2	1.0	0.4
Mountain ash	3.0	2.0	1.8	1.5	1.0	0.6
Paper birch	13.8	11.8	9.8	5.4	3.2	1.8
Redosier dogwood	9.5	5.3	4.9	4.3	2.9	1.7
Red maple				1.5	**	0.1
Sumac sp.	3.0	1.4	1.2	**		
White pine	0.4	0.2	0.2	0.2	0.1	0.1
Willow sp.	8.6	6.8	5.7	3.5	2.0	1.0
Medium						
Beaked hazelnut	4.1	4.1	3.2	2.6	1.9	1.7
Bush honeysuckle	1.9	1.5	2.3	2.2	1.8	1.3
Canadian honeysuckle	2.2	1.8	1.4	1.5	1.2	1.3
Mountain alder	2.3	2.0	1.9	2.4	2.3	2.9
Mountain maple	2.7	2.1	2.1	2.7	2.2	1.6
Rose sp.	0.6	0.6	1.0	0.7	0.6	0.4
Sugar maple		0.1		0.2	0.2	0.2
Yellow birch		0.1				
Low						
Juniper			0.5	0.2	0.8	1.4
Red-berried elder	0.2	0.2	0.2	0.1	0.1	0.2
Speckled alder	1.9	1.8	1.7	3.0	2.0	1.6
Spruce sp.	1.3	1.4	1.7	2.5	3.8	5.9
White-cedar	1.6	1.3	1.6	1.9	2.7	4.2

*184 plots in 1945; 306 plots in 1948, 1950, 1961, 1965, and 1970.
**Less than 0.1 percent.

spruce climax type; it occupies about 18,000 acres (about 30 percent) of the area. This type consists mainly of three species: paper birch; balsam fir; and white spruce. In some stands, yellow birch is a major component; white-cedar is a minor stand component. According to Cooper (1913), the type is climax. However, the Halliday (1937) and Rowe (1959) classifications suggest that it relates more closely to the Great Lakes-St. Lawrence Region since it is not typically boreal. Also, the type has become open and parklike because of more than 60 years of moose browsing. Therefore, more shrub browse occurs than is usually found in a typical boreal forest. Because the stand mixtures in this type are so variable, shrub species vary accordingly. Usually the shrub species include bush honeysuckle, Canadian honeysuckle, juneberry, mountain maple, mountain ash, redosier dogwood, red-berried elder, and ground hemlock sprigs.

The sugar maple-yellow birch climax type occupies about 10,000 acres (7 percent) of the island. The entire type is confined to the Greenstone Ridge in the southwest area where it covers 20 percent of the area. This forest has had little disturbance the past 120 years. Yellow birches are about 150 years old, sugar maple 220 years, and white-cedar 300 years of age. Balsam fir and some red maple also occur in the type. The shrub layer is dominated by sugar maple reproduction, but it has some white-cedar.

The black spruce–white–cedar swamp forest type covers about 10,000 acres (7 percent) of the island. About 9,000 acres (18 percent) is covered by this type. The swamp forest stands represent the island's third line of successional development. Stand components vary, but various combinations of black spruce, white-cedar, and tamarack are present. Predominant shrubs vary by different stand mixtures. They may contain such species as speckled alder, redosier dogwood, Canadian honeysuckle, mountain maple, and ground hemlock.

Thirteen-thousand acres (26 percent) of the area are covered by the aspen-birch type (5,000 acres), the birch-fir type (5,000 acres), and the 1936 burn type (3,000 acres). These communities vary in stand development and species composition. All are related to past fire disturbances.

Population fluctuation

Pellet group counts were made on seven transects in the southwestern area (figure 14), and similar counts were made on Beaver and Washington Island during the period.

The southwestern area counts showed a significant downward trend in population from 1948 to 1950 ($P < .01$). And from 1950 to 1970, the tallies indicated a significant upward trend in the population ($P < .01$). Each of the seven transects also showed similar significant population decreases and increases. The counts in the 1936 burn in the central area (Siskiwit Lake) showed a significant downward trend in population from 1950 to 1970. In contrast, counts in the southwestern area showed a significant upward trend from 1950 to 1970. Apparently, the better interspersion of unburned

Table 12. Percentage of each species in the diet in the southwestern area of Isle Royale.

Species and preference	Year					
	1945	1948	1950	1961	1965	1970
High						
Aspen	18.4	18.5	14.2	10.9	9.1	5.9
Balsam fir	6.7	7.8	1.2	16.8	14.1	22.7
Balsam poplar	0.1	0.5	1.1	0.2	0.1	0.1
Black ash		0.1	0.2			
Cherry sp.	3.1	2.8	3.3	3.1	8.0	6.0
Ground hemlock	0.8	0.4		1.3		0.1
Highbush cranberry	0.6	1.3	0.7	0.2	0.2	0.4
Juneberry sp.	4.4	4.2	5.4	3.6	3.6	2.4
Mountain ash	22.7	20.1	18.8	33.4	24.6	14.9
Paper birch	16.2	15.7	15.7	6.4	5.2	5.4
Redosier dogwood	5.3	8.1	9.5	7.7	11.9	9.7
Red maple					0.4	0.4
Roundleaf dogwood	0.2	0.2				
White pine		0.1	0.4	0.3	0.2	0.1
Willow sp.	4.9	7.0	10.9	3.5	6.8	4.6
Medium						
Beaked hazelnut	4.5	3.8	7.0	7.8	10.5	12.9
Mountain alder	0.4	0.5	1.0	0.2	0.4	0.6
Mountain maple	2.9	2.5	2.1	0.7	2.8	2.0
Sugar maple	6.7	3.7	6.8	1.9	0.8	10.3
Yellow birch	1.2	1.5	1.2	0.8	0.8	0.6
Low						
Red-berried elder	0.1	0.1				
White-cedar	0.1	0.3		0.3		0.4

patches of timber in the southwestern area burn made possible sustained longer use by the moose. On both Beaver and Washington Island, the counts showed the same population trend decrease (1948-1950) and increase (1950-1970).

Percentage of each species in the diet

Browse surveys in the southwestern area have been summarized by years for the period 1945 to 1970 and by preference groups (high, medium, and low) (table 12). The 1945 survey showed that 15 high preference group species formed 83 percent of the diet; in 1970, this species group formed 73 percent of the food eaten. Six species in the medium preference group increased from 16 percent of the food eaten in 1945 to 26 percent in 1970. The low preference species furnished less than 1 percent of the food eaten. High preference species that decreased strikingly in the diet from 1945 to 1970 were aspen, mountain ash, and paper birch (figure 21). Striking increases in the diet during the period were for balsam fir, cherry, and redosier dogwood (figure 21).

The Island Mine-Lake Desor-Windigo transect is of special importance; it's the only transect having the sugar maple-yellow birch climax type. Use by moose is confined to the spring, summer, and early fall – not winter. High preference species accounted for 21 percent of the diet in 1945 and only 9 percent in 1970. Mountain ash is the major species, and the diet has fluctuated from 3 to 13 percent. The species made up 9 percent of the diet in 1945 and only 3 percent in 1970. The medium preference group accounted for the major part of the diet each year. Sugar maple alone accounted for most of the food eaten during the period. The low preference species made up less than 3 percent of the diet.

Fluctuation in available browse

In the southwestern area, the available browse supply (average cover percentage) in the high preference group decreased significantly ($P < .01$) from 1945 to 1970 (table 13). The medium

Table 13. Fluctuation in available browse in the southwestern area of Isle Royale.*

Species and preference	Year					
	1945	1948	1950	1961	1965	1970
	Average cover percent					
High						
Aspen	6.9	5.0	3.8	2.7	1.6	1.0
Balsam fir	3.7	3.2	3.3	3.9	4.7	5.4
Balsam poplar	0.5	0.4	0.3	0.2	0.3	0.3
Black ash	0.7	0.2	0.3	**	**	0.1
Cherry sp.	2.6	1.7	1.5	1.3	1.5	1.0
Ground hemlock	1.8	1.2	1.0	1.1	1.1	1.2
Highbush cranberry	1.5	0.8	0.7	1.0	1.0	0.8
Juneberry sp.	2.3	1.7	1.5	1.2	1.2	1.6
Mountain ash	8.9	6.9	5.5	4.3	3.5	2.7
Paper birch	8.3	5.6	4.4	2.6	2.2	2.0
Redosier dogwood	2.6	3.0	2.8	2.0	1.9	1.8
Red maple	0.5	0.5		**	0.2	0.3
Roundleaf dogwood	0.8	0.3	0.3	0.1	0.3	0.2
Sumac sp.				0.6	0.1	
White pine	0.1	0.1	0.1	0.2	0.1	0.1
Willow sp.	3.1	2.7	2.0	1.1	1.1	0.3
Medium						
Beaked hazelnut	2.8	2.7	2.8	2.8	3.0	3.0
Bush honeysuckle	1.1	1.6	1.6	1.2	1.2	1.2
Canadian honeysuckle	2.0	1.6	1.5	1.5	1.5	1.4
Mountain alder	0.7	0.8	0.8	0.5	0.5	0.3
Mountain maple	4.3	3.5	3.6	3.3	3.3	2.9
Rose sp.	0.2	0.3	0.3	0.3	0.2	0.2
Sugar maple	16.2	12.4	13.1	13.1	13.1	12.5
Yellow birch	3.0	1.6	1.4	1.0	0.9	0.9
Low						
Juniper		**	**	**		**
Red-berried elder	1.3	1.4	0.8	0.7	0.9	0.7
Speckled alder	1.7	1.6	1.1	1.3	1.2	0.8
Spruce sp.	1.3	1.5	2.0	3.3	3.5	4.3
White-cedar	4.0	3.1	3.2	3.1	3.3	3.3

*266 plots in 1945; 333 plots in 1948, 1950, 1961, 1965, and 1970.
**Less than 0.1 percent.

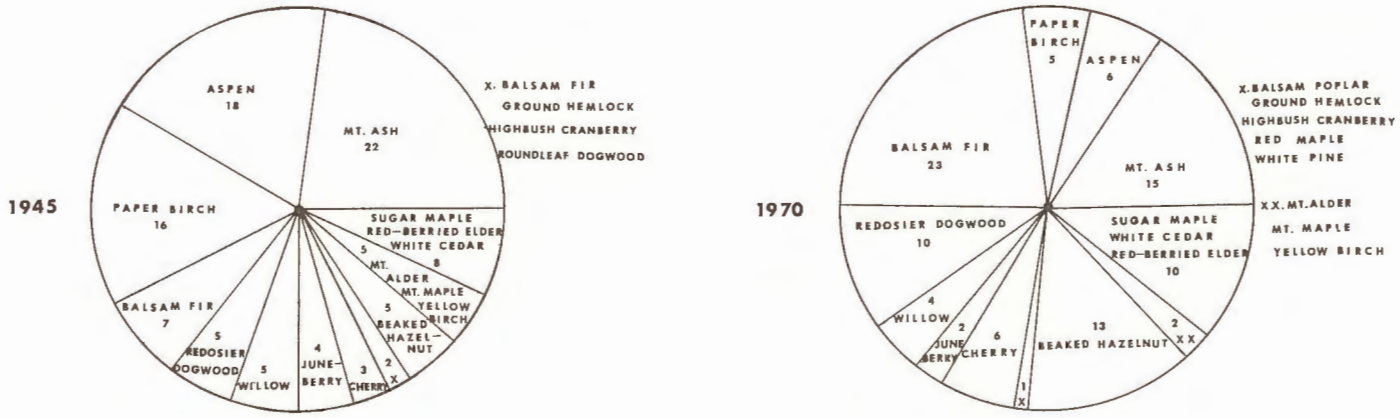


Figure 21. Percentages of each species in the diet in 1945 and 1970 are compared for the southwestern area of Isle Royale.

preference species also decreased significantly ($P < .01$), while the low preference group showed no significant change. Aspen, mountain ash (figure 19), paper birch, redosier dogwood, and willow decreased significantly ($P < .01$); balsam fir (figure 19) and spruce increased significantly ($P < .01$). For beaked hazelnut and white-cedar, there was no significant difference from 1945 to 1970.

Fluctuations in available browse in the Feldtmann 1936 burn showed a significant decrease for the high preference species ($P < .01$). The medium and low preference species had no significant differences during the period. Species that had significant decreases were aspen, paper birch, and willow ($P < .01$).

The Island Mine-Lake Desor-Windigo transect showed no significant differences for the high, medium, and low preference groups. Similar results were found on Beaver Island and on Washington Island for these groups. On Washington Island, significant decreases occurred for cherry and ground hemlock ($P < .01$) and paper birch ($P = .05$). Spruce increased significantly ($P < .01$).

Main island

Population fluctuation

The island's history of moose population fluctuations has been discussed previously in this report. For the period 1948 to 1970, pellet group counts made in 1948, 1950, 1961, 1965, and 1970 have provided the most significant population trend data (figure 12). From 1948 to 1950, the counts decreased significantly ($P < .01$). The counts substantiate the die-off of the moose during that period (Krefting, 1973). After 1950, general observations, range surveys, and pellet group counts have shown that the moose herd increased significantly ($P < .01$).

Percentage of each species in the diet

Percentage data of each food eaten on the entire island (excluding nearby islands) show the winter diet for the period consisted of 24 species (table 14). Fifteen were in the high preference group; seven were medium preference species; and two species were in the low preference group. The high preference group made up more than 80 percent of the diet. Some species in the high preference group decreased, while others increased. Aspen, paper birch, and willow decreased (figure 22). In contrast, balsam fir increased. The medium preference species increased slightly. Of these, the greatest increase was beaked hazelnut – from 4 to 8 percent in the diet. Low preference species formed less than 1 percent of the diet.

Additional information on the moose's winter food habits came from the occurrence of conifer needles in moose pellets collected in 1961. A total of 3,135 individual pellets was collected from 237 pellet groups located randomly throughout the island. The number of randomly selected pellets from each group ranged from 8 to 28. The examination revealed no white-cedar or white pine. The frequency of balsam fir needles was 67 percent. For ground hemlock, it was 14 percent. Also, the occurrence of balsam fir in the browse plots was 51 percent. For ground hemlock, the frequency was 14 percent – the same frequency as determined from the pellet study.

On St. Ignace and Simpson Islands, Ontario, Peterson (1953) examined 170 pellets from 34 samples in 1947. He found all had balsam fir needles and 42 percent contained white-cedar. The 1948 collection from these islands consisted of 460 pellets from 92 samples. All had balsam fir needles, and 29 percent contained white-cedar.

Fluctuation in available browse

The data on available browse (average cover percentage) for the main island are based on 30 species. Sixteen species were in the high preference group; nine were in the medium pref-

Figure 22. Percentages of each species in the diet in 1945 and 1970 are compared for the main island of Isle Royale.

Table 14. Percentage of each species in the diet on the main island of Isle Royale.

Species and preference	Year*					
	1945	1948	1950	1961	1965	1970
High						
Aspen	20.5	16.0	14.5	11.8	10.8	8.3
Balsam fir	9.2	11.1	4.8	13.4	14.3	26.2
Balsam poplar	0.4	0.5	0.8	0.3	0.4	0.3
Black ash	0.1			0.2		
Cherry sp.	2.5	3.0	3.1	2.9	4.6	3.7
Ground hemlock	0.3	0.3		1.1	0.1	0.1
Highbush cranberry	1.1	1.7	1.2	1.4	2.2	1.5
Juneberry sp.	4.3	4.2	5.4	5.3	5.6	7.1
Mountain ash	11.9	11.3	8.8	19.8	15.6	11.5
Paper birch	17.9	17.3	23.9	10.6	7.1	5.5
Redosier dogwood	8.8	10.3	10.8	12.4	15.3	11.3
Red maple	0.1	0.2	0.3	0.5	0.6	0.4
Sumac sp.	1.1	0.2	0.4			
White pine	0.3	0.2	0.3	0.2	0.1	0.3
Willow sp.	10.1	10.6	13.1	7.8	7.9	5.3
Medium						
Beaked hazelnut	4.2	5.5	6.5	7.6	8.9	7.9
Bush honeysuckle				0.3	0.5	
Canadian honeysuckle		0.3				
Mountain alder	1.7	2.0	1.5	1.2	2.3	1.7
Mountain maple	1.6	1.9	1.9	1.2	2.2	2.7
Sugar maple	2.5	1.5	1.9	0.8	0.3	4.7
Yellow birch	0.5	0.6	0.4	0.2	0.3	0.3
Low						
Speckled alder				0.1	0.1	
White-cedar	0.1	0.4		0.4		0.5

*592 plots in 1945; 844 plots in 1948, 1950, 1961, 1965, 1970.

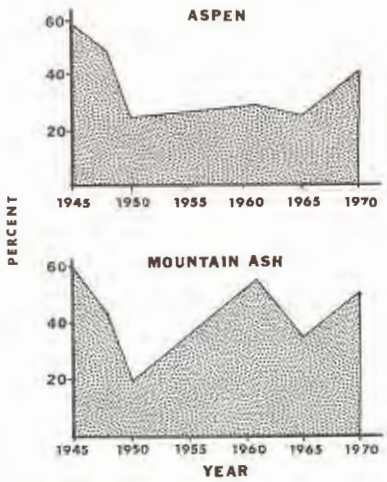


Figure 23. Fluctuations are shown in the average degree of browsing on aspen and mountain ash on the main island of Isle Royale.

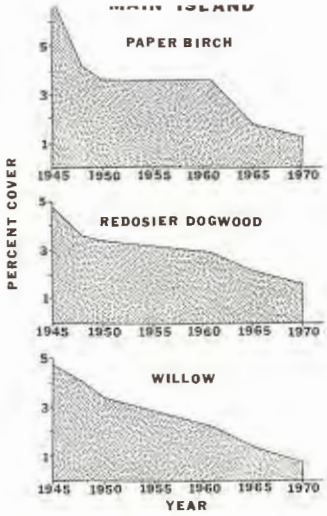


Figure 24. Fluctuations are shown in the available browse supply of paper birch, redosier dogwood, and willow on the main island of Isle Royale.

erence group; and five were in the low preference group (table 15). The high preference group decreased significantly from 1945 to 1970 ($P < .01$). Species that decreased significantly ($P = .01$) were aspen, mountain ash (figure 23), paper birch, redosier dogwood, and willow (figure 24). Balsam fir decreased significantly from 1945 to 1950 ($P = .05$) and increased significantly ($P = .05$) from 1950 to 1970 (table 15). In the medium preference group, fluctuations in the available browse supply were not so great between years. There was a significant decrease from 1945 to 1948 and from 1945 to 1970. However, there were no significant differences from 1948 to 1950, from 1950 to 1961, from 1961

Table 15. Fluctuation in available browse on the main island of Isle Royale.*

Species and preference	Year					
	1945	1948	1950	1961	1965	1970
	Average cover percent					
High						
Aspen	9.2	5.3	4.3	3.7	2.1	1.5
Balsam fir	5.3	3.5	3.5	4.4	4.7	5.6
Balsam poplar	0.7	0.4	0.3	0.2	0.2	0.2
Black ash	0.5	0.2	0.2	0.2	0.2	0.1
Cherry sp.	2.3	1.7	1.4	1.2	1.1	0.8
Ground hemlock	1.7	1.0	0.9	0.8	0.7	0.6
Highbush cranberry	1.5	1.0	1.1	1.2	1.0	0.9
Juneberry sp.	3.1	1.7	1.8	1.7	1.5	1.5
Mountain ash	8.8	3.7	3.1	2.7	2.1	1.4
Paper birch	6.9	4.2	3.6	3.6	1.8	1.3
Redosier dogwood	4.7	3.6	3.4	2.9	2.1	1.6
Red maple	0.4	0.5	0.8	0.7	0.8	0.5
Roundleaf dogwood	0.8	0.3	0.3	0.1	0.2	0.2
Sumac sp.	2.4	0.4	0.4	0.6	0.1	**
White pine	0.2	0.2	0.2	0.2	0.3	0.2
Willow sp.	4.8	4.1	3.4	2.2	1.4	0.7
Medium						
Beaked hazelnut	4.8	3.8	3.6	4.1	4.0	4.1
Bush honeysuckle	1.5	1.3	1.9	2.2	0.8	1.6
Canadian honeysuckle	3.0	1.5	1.3	1.2	1.3	1.2
Jack pine	0.2	0.2	0.2	0.2	0.1	**
Mountain alder	3.0	1.5	1.8	1.9	1.9	1.7
Mountain maple	2.9	2.3	2.4	2.4	2.4	2.1
Rose sp.	0.4	0.5	0.7	0.6	0.5	0.4
Sugar maple	7.2	4.9	5.1	5.1	5.2	4.9
Yellow birch	0.3	0.1	0.2	0.1	0.2	0.1
Low						
Juniper	0.1	0.1	0.1	0.3	0.1	0.4
Red-berried elder	1.0	1.0	0.8	0.8	0.7	0.7
Speckled alder	1.5	1.6	1.3	2.0	1.5	1.0
Spruce sp.	1.3	1.5	1.8	2.8	3.6	4.9
White-cedar	2.4	1.8	2.0	2.2	2.4	3.0

*592 plots in 1945; 844 plots in 1948, 1950, 1961, 1965, and 1970.
**Less than 0.1 percent.

to 1965, and from 1965 to 1970. Beaked hazelnut, the major species, showed no significant differences during the period. For the low preference group, the browse supply remained the same in 1945, 1948, and 1950 before it increased significantly (P = .01) by 1970. Spruce, a nonbrowse species, and white-cedar, sometimes browsed, increased significantly from 1945 to 1970 (P = .01).

In summary, these data demonstrate conclusively that the browse supply on Isle Royale reached a critical level by 1970. In 1945, major high preference key species – such as aspen, mountain ash, paper birch, redosier dogwood, and willow – made up the bulk of the diet. And in 1970, these species furnished far less browse. Only balsam fir increased, and most of this increase was in the northeastern area. The browse furnished by the medium preference group did not fluctuate widely. And the low preference group supply remained the same for about 5 years. Then it increased during the next 20 years. Since the moose thrives best during the seral stage of plant succession, major disturbances will be needed to create this kind of habitat. Unfortunately, most of the forest cover types have matured; they furnish far less browse than they did in 1945. Even in the 1936 burn area, the tree species which once furnished an abundant supply of browse produce very little browse within reach. The feasibility of introducing fire into the ecosystem must be explored. Fire may be a means to increase browse.

Fluctuation in average degree of browsing

For the period 1945 to 1970, data on the average degree of browsing were subjected to chi-square tests for eight species on the main island (table 16). For mountain ash, there was a significant decrease from 1945 to 1948 and from 1948 to 1950 (P = .01). This was followed by a significant increase from 1950 to 1961 (P = .01), a significant decrease from 1961 to 1965 (P = .01), and a significant increase (P = .01) from 1965 to 1970. For aspen, the average degree of browsing also decreased significantly from 1945 to 1948 and from 1948 to 1950 (P = .01). But from 1950 to 1965, there was no significant difference in the average degree of browsing. However from 1965 to 1970, there was a significant increase in browsing (P = .01) (table 16). To a great extent, browsing on willow followed the same pattern as for aspen. There were significant decreases from 1945 to 1948 and from 1948 to 1950. No significant differences occurred from 1950 to 1965, but from 1965 to 1970 there was a significant increase (P = .01).

For paper birch, there were significant decreases from 1945 to 1948 (P = .01), from 1948 to 1950 (P = .01), and from 1950 to 1965 (P = .05). From 1965 to 1970, there was a significant increase in browsing (P = .05). The average degree of browsing for balsam fir remained the same from 1945 to 1948 and decreased significantly from 1948 to 1950 (P = .01). This was followed by a significant increase from 1950 to 1961

Table 16. Average degree of browsing for all species on the main island of Isle Royale.[1]

Species	Year					
	1945	1948	1950	1961	1965	1970
	Percent					
Mountain ash	60	44	20	56	35	51
Aspen	58	46	24	28	26	40
Willow sp.	57	39	28	30	32	42
Paper birch	53	35	26	18	13	18
Red maple	52	37	20	22	17	30
Balsam fir	46	45	10	24	16	36
Redosier dogwood	41	44	23	36	31	41
White pine	41	16	19	22	10	27
Juneberry sp.	40	34	19	24	20	36
Balsam poplar	37	38	13	25	23	29
Cherry sp.	31	28	16	22	27	37
Beaked hazelnut	27	24	14	18	14	16
Highbush cranberry	26	34	11	11	15	17
Roundleaf dogwood	22	31		3		1
Yellow birch	21	27	8	12	10	13
Mountain alder	19	27	7	7	7	9
Mountain maple	14	12	6	4	5	11
Black ash	13	15		22	5	9
Sugar maple	9	4	3	1		8
Ground hemlock	7	5		13	1	2
White cedar	2	3		2		2
Red-berried elder	2	2				
Canadian honeysuckle		4				
Rose sp.				2		
Bush honeysuckle				1	2	

[1] Species with average degree of browsing of 1 or more.

(P = .01), a significant decrease from 1961 to 1965 (P = .01), and a significant increase from 1965 to 1970 (P = .01). The browsing on redosier dogwood and balsam fir were much the same. It remained the same from 1945 to 1948, decreased significantly from 1948 to 1950 (P = .01), and increased significantly from 1950 to 1961 (P = .01). There was no significant change from 1961 to 1965, but a significant increase occurred from 1965 to 1970 (P = .01).

For juneberry, browsing decreased significantly from 1945 to 1948 and from 1948 to 1950 (P = .01). From 1950 to 1961, browsing increased significantly (P = .05). This was followed by a significant decrease in browsing from 1961 to 1970 (P = .05). For cherry, there was no significant difference in browsing from 1945 to 1948, but there was a significant decrease from 1948 to 1950 (P = .01). This was followed by significant increases from 1950 to 1961, from 1961 to 1965, and from 1965 to 1970 (P = .01).

The average degree of browsing for the eight species on the main island suggests that browsing was apparently influenced by snow depth, winter temperature, and the availability of high preference species. From 1945 to 1948, browsing decreased significantly (P = .01) for only five of the eight species. From 1948 to 1950, browsing for all species decreased significantly (P = .01) (table 16). The decrease from 1948 to 1950 reflects the known die-off of the herd during that period. Since the population trend was upward from 1950 to 1961, five of the eight species showed significant increases in browsing (P = .05), two species showed no change, and one decreased significantly (P = .05). From 1961 to 1965, the browsing for only one species increased significantly (P = .05), four species decreased significantly (P = .05), and three species showed no change. However from 1965 to 1970, seven of the eight species increased significantly (P = .01), while one decreased significantly (P = .01). Since the browse supply for most high preference species was at a low point in 1970 and the population trend had increased significantly from 1950 to 1970, the increased browsing suggests the moose herd had exceeded the carrying capacity of the winter range.

FACTORS AFFECTING THE MOOSE RANGE

Effect of insects and diseases

Many investigations have demonstrated the importance of balsam fir in the moose's winter use patterns (Murie, 1934; Hickie, 1936; Aldous and Krefting, 1946; Krefting, 1951; Pimlott, 1953, 1961; and Krefting, 1973). The older stands provide important winter cover, and the young growth provides winter browse. In 1970 on Isle Royale, balsam fir made up 26 percent of the winter browse in the diet. Since balsam fir is defoliated and killed by outbreaks of the spruce budworm *(Christoneura fumiferana),* the role of this insect is of great significance.

Case histories of budworm outbreaks have been reported by Blais (1968) and Kulman (1971). Bakuzis and Hansen (1965) have also reviewed epidemics that occurred in Minnesota and Ontario from about 1880 to 1956. Peterson (1955) noted budworm attacks in Ontario in 1946. Earlier attacks there killed 50 to 100 percent of the balsam fir in some areas. In 1952, a large budworm-damaged area resulted from simultaneous outbreaks in the Hudson, LacSeul, and Lake of the Woods areas, extending into northeastern Minnesota (McGugan et al., 1953; Batzer, 1969). In 1956, moderate to heavy defoliation occurred on 419,000 acres in Minnesota (Bean and Graeber, 1957). Within the spruce–fir type in northeastern Minnesota, the defoliation area increased from 96,000 acres in 1960 to 240,000 acres in 1961 (Batzer and Bean, 1962).

Although the budworm mostly kills overstory, removal of winter cover benefits moose in the long run. The overstory removal releases the advanced reproduction of balsam fir and also enhances shrub growth. Cumming (1972) noted: "High densities of moose which built up in northeastern Ontario some 10 to 20 years ago, probably resulted from the great spruce budworm outbreak in that area." In northwestern Ontario, Simkin (1963) observed that, when budworm-killed stands are burned, the successional growth provides excellent moose habitat. These stands permitted more sunlight to reach the forest floor. This sunlight, in turn, stimulated the growth of such important hardwood species as aspen, paper birch, willow, juneberry, mountain ash, and beaked hazelnut.

On Isle Royale, the first known budworm attacks occurred in the early 1930's. Along the entire south shore of the island, 75 to 100 percent of the balsam fir stands were killed (Brown ca., 1935). Hickie (1936), too, reported 90 to 100 percent of the balsam fir reproduction that projected

above the snow was killed. The budworm-killed trees probably furnished additional fuel for the 1936 fire which burned over approximately one-fifth of the island (Krefting, 1973). Krefting concluded that this fire reduced plant succession to the early seral stage. It probably was responsible for the subsequent marked increase in the moose herd.

A limited insect and disease survey made in 1964 by the U.S. Forest Service showed the budworm had caused scattered mortality in older balsams before the fire (Letter of Sept. 3, 1964, from the Superior National Forest, Duluth, Minn.). The survey showed that current defoliation was light and limited largely to the unburned area west of Siskiwit Bay.

Budworm outbreaks are, therefore, natural events which will continue to affect forest types dominated by balsam fir. Future periodicity, extent, and severity of these outbreaks will be difficult to predict. Some investigators have speculated that the epidemics occur at intervals of 50 to 70 years (Swaine et al., 1924; Graham and Orr, 1940). McLintock (1949) suggested a cycle of 30 to 35 years for the northeastern United States. Spruce budworm epidemics must be considered beneficial to moose.

Two tree diseases are of importance to Isle Royale moose: white pine blister rust (*Cronartium ribicola*); and the brown cubical rot on balsam fir (*Polyporus balsameus*). The establishment and growth of white pine reproduction has been hampered by the widespread distribution of the rust. By 1945, tree rust had almost eliminated reproduction. White pine, a high preference browse species, made up 0.3 percent of the winter diet in 1945 – in 1970, the amount in the diet was the same. The brown rot is both detrimental and beneficial. Overstory balsams become weakened because of the rot and are, therefore, more vulnerable to wind breakage. Removal of these overstory trees by wind also opens up the stand and enhances the growth of the ground vegetation for browse.

Effect of wind damage

Much has been written about wind damage to the forest, especially concerning winds of hurricane velocity (Grisez, 1955). Studies have shown that forest stands' species composition and form affect the extent of damage less than do aspect and exposure (Baxter, 1952; Jensen, 1941; Lundgren, 1954). Trees growing on ridgetops are especially vulnerable to windthrow, particularly if the storm occurs during the wet season when the soil is loose and wet (Toumey and Korstian, 1947). Studies have shown blowdown of pulpwood stands in eastern Canada was most frequent in narrow valleys, at lake ends, on ridges, on south or southeast-facing slopes, and on shallow soils in mature stands having dominant species of spruce and balsam (Zon, 1914).

Schantz-Hansen (1937) reported that, during one storm, 27 percent of the balsam fir in the Cloquet, Minn., Forestry Center were windthrown. Cheyney (1942) in Minnesota also concluded that more wind damage occurs on wet sites than on dry sites.

An early study reported balsam fir in the Adirondacks was vulnerable to windthrow because of shallow root systems and decay which the root systems usually contain (Behre, 1921). Zon (1914) also noted balsam fir is easily uprooted by wind because the root system is shallow and the bole is brittle. As mentioned previously, balsam fir is susceptible to butt rot, making it more vulnerable to windthrow.

Dodds (1973) reported that blowdown areas are common in the moose range in the Atlantic Provinces of Canada, particularly in Nova Scotia and Newfoundland. Also, Wright (1956) refers to the Saxby Gale of 1869 which created many blowdowns in southern New Brunswick.

At Itasca State Park, Minn., windthrow damage to balsam fir was greater on ridge tops than on swampy areas (Lundgren, 1954). Lundgren found only one tree standing out of an original 58 balsam fir. Uprooting was the major cause of balsam fir loss; the trees had both root and butt rot.

Lack of leaves usually permits hardwoods to survive severe windstorms in the dormant seasons. However, damage to conifers is often increased when a stand's hardwood trees are leafless (Bowman, 1944, and Hawley and Stickel, 1948).

Isle Royale is particularly vulnerable to wind damage. This is because of its isolation as an island, its location in northwestern Lake Superior, and its ridges, narrow valleys, and lakes. The extensive southeast-facing slopes, shallow soils, and extensive mixed stands of spruce and balsam fir also make it more susceptible to windthrow. Severe timber blowdowns are known to have occurred during the past century or before. The species most affected have been balsam fir, black spruce, and white spruce. In 1951, an extensive blowdown area occurred in the aspen-paper birch-balsam fir-spruce type in the northeastern end of the island. Also in the fall of 1969, an estimated 30 acres blew down on Houghton Ridge which had very shallow soils. In late fall of 1971, heavy winds created balsam fir blowdowns in many parts of the island. In the summer of 1937, the edges of the 1936 burn area had extensive blowdowns of white-cedar, balsam fir, black spruce, and white spruce. The fire damaged the root systems of these trees and made them more vulnerable to windthrow. Unfortunately, although it is known that windthrow has occurred commonly on Isle Royale, the dates, number, and extent of blowdowns have not been systematically recorded. However, these blowdowns are important and must be considered beneficial to moose. They permit more sunlight to reach the forest floor, thereby enhancing the growth of tree reproduction and shrubs. In addition, the balsam fir blowdowns also provide an important source of temporary winter browse.

Effect of forest cutting

Logging has been the principal method of removing the older-age timber with young browse-producing stands for deer and moose (Telfer, 1970a). After logging, new vegetation is in the early successional stage, containing a greater variety and quantity of high quality browse than does the mature forest (de Vos, 1962; Cowan et al., 1950). Apparently, logging and wildfire, plus land clearing for settlement, was responsible for the extension of moose in the part of Ontario north of Lake Superior (Peterson, 1955).

On Isle Royale, the assumption has been that cutting first occurred in the 1930's. However, Rakestraw (1963)

has demonstrated that timber cutting on the island took place as early as 75 years before the arrival of the moose in the early 1900's. His report is the major source for the following discussion.

The American Fur Company operated several field stations on the island. These stations were engaged in fishing from 1835 to 1837 (Nute, 1926). When the island was surveyed in 1847-1848, fishermen of the American Fur Company and succeeding fishermen cut white pine to make barrel staves (Ives, 1848). During the three periods of copper mining (1843-1855, 1873-1881, and 1889-1893), much lumber was used for mine timber, shaft houses, ore docks, dwellings, and business houses. These mines were located around the periphery of the island from Malone Bay to Rock Harbor and Washington Harbor. White pine, when available, must have been used for construction lumber. Tamarack was probably preferred for mine timbers where strength and durability were important. Rakestraw (1968) reported, "In the areas around the recent mines one can still see the effect of heavy cutting. In the Saginaw mine area, pine stumps, with axe marks still visible, are plentiful." Rakestraw also noted stumps of large white pine still remain in the Island mine area. Also, the clearings show evidence of heavy cutting near Card Point, Hay Bay, Epidote mine, and the Siskiwit mine settlements.

Rakestraw pointed out there is also evidence of commercial timber cutting. For example, an old logging road in the Checker Point area shows evidence of extensive and destructive logging for white pine. It appeared far beyond that needed for the Island mine settlement. This logging must have occurred after 1880 when cross cut saws began being used. Rakestraw also indicates a sawmill on Rock Harbor carried on extensive logging for several years. In addition, a lumber firm made their headquarters at the head of Hay Bay. The 300 inhabitants of the logging camp cut all the valuable timber from Hay Bay to Washington Harbor. The logs may have been rafted to Duluth. The next and last logging occurred in 1935 and 1936 at the head of Siskiwit Bay. There, 2,500 acres were clear-cut for pulpwood (Hickie ca., 1943).

Timber cutting on Isle Royale has been minor, and logging has not been important in initiating secondary successions. The influence of timber cutting on the moose herd has been insignificant.

Effect of fire

Ahlgren and Ahlgren (1960) reviewed the literature on the ecological effects of forest fires in the Lake States. This review demonstrated the importance of forest fires in the establishment and development of even-aged stands of aspen, birch, and pine.

Maissurow (1941) reported on the role of fire in the perpetuation of the virgin forests of northern Wisconsin. He found that 95 percent of these forests had been burned within the last 500 years. Maissurow concluded that these fires were "periodic and ecologically normal events in the life of the forest."

In Itasca State Park, Minn., research showed that at least 32 fires occurred between 1650 and 1922. Twenty-one of these were major fires, and 16 resulted in pine regeneration (Frissell, 1973). Fires occurred in the area an average of 8.8 years; major fires occurred every 10.3 years. Frissell concluded that: "While attempting to preserve these biotic communities by protecting them, man has actually interfered with the natural process. This interference has resulted in serious deviation from natural conditions. If the preservation of natural biotic communities is the objective of Itasca Park, then a more active management program must be adopted that recognizes the role of fire and take steps to return this all-important natural factor to the system."

Vogl (1967) summed up his views regarding controlling fire in Wisconsin: "Wisconsin landscape has moved from a rich mixture of prairies, barrens, clearings, savannas, and forests to an unproductive, monotonous, homogeneous, and almost endless forest. This transition has produced a loss of valuable open lands for wildlife and a loss of game producing edges. Much of Wisconsin has become a place where 'you can't see the forest for the trees,' and consequently, a place where you can't see (or find) the wildlife for the trees."

Krefting (1973) reviewed the literature of moose distribution and habitat selection in north central North America. He reported that the most desirable habitats for moose occur in the early seral stages of plant succession. Fire has undoubtedly been the major agent for establishing these secondary successions which are not only desirable for moose, but also for deer, beaver, and snowshoe hare. Krefting also reviewed the status of recent fires in Manitoba, Ontario, and the Lake States. He concluded that fire protection during the past half century has reduced the amount of high quality moose habitat.

Hayes' early observations (1938) on forest fires and wildlife stressed the ecological importance of fire. He noted: "It may be agreed that fire has been an ecological factor, even in the forest primeval, and that in favoring certain types of forest and wildlife, it produces a natural condition." Natural fire occurred quite often in most parts of the boreal forest, preventing the forest from reaching maturity.

In the Taiga of Alaska, Viereck (1973) reported that: "Some wildlife species, such as moose and snowshoe hare, depend upon fire and its resultant successional plant communities, whereas fire may have deleterious effects on caribou winter range."

The importance of fire in the boreal forest has been evaluated by Rowe and Scotter (1973). These authors concluded that fire should be considered a normal ecological process and that a thorough knowledge of its long term role in terrestrial and aquatic ecosystems is needed.

In northern Manitoba, the manipulation of the range, mostly by forest fires, was the most important factor in moose abundance and distribution (Bryant, 1955). In Ontario, Cumming (1972) wrote: "It has been observed over and over again that some of the greatest moose concentrations are in areas previously burned. It seems likely that the nutrients released in ashes from burned vegetation enrich the area and produce more nutritious foods."

Within the moose range in northeastern Minnesota, fire history research by Heinselman (1969 and 1970) has shown the oldest stand dated from 1595; the youngest of any size dated from 1936. From 1600

A.D. to 1920, fires occurred at 5 to 50 year intervals. For some, the interval was as short as 10 years; for others, it was as long as 200 to 300 years. Heinselman noted that, "The animal component of these forest ecosystems was adapted to a fire ecology. Some of the most abundant herbivores – deer, moose, elk, snowshoe hare, and beaver – are best adapted to recent burns and the early successional stages of the forest – not climax forests."

In more recent research, Heinselman (1973) noted: "Fire largely determined the composition and structure of the presettlement vegetation of the Boundary Waters Canoe Area as well as the vegetation mosaic on the landscape and the habitat patterns for wildlife." He said that prescribed burning should be reintroduced and lightning fires should be monitored.

On the Kenai Peninsula, Alaska, Spencer and Hakala (1964) said, "Viewed solely from the standpoint of moose management, forest fires in this zone have generally been beneficial through the production of winter browse in sufficient quantity to maintain large moose herds. Duration of browse growth and volume produced is highly variable. Some areas have produced no browse growth following fires."

Isle Royale fire history information is rather sketchy. However, a recent vegetation-type map demonstrates that the island has a mosaic of forest cover types of different sizes and ages (Krefting et al., 1970). Most of these cover types have been produced by past forest fires. Ives' field notes concerning his linear survey of the island referred to burned over areas – especially in the northeastern section (Ives, 1848). Also during the three copper mining periods from about 1843 to 1893, copper prospectors set fires intentionally (Brown ca., 1935; Rakestraw, 1965).

Table 17. Recent fires on Isle Royale.*

Year	Number by origin			Acreage
	Lightning	Other	Total	
1940	–	–	–	–
1941	1	2	3	–
1942	1	–	1	6.80
1943	–	–	–	–
1944	–	–	–	–
1945	1	–	1	8.30
1946	1	–	1	1.26
1947	2	–	2	2.00
1948	2	–	2	1,440.75
1949	3	–	3	–
1950	–	–	–	–
1951	–	–	–	–
1952	–	–	–	–
1953	–	–	–	–
1954	2	6	8	6.53
1955	2	1	3	0.90
1956	–	1	1	–
1957	–	2	2	–
1958	5	2	7	1.07
1959	2	–	2	0.16
1960	–	3	3	–
1961	1	–	1	–
1962	1	4	5	0.37
1963	–	–	–	–
1964	2	1	3	–
1965	–	–	–	–
1966	–	4	4	A**
1967	–	1	1	A
1968	1	–	1	A
1969	3	–	3	A
1970	2	6	8	7A, 1B***
1971	–	–	–	–
1972	–	5	5	4A, 1B
	32	38	70	1,504.67****

*Data from fire reports, National Park Service, Houghton, Mich.
A**0.25 acres or less. B***0.26 to 9.99 acres.
****Approximate acreage burned in 32 years.

Isle Royale fire records from 1940 to 1972 show that, out of a total of 70 fires, 32 were lightning-caused and 38 were man-caused (table 17). The average was one lightning fire a year. Lightning fires occurred during 17 of the 32 years. The 70 fires burned approximately 1,505 acres. This amount is not related to the acreage that might have been burned by unchecked fires from natural causes (Hansen et al., 1973). However in recent years, naturally caused fires have been permitted to burn if they would not destroy valuable property or special scenery.

The second largest fire during the 32 year period occurred in 1948. It burned 1,440 acres within the 1936 burn area, covering the area south of Lake Desor.

The severe and extensive 1936 fire burned about 26,000 acres (19 percent) of the island (figure 25). "This fire was destined to have a more profound effect on the vegetation and animal life of the island than any other single historical event" (Hansen et al., 1973). Aldous and Krefting (1946) wrote: "In 1936 fires burned over approximately one-fourth of one island. These eliminated a large part of the browse supply for 2 or 3 years, but in the long run have been one of the greatest factors in permitting a comeback of the moose. Today (1946) the 1936 burned area supplies more browse than the remainder of the island combined." This fire has been described in detail by Hansen et al., 1973.

Today, most of the aspen and paper birch are over 30 years old. They are out of reach of moose, and in many stands, the understory shrub growth is shaded out (figures 26 and 27). White spruce was also one of the first species to become established in the burn, together with scattered amounts of white pine and white-cedar (figure 28). These stands are also shading out the shrub understory.

Effect of consumers on the vegetation

In order of importance, the major consumers of the island's vegetation are: moose; beaver; and snowshoe hare. Ungulates that have disappeared from the island are the woodland caribou and the white-tailed deer.

Woodland caribou

The woodland caribou apparently resided on Isle Royale for more than 100 years. The species was probably the first ungulate to occupy the island in recent history. John Tanner reported killing two caribou on the island in the early 1800's (James, 1830). In 1840, a solitary herd of "reindeer" was reported (U.S. Indian Bureau Ann. Rept., 1840, p. 354). In 1890, Scott (1925) observed caribou in the Washington Harbor area. Adams (1909) and other scientists' biological survey of the island in 1904 and 1905 provided reliable reports of caribou. A fisherman observed two caribou at Blakes' Point on March 27, 1904; the same day, two more caribou were seen on the ice on Rock Harbor. Later in 1904, fishermen reported seeing nine caribou near the Rock Harbor Lighthouse. In 1911, Warren (1926) noted a single caribou on a beach of Caribou Island at Rock Harbor. On the basis of the number of tracks found a few years before 1911, Warren estimated five to 10 animals were present. Wood (1917) also reported two large caribou herds on the island in 1911. Hickie (ca., 1943) noted that James MacGillvray photographed a cow with twin calves at the head of McCargoe Cove in 1926. On the basis of this record, Dustin (1946) concluded the caribou apparently became extirpated in 1926.

The caribou on Isle Royale may have disappeared because of extensive fires that destroyed the ground and tree lichens. Two factors, more widespread, may have also led to their extinction. There could have been a climatic change – a warming could have led to more crusting of the snow cover, creating tough feeding conditions. Caribou are also extremely susceptible to *Parelophostrongylus*. This parasite could have been introduced to Isle Royale when the nine white-tailed deer were introduced about 1912. Simkin (1965) reported: "Caribou are a species of the coniferous forest, a habitat in which ground and tree lichens grow most luxuriantly." They still persist on the Slate Islands in Lake Superior, Ontario. Krefting observed six caribou on these islands in 1970 where a herd of 40 to 50 lives presently. Cringan (1957) reported the Slates' supply of ground and tree lichens was critical; however, browsing woody plants was unimportant. Based on Cringan's findings, it seems that the Isle Royale caribou herd had little or no impact on the tree and shrub growth at any time. The supply of ground and tree lichens probably was affected more by fire than by the feeding activities of the caribou.

White-tailed deer

White-tails were not native to Isle Royale. In about 1912, nine animals were stocked on the island by the Michigan Conservation Commission (Warren, 1926). Fergusson (1919) reported, "The deer, I believe are all gone. Some four years ago, my wife and I saw five deer and fawns up behind Siskiwit and two years ago I saw deer tracks on the Lake Desor trail, but neither last year nor this year did I see any sights of deer."

Warren (1926) also noted, "Lately they are occasionally caught sight of and their tracks more often seen. This past season (1925) we saw a buck and two does, each at a separate place and time, and saw tracks of six or eight in other places."

These are the only authentic records for deer on Isle Royale. The deer survived from 1912 to 1925 and then disappeared for unknown reasons. With an abundant supply of nutritious browse species, such as ground hemlock, white cedar, mountain ash, and mountain maple, it seems that a sizeable herd would have become established together with the rapidly increasing moose herd. Apparently, illegal hunting kept the population at a low level and finally resulted in extirpation. Therefore, it can be assumed that the small number of deer had little or no impact on the Isle Royale vegetation.

Snowshoe hare

The snowshoe hare is the third most important consumer of the island vegetation. During 1904-1905, 1916-1917, and in the early 1930's, hares were numerous, and their distribution on the main island was quite general (Krefting, 1969). Murie (1934) noted hares were very scarce in 1930. In 1958, the hare population started increasing; and by 1962, the species was abundant (Krefting, 1969). On

Figure 25. Here's the 1936 burn area in the spring of 1937. The extremely hot fire began July 25. It destroyed the humus layer in addition to the overstory and ground vegetation. (Photo is by the National Park Service.)

Figure 26. This 33-year-old paper birch stand is in the 1936 burn area on Isle Royale. Dense stands of paper birch have grown out of reach for browse. Shrubs have been killed because of overhead shading.

Figure 27. This 36-year-old aspen stand is in the 1936 burn area on Isle Royale. Aspen is less common than is paper birch. It is usually confined to smaller areas where site conditions are better for its growth.

Figure 28. This is a 36-year-old white spruce stand in the 1936 burn area on Isle Royale. It is one of the first species to become established in the burn, together with white-cedar and white pine.

Passage Island, where moose are absent, hare browsing was severe in 1945 (Krefting, 1969). A browse survey on Passage Island that year showed the percentage of each food eaten was: cherry, 44; mountain ash, 22; balsam fir and ground hemlock, each 14; and mountain alder, redosier dogwood, and highbush cranberry, each 2 percent. In 1962, Johnson (1969) observed severe hare nipping and barking of white spruce, white-cedar, white pine, jack pine, and aspen at Chippewa Harbor and at the swamp at the head of Siskiwit Bay. The vegetation tallies at the Daisy Farm exclosure in 1949, 1952, 1956, 1959, 1961, 1963, and 1972 revealed no nipping by the snowshoe hare. A tally at the Windigo exclosure for the same years and in 1971 also indicated no hare nipping. However, the Siskiwit Lake and Siskiwit Camp exclosure tallies (1949, 1952, 1956, 1959, and 1961) showed some nipping of vegetation. At Siskiwit Lake in 1959, 4 percent of a total of 148 stems were nipped by hares. Paper birch, willow, and balsam fir were the species eaten. In 1961, 12 percent of a total of 120 stems were nipped. The species were: willow; paper birch; redosier dogwood; and balsam fir. At the Siskiwit Camp exclosure (1950, 1952, 1956, 1959, and 1961), 27 percent of 59 stems was nipped in 1961. Fire cherry, paper birch, mountain maple, white-cedar, and highbush cranberry made up the list of species nipped. From this study and from general observations made on Isle Royale, it appears that the snowshoe hare is not generally a serious deterrent to Isle Royale vegetation. Most nipping is done when the species is at the peak of its cycle. Then, its predators are less effective in holding the population in check. Like the beaver and moose, the snowshoe hare thrives best in the early stages of plant succession. It is best adapted to a fire-induced ecosystem.

Beaver

In the following discussion, the major source of information is based on the research of Krefting (1963). As early as 1847, old aspen-cut stumps and old beaver dams were found which indicated the earlier presence of beaver. The first fresh beaver signs were reported in 1878. Beaver were probably absent or scarce until 1921. They continued to increase so that, by 1930, the species was common. The increase continued, especially from 1937 to 1942, when they were widely dispersed in all the lakes and streams on the island. In the late 1940's, the number of colonies was estimated at 200 – an average of one colony per square mile. About 1948, a study showed that a die-off of beaver occurred. Evidence suggested that the die-off was due to a depleted food supply (Krefting, 1963). However in Minnesota and Ontario, a beaver die-off occurred about the same time. That one was attributed to a tularemialike disease. This disease may have been present on Isle Royale, contributing to beaver mortality. Predation by the coyote may have been a secondary cause of the die-off. From 1959 to 1963, the number of active colonies was estimated at 140, about 900 beaver. Field observations in 1972 indicated that the population was high, especially in the northeastern area of the island. This area contains the island's largest acreage of pole-sized aspen.

The beaver is the second most important consumer of the island's vegetation. Its impact on the vegetation is due to its tree-cutting and dam-building activities. At most colony sites, sizeable areas of timber are flooded and killed. The beaver prefers aspen, and that is the species cut first at new colony sites. Willow and paper birch are apparently second-choice foods (Krefting, 1963). Shelton (1966) concluded that aspen is the most preferred and nutritious species.

Beaver dams provide important aquatic habitat for moose, cavity-nesting birds, ducks, shore birds, muskrats, and brook and rainbow trout (Krefting et al., 1966). At abandoned colony sites, permanent openings are created which benefit moose and other wildlife. The openings usually develop into grassy meadows. Borders of these grassy meadows grow up to willow and other shrub species preferred by moose. Like the moose, the beaver thrives best in the early seral stages of plant succession. Unfortunately, aspen will be replaced by balsam fir and white spruce when the stand reaches the climax. Therefore, the beaver is best adapted to a fire-induced ecosystem; it is not a climax forest species.

Moose

The moose is, by far, the most important consumer of the island's vegetation. Since the moose arrived in the early 1900's, the range vegetation has been subjected to more than 60 years' browsing. Fortunately, the history of the impact on several browse species can be determined; information is available about conditions before the moose arrived. Jackson (1849) briefly described the island's vegetation, and Foster and Whitney (1850) gave an even more inclusive description of the Isle Royale forest. Ives' (1848) land survey notes and plats referred to certain plants, namely hazelnut and ground hemlock, that were abundant over most of the island. W.P. Holt (p. 235 in Adams, 1909) regarded ground hemlock to be: "Everywhere abundant in the upland forest of the island. On account of its low spreading growth, it forms one of the greatest impediments in penetrating the island's forests. The rankest growth was noted in the lower forest region around Washington Harbor where it attains a height of four or five feet."

In 1909 and 1910, Cooper (1913) considered ground hemlock to be the most important species of all the understory vegetation. W.P. Holt (p. 224 in Adams, 1909) reported that balsam fir was the most common conifer; it was superseding black spruce, white spruce, and tamarack.

In the early 1930's, Murie (1934) noted: "Ground hemlock (yew), an evergreen shrub attaining a height of four or five feet is another important source of food which has been practically exhausted. Today nothing remains of this spreading shrub except dead branches and a few leaves near the roots. The fact that this shrub is eaten the year round hastened its destruction. Ground hemlock at one time furnished a large amount of food for the moose. Its disappearance has resulted in concentration on the remaining species utilized in winter."

About the same time, Brown (ca., 1935) said: "Rank growth of healthy, green, ground hemlock was not found anywhere on the main island in what could be called abundance, or in sufficient abundance to be an impediment to walking. Much ground hemlock was seen which was straggly in appearance and which appeared to

have been either severely browsed or trampled, or perhaps both. Outlying islands such as Smithwick Island, Mott Island, and Passage Island have large amounts of rank growth of ground hemlock which have not been browsed or slightly so."

Brown (ca., 1935) also noted: "The feeding on balsam shows up in two ways – the browsing of small branches and twigs followed on small trees by the breaking of the leader sometimes 3 or 4 feet from the tip, and the stripping of the bark. Balsam is one of the principal foods left following the exhaustion of the ground hemlock as an important food source for moose."

Murie (1934), too, regarded balsam fir as one of the important sources of winter food. Murie reported: "Its utilization is not so complete on the east end as it is on the western two-thirds of the island. At Chippewa Harbor, on some of the steep slopes of Greenstone Ridge, and along Lane Cove there are areas where it is not very heavily browsed. From Chickenbone Lake westward I did not note a single balsam unbrowsed; most of it was heavily browsed, the branches closely trimmed and the tops broken off. Undoubtedly well over fifty percent of the original supply of balsam has been utilized."

Murie also made this reference to browsing on poplar and paper birch: "Thousands of the smaller trees have been broken over by moose. Many are dead, others have but a few twigs bearing leaves. Both species are greatly overbrowsed, as is also the mountain ash . . . Most of the shrubs (except for the alders) have been heavily utilized."

McMurray (ca., 1933) made a geographical report of the Isle Royale vegetation based on field work in the summers of 1929 to 1931. He estimated that the ground hemlock type originally covered some 40,000 acres, about one-third of the main island. His survey revealed: "It is only on a few isolated islands that small uninjured stands (ground hemlock) can be found (figure 29). It has been searched out and eaten in every nook and cranny, and in general the result has been the complete destruction of the stand. Miles of line were run through areas where the original ground cover of this type was attested only by the dead stems, and a few twigs which retained a feeble vestige of life."

Figure 29. In 1931, dense growth of ground hemlock was growing on Wright Island near Isle Royale. This was before the moose arrived on that island. (Photo is by the Michigan Department of Natural Resources.)

Regarding hazel, McMurray said: "Although estimated as originally covering only 12,000 acres, this growth was very thick, and its total must have made up a very large amount of browse. In places, this has been carried on so systematically that the stand has been killed outright, and only dead stems remain . . . It would seem that a few more years must reduce the hazel to the condition of the ground hemlock."

Balsam fir has been heavily browsed throughout most of the island. In many cases, the young growth had been completely destroyed. McMurray noted: "It is estimated that perhaps two-thirds of this important food supply has been destroyed, and the balance is disappearing rapidly." In addition, much of the mountain ash and cherry had been killed by browsing or bark stripping. He concluded: "But it is inevitable, in view of these clearly evident effects upon the food supply, that unless some factor enters to reduce their numbers, they must soon approach the end of the food supply. Unfortunately, even if the moose are reduced either by starvation, migration, or removal, it will take a long period to reconstitute the original ground cover and young forest stands."

Hickie (ca., 1943) referred to 1931 Isle Royale forage conditions, based on a brief report by J.H. Stephenson and I.H. Bartlett of the Michigan Game Division (p. 15). Stephenson wrote: "It is a somewhat startling fact that hardly a tree of suitable size to provide browse of the varieties listed" (he named hardwoods, balsam, willows, fire cherry, poplar, mountain ash, and various shrubs including ground hemlock) "bears any available browse. Either the trees are stripped of all twigs or browse are killed from overbrowsing or girdling. And there is no evidence of recent reproduction." He concluded that, "It is my opinion that the present herd cannot long endure without artificial help, as the available winter food is limited, to say the least."

In the spring of 1944, a preliminary browse survey was initiated. This was followed by an islandwide survey in May 1945 (Aldous and Krefting, 1946). Aldous and Krefting reviewed the past and present status of ground hemlock, noting: "The dead twigs of the species referred to by Murie are mostly gone and now only small fronds are present that have grown up since the past high population."

Balsam fir reproduction was being kept down by repeated browsing. Along Rock Harbor, most young trees were less than 2 feet tall. One tree a foot in height was 20 years old. Aspen was severely overbrowsed everywhere.

Figure 30. Old moose-barking scars on aspen are from the 1930's die-off on Isle Royale. The scars were 12 years old when the photo was taken in 1944. (Photo is by S.E. Aldous, Fish and Wildlife Service, USDI.)

Fallen trees were being barked extensively, but standing trees were not being barked to any great extent. Old scars on aspen showed that, around 1932, they had been eaten severely back (figure 30). Mountain ash was severely browsed, and barking occurred on standing trees.

Range surveys were repeated in the springs of 1948 and 1950 (Krefting, 1951). Mainly during the 1948-1949 winter, starvation reduced the herd by an estimated one-third. Barking of standing aspen – considered rare in 1945 – was common in 1948 (figure 31). A few years later, aspen showed signs of recovery (figure 32).

Balsams less than 3 feet tall were more than 30 years old, and much of the stock had been killed. On Hay Point, balsam mortality was 600 trees per acre. The former dense growth of ground hemlock had been reduced to small twigs; the only place ground hemlock was recovering was within a moose exclosure established at Windigo in 1948. In that year for the first time, ground hemlock was browsed on Smithwick Island. The study concluded: "If the moose are not held in check by some other means than allowing them to stabilize themselves by depleting their food supply, it will be impossible to conserve the island's plant life."

Barking of standing trees has also been evaluated in relation to fluctuations of moose population and food shortages. In the 1930's, Murie (1934) reported some areas where 90 percent of aspen trees had been barked and one area where the bark had been stripped and eaten from 40 or more white cedar. These data were gathered prior to the herd's first crash decline and reflect the effect several thousand moose had had on the island. The barking data gathered since 1947 on standing and down trees correlate quite well with the known population fluctuations and die-off of the moose (table 18). The trees barked per 100 miles of transect in 1947 were 36 for standing trees, 212 for down trees, and 248 for all trees. Severe barking also occurred during the 1948-

Table 18. Moose barking on Isle Royale.

Year	Miles of transect	Species	Total trees barked per 100 miles of transect		
			Standing trees	Down trees	All trees
1947	42	Aspen,	9.5	212.0	247.6
		mountain ash,	16.7		
		balsam fir	9.5		
			35.7		
1948	140	Aspen,	15.7	52.8	74.3
		mountain ash,	4.3		
		red maple	1.4		
			21.4		
1949	36	Aspen,	44.4	58.3	113.8
		tamarack,	2.7		
		balsam poplar		8.3	
			47.1		
1950	137	Aspen	8.0		
1961	140	Aspen	20.7		
1965	140	Aspen,	0.7	8.6	10.0
		mountain ash	0.4		
			1.4		
1970	140	Aspen,	20.0	5.7	27.1
		fire cherry,	0.7		
		sugar maple	0.7		
			21.4		

1949 die-off. In 1950, 1961, and 1965, less barking occurred; from 1965 to 1970, there was a striking increase in barking. A total of 134 trees was barked on the transects; 83 percent was aspen, and 10 percent was mountain ash.

In 1967, a special study obtained information on the growth rate of balsam fir in response to browsing pressure by moose. Balsams from six sites were measured for height, diameter, and age. A total of 116 cross section samples of trunks at ground level were collected. Mostly, the sampled trees were under 4 feet tall. Fifty-eight age core samples were taken from large balsam trees. Eight balsams within the Windigo exclosure (established in 1948) averaged 2.7 inches d.b.h. (diameter at breast height, 4½ feet above ground) and 15.6 feet in height. Eighty-three trunk sections outside the exclosure averaged 1.2 inches in diameter at the ground line and 3.7 feet in height. The age of protected trees averaged 23.2 years compared to 29.6 years for the unprotected trees. The known die-off of the moose herd from 1948 to 1950 was compared with the closeness of the annual growth rings. There was an apparent correlation with some samples. However, factors other than moose browsing – such as moisture, temperature, sunlight, and defoliation by the spruce budworm – may have been equally important (figures 33 and 34). The growth rings on the 58 age core samples showed no correlation with the 1930 moose die-off.

Exclosure study findings, 1948-1972

To evaluate the long term effects of browsing by moose on woody vegetation, four moose exclosures were established in representative forest cover types. Two were built in the 1936 burn area, one in the aspen–birch–conifer type, and one in the spruce–fir–birch climax forest type. They were established in cooperation with the Park Service at these locations: in the northeastern section near the Daisy Farm Campground; in the central section on the shore of Siskiwit Lake; in the southwestern section near Halloran Lake; and again in the southwestern section (figure 35) along Washington Creek at Windigo. The

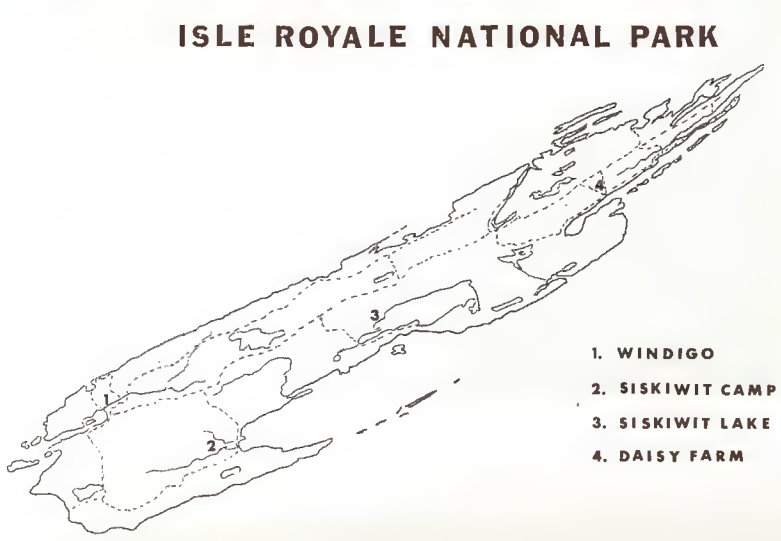
Figure 31 (above). Barking by moose on standing aspen reached a peak on Isle Royale just before the 1948-49 die-off of moose.

Figure 32 (right). Aspen recovery followed the 1948-49 die-off of moose in the Feldtmann 1936 burn area on Isle Royale. The deformed branch growth shows the old browse line and the good growth that followed.

Figure 33 (below). Cross section of a stem of balsam fir shows good growth in the absence of moose browsing on Isle Royale. The tree was 10 feet tall, 18 years old, and 1.5 inches in diameter at the ground level.

Figure 34 (below). Cross section of a stem of balsam fir shows poor growth due to moose browsing on Isle Royale. The tree was only 2.8 feet tall, 29 years old, and 1.4 inches in diameter at the ground level.

Figure 35 (below). Locations of moose exclosures are indicated on this map.



specific objectives were to determine the effects of moose browsing on the survival and height growth of key species of trees and shrubs at four locations on the island.

At each site, the exclosure (fenced area) was 50 x 50 feet. Each exclosure had an adjoining control or unfenced area of the same dimensions. White-cedar posts were set 12½ feet apart to form the squared area. The exclosures had woven fencing 8 feet high. To help protect the fence from windfalls, a single strand of barbed wire was fastened to the posts 2 feet above the woven wire.

Within each exclosure and on each unfenced control, a vegetation study area 33 x 33 feet square was laid out. This area was subdivided into 25 mil-acre plots (6.6 x 6.6 feet) (figure 36). All woody plants within each study area (exclosure and control) were tallied by species and measured for height (feet and tenths of feet); similar tallies were made at intervals after that. When tree species were large enough, the diameters were measured in inches and tenths of inches at the 4½ foot height level.

At the Siskiwit Camp and Siskiwit Lake sites, 10 of the randomly located mil-acre plots were tallied on each occasion (figure 36); at the Daisy Farm and Windigo sites, all 25 mil-acre plots were tallied each time a tally was made.

Camera points were also established at each location. Photographs of the vegetation were taken periodically until the views at each location were obstructed by tree and shrub growth.

Data have been summarized by species, number of stems, and mean height of stems for the exclosure and control plot at each site. Mean height growth was used to compare exclosure and control plots since the mean takes into account the number of stems.

Figure 36. This was the plan for sampling the vegetation within the exclosure and control plots on Isle Royale.

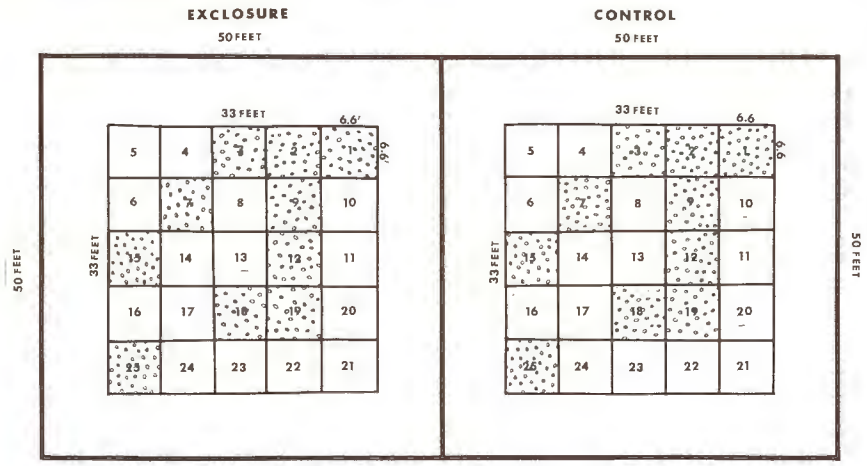


Figure 37 (below). This is the vegetation within the Daisy Farm exclosure after 3 years of protection.

Daisy Farm

The exclosure and control plots were established within the aspen–paper birch–balsam fir–spruce type in May 1949 (figure 37). Most of this 100-year-old type is located in the northeastern area of the island. It was subjected to extensive forest fires a century or more ago. The type covers about 69,000 acres. It is characterized by extensive stands of aspen and paper birch which are even-aged because of their fire origin. In recent years, conifer reproduction (mostly balsam fir and white spruce) has been increasing in most of this type. Understory shrubs are a mixture of juneberry, mountain alder, mountain ash, redosier dogwood, willow, and highbush cranberry. Some areas also have extensive areas of thimbleberry, bush honeysuckle, and beaked hazelnut. The northeastern area also has many permanent rock outcrop openings. Because of erosion after past forest fires, these openings are destitute of soil. Their tree and shrub growth is stunted due to the poor sites. However, these openings are important because slow tree and shrub growth has allowed the moose to keep browse within reach.

The mean height of aspen in the exclosure increased from 2.8 feet in 1949 to 16.7 feet in 1966; on the control, the mean height only increased from 1.1 to 5.8 feet during the period (tables 19 and 20). During the 17 year period, the mean height of aspen within the exclosure has been significantly greater than for the trees on the control ($P < .01$). A remeasurement in 1972 showed the tallest aspen on the control was only 7 feet. Its mean height was 3.2 feet, and this

Table 19. Number of stems of woody vegetation in the Daisy Farm exclosure and control plots on Isle Royale.[1]

Species	1949		1952		1956		1959		1961		1963		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	29	20	30	23	26	20	24	18	24	24	28	21	26	20
Balsam fir	344	318	347	341	293	317	214	248	236	303	171	244	192	207
Canadian honeysuckle	5		4		4		4		2		4		2	
Ground hemlock		2		2		1		1		1		1		
Juneberry sp.		1		1	1	1		1		1		1		1
Lowbush cranberry	15		15		9		6	1	8	1	6	1	3	1
Mountain alder	5	7	4	5	4	4	4	10	4	10	4	7	2	3
Mountain ash		11	1	12		15		11		9		13		8
Mountain maple		2		2		1								
Paper birch	8	9	6	9	7	8	7	9	10	6	6	4	5	5
Ribes sp.	3	3	5	3	4	3				3		2		
Redosier dogwood	103	12	99	12	98	14	94	17	96	19	83	13	80	18
Speckled alder														2
White spruce	12	6	12	8	9	6	8	6	11	6	10	6	13	7
	524	391	523	418	455	390	361	322	391	383	312	313	323	272

[1] 25 mil-acre plots.

Table 20. Mean height of woody stems in the Daisy Farm exclosure and control plots on Isle Royale.[1]

Species	1949		1952		1956		1959		1961		1963		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	2.8	1.1	4.4	1.7	8.1	2.1	9.0	2.4	11.7	3.0	12.2	3.9	16.7	5.8
Balsam fir	0.5	0.6	0.7	0.7	1.2	1.2	2.3	1.9	2.4	2.5	4.7	3.4	5.4	4.9
Canadian honeysuckle	0.3		0.4		1.4		1.2		1.0		1.6		2.9	
Ground hemlock		0.4		0.6		0.7		0.7		0.9		1.0		
Juneberry		1.0		2.1	1.2	3.3		4.8		3.2		5.1		5.0
Lowbush cranberry	0.5		0.7		1.0		1.4	1.6	1.4	1.1	2.0	2.3	2.6	2.5
Mountain alder	0.5	4.5	0.8	3.5	1.1	3.9	1.1	2.8	1.7	3.0	2.3	3.4	4.4	5.5
Mountain ash		0.4	0.3	0.7		1.1		2.1		2.0		1.8		2.5
Mountain maple		0.6		0.9		1.2								
Paper birch	0.6	1.5	1.3	1.5	2.3	1.8	3.3	2.8	3.6	3.0	6.1	3.5	7.8	4.1
Ribes sp.	0.6	0.8	0.8	1.4	1.2	1.5				0.8		1.6		
Redosier dogwood	1.0	0.4	1.8	0.5	2.7	0.7	4.1	0.9	3.3	1.2	4.5	2.2	5.9	2.2
Speckled alder														3.2
White spruce	0.3		0.4		0.7		1.0		1.4		2.4		2.8	
All Species	0.7	0.7	1.1	0.9	1.9	1.3	2.8	2.0	3.2	2.1	5.1	3.4	6.3	4.8

[1] 25 mil-acre plots.

aspen's average diameter was 1.9 inches.

For balsam fir, the exclosure and control plot trees had about the same mean height in 1949. By 1966, the mean height of the exclosure trees was significantly greater than was the height of control plot trees ($P = .10$). In 1966, the largest balsam in the exclosure was 14 feet tall and 2.7 inches in diameter. On the control, the largest balsam was 1 inch in diameter and 10 feet tall. In 1972, the tallest balsam on the control was 16 feet, the mean height was 5.9 feet, and the average diameter was 0.6 inches. The tallest balsam in the exclosure was 25 feet, and the mean height was 9.4 feet. The average diameter was 2.8 inches.

For paper birch, the mean heights in 1949 were 0.5 feet in the exclosure and 1.5 feet in the control. By 1966, the mean height of the exclosure trees was significantly greater ($P = .10$) than was that of the control plot. During the 17 year period, the number of stems in the exclosure and control plots were the same.

For redosier dogwood in 1949, there were about nine times more stems in the exclosure than in the control; by 1966, there were about four times more stems. This decrease can be attributed to the killing of stems by shading. By 1966, the mean height of exclosure stems was significantly greater than that of control plot stems ($P < .01$).

These data show that browsing by moose has had a significant effect on the height growth of aspen, balsam fir, redosier dogwood, and paper birch.

The severity of browsing varied from 1949 to 1972, but several tree species gradually rose above the 10-foot browse line for moose (table 21). Within the exclosure, a satisfactory stocking of aspen was reached by 1972 when the density reached 480 trees per acre. None of the aspen on the control plot reached 10 feet in height. Balsam fir reached a density of 480 trees per acre by 1963 and increased three times by 1972. The control plot balsams only reached a density of 240 trees by 1972. Within the exclosure, the density of paper birch reached only 80 trees per acre by 1972. None of the control plot birch reached the 10-foot level by 1972. White spruce, a nonbrowse species, did not reach a satisfactory stocking by 1972.

Tallies of browsing by moose showed the average number of all stems browsed was 22 percent in 1949, 46 percent in 1946, and 29 percent in 1963 (table 22). The average (percent) for the period was balsam, 28; mountain ash, 46; paper birch, 71; aspen, 90; and juneberry, 100.

Siskiwit Lake

The exclosure and control plots were established within the aspen–birch type in the 1936 burn area in May 1949. The plots were located on the southwestern end of Siskiwit Lake. The 1936 burn type occupies 26,000 acres (19 percent) of the island. Aspen and paper birch saplings formed the overstory; understory shrubs were mainly redosier dogwood, speckled alder, and willow.

For aspen, the analysis of variance to compare mean height growth between plots showed a significant difference between the control and exclosure (table 23 and 24) (P = .05). There was also a significant difference in mean height growth among years (P = .05). The analysis of variance showed a significant difference in mean height growth in the control plot among years (P = .05). The mean height growth in 1966 was also significantly greater than for all other years except 1961 (P = .05). However, the analysis of variance to compare the number of aspen stems among years in the control plot showed no significant difference.

For paper birch, the analysis of variance to compare mean height growth between plots showed a significant difference between the control and the exclosure. There was also a significant difference in mean height growth among years within the exclosure (P = .05).

For redosier dogwood, a paired t-test was used to compare mean differences in height growth between years. The probability that the yearly means are not the same is 62 percent. Analysis of variance was also used to compare mean height growth in the control among years. There were no significant differences. The analysis of variance was used to compare number of stems among years, and these were

Table 21. Number of trees per acre 10 feet or taller at four exclosure sites.

Windigo

Species	Year			
	1961		1966	
	Exclo.	Cont.	Exclo.	Cont.
Balsam fir	300	0	800	0
Paper birch	100	0	500	0
White spruce	200	100	200	100

Daisy Farm

Species	Year							
	1961		1963		1966		1972	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen					280	0	480	0
Balsam fir	80	0	480	0	900	100	1280	240
Paper birch							80	0
White spruce							80	240

Siskiwit Lake

Species	Year							
	1949		1952		1956		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	0	100	0	600	700	900	1200	1400
Paper birch					1400	200	2200	1500
White spruce							0	300

Siskiwit Camp

Species	Year							
	1952		1956		1959		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Paper birch	100	0	2900	100	3100	1500	3400	1900

Table 22. Number and percentage of woody stems browsed in the Daisy Farm control plot on Isle Royale.[1]

Species	1949			1952			1956			1961			1963			1966		
	No. Stems	Moose browsing No.	%	No. Stems	Moose browsing No.	%	No. Stems	Moose browsing No.	%	No. Stems	Moose browsing No.	%	No. Stems	Moose browsing No.	%	No. Stems	Moose browsing No.	%
American yew	2			2			1			1			1			1		
Aspen	7	7	100	11	10	91	11	10	91	6	6	100	12	10	83	9	7	78
Balsam fir	95	15	15	148	44	29	142	52	37	105	44	42	165	43	26	148	38	26
Juneberry sp.	1	1	100	1	1	100	1	1	100	1	1	100	1	1	100	1	1	100
Mountain alder	7			5			4	3	75	10			10			7		
Mountain ash	11	1	9	12	2	17	15	11	73	11	8	73	9	5	55	13	6	46
Mountain maple	2	1	50	2	1	50	1	1	100									
Paper birch	9	6	66	9	7	78	8	8	100	8	5	63	5	3	60	3	1	33
White spruce	4			5			3			3						3		
Total	138	31	22	195	65	33	186	86	46	145	64	44	203	62	30	185	53	29

[1] 10 mil-acre plots randomly located.

Table 23. Number of stems of woody vegetation in the Siskiwitt Lake exclosure and control plots on Isle Royale.[1]

Species	1949		1952		1956		1959		1961		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	20	32	15	33	15	32	15	21	13	24	12	17
Balsam fir				1		1	1	3	1	4	1	8
Juneberry sp.												1
Mountain ash					1							
Paper birch	49	32	50	35	55	53	35	39	25	22	22	23
Pin cherry				1		2		2		2		1
Redosier dogwood	12	2	20	6	29	16	35	32	45	39	43	64
Ribes sp.												5
Speckled alder	6		16		27		33	3	33	5	28	15
White-cedar				1	1	1		1		1		3
White spruce		3		2		2		2		2		2
Willow sp.	17	39	11	34	11	41	13	45	2	21		25
Total	104	108	112	113	139	148	132	148	119	120	106	164

[1] 10 mil-acre plots.

Table 24. Mean height of woody stems in the Siskiwit Lake exclosure and control plots on Isle Royale.[1]

Species	1949		1952		1956		1959		1961		1965	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	2.8	4.8	5.6	6.0	11.3	7.4	15.0	9.2	19.0	9.8	28.0	16.9
Balsam fir				0.6		1.3	0.5	1.9	1.2	1.8	4.2	1.8
Juneberry sp.												1.0
Mountain ash					0.8							
Paper birch	3.4	2.8	3.4	3.3	6.7	3.6	11.0	4.8	14.4	5.4	19.1	9.9
Pin cherry				0.5		0.9		1.2		2.2		7.5
Redosier dogwood	0.8	1.7	1.3	2.2	2.0	2.0	2.5	2.9	2.8	2.4	4.2	3.8
Ribes sp.												1.0
Speckled alder	1.0		1.5		2.3		3.7	5.3	7.3	5.8	11.6	8.0
White-cedar				0.4	1.0	1.3		0.2		0.3		1.6
White spruce		1.0		1.5		3.5		6.0		6.3		12.1
Willow sp.	4.0	5.3	2.6	6.9	3.8	8.2	2.4	5.8	5.0	3.9		8.4
All species	3.0	4.2	3.0	4.1	5.1	5.5	6.5	5.2	8.3	4.9	12.0	7.0

[1] 10 mil-acre plots.

found to be significantly different (P = .05).

For willow, mean yearly height growth was compared between plots for the control and exclosure. A paired t-test was used to compare yearly differences. The probability that the means are not the same is 79 percent. Analysis of variance to compare mean height growth among years in the control plot showed the differences were not significant. Analysis of variance to compare mean number of stems per plot among years in the control showed no significant difference.

Results show that moose browsing has had a significant effect on height growth of aspen, paper birch, redosier dogwood, and willow. With the exception of redosier dogwood, browsing had no effect on mean number of stems. When the exclosure was established in 1949, the density of aspen trees taller than 10 feet was 100 per acre on the control; by 1952, the density increased to 600 per acre (table 21). None of the exclosure aspen reached the 10-foot level until 1956 when the density was 700 stems per acre. By 1956, paper birch reached a stocking of 1,400 stems per acre within the exclosure; the control plot density was 200 trees per acre.

Figure 38. This vegetation is within the Siskiwit Camp exclosure after 12 years of protection from moose browsing.

Table 25. Number and percentage of woody stems browsed in the Siskiwit Lake control plot on Isle Royale.[1]

Species	1949			1952			1956			1959					1961				
	No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Hare browsing		Moose browsing		No. Stems	Hare browsing		Moose browsing	
		No.	%		No.	%		No.	%		No.	%	No.	%		No.	%	No.	%
Aspen	32	23	72	33	19	58	32	21	66	21			8	38	24			6	25
Balsam fir				1			1			3	1	33			4	2	50		
Fire cherry				1			2			2					2				
Paper birch	32	11	34	35	15	43	53	32	60	39	3	7	17	43	22	4	18	3	14
Redosier dogwood	2	2	100	6	2	33	16	5	31	32					39	2	5		
Tag alder										3					5				
White-cedar				1			1			1					1				
White spruce	3						2			2					2				
Willow sp.	39	23	59	34	17	50	41	23	56	45	2	4	18	33	21	6	28		
Total	108	59	54	111	53	48	148	81	55	148	6	4	40	27	120	14	12	9	7

[1] 10 mil-acre plots randomly located.

Tallies of browsing by moose and of hare clipping on the control have been summarized by species and years (table 25). The percent of stems browsed was about 50 percent in 1949, 1952, and 1956. In 1959 and 1961, there was less hare nipping than moose browsing.

Siskiwit Camp

The exclosure and control plots were established within the aspen–birch type in the 1936 burn area in May 1950 (figure 38). This 3,000 acre part of the 1936 burn area is located in the southwestern section of the island in the Feldtmann area. At the study area site, paper birch was the main tree species in 1950. The principal shrubs were mountain maple and pin cherry. Most of the tree growth of aspen and paper birch had been suppressed by severe moose browsing for 15 years (1936-1951). Since that time, the trees have recovered from browsing.

For pin cherry, a paired t-test was used to compare mean yearly differences in mean height (tables 26 and 27). The yearly difference was significantly greater in the exclosure than in the control (P = .05).

The analysis of variance to compare

Table 26. Number of stems of woody vegetation in the Siskiwit Camp exclosure and control plots on Isle Royale.[1]

Species	1950		1952		1956		1959		1961		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	1		1									
Black spruce	1	1		1		1						
Canadian honeysuckle	4		15	2	12	2	12	2	12	5	23	7
Choke cherry	2				2		5		5	2	5	
Hawthorn sp.								2				2
Lowbush cranberry						1		2		1		2
Mountain ash	1		3		4	1	4	1	3	1	1	1
Mountain maple	42	1	47	1	15	4	14	5	12	4	15	4
Paper birch	42	22	46	25	46	25	41	28	32	31	32	25
Pin cherry	1	10	4	10	15	9	16	12	14	9	22	16
Red-berried elder	4	3	4	6	7	4	8	4	6	4	7	5
Redosier dogwood	2		2									
Ribes sp.			17		10		8		7		9	
White-cedar	2		2		2		2		2	1	1	
White spruce								1		1		
Willow sp.	2		2		2		1		2		4	
Total	104	37	143	45	115	46	111	57	95	59	119	62

[1] 10 mil-acre plots.

Table 27. Mean height of woody stems in the Siskiwit Camp exclosure and control plots on Isle Royale.[1]

Species	1950		1952		1956		1959		1961		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	3.0		1.5									
Black spruce	0.6	1.1		1.4		3.5						
Canadian honeysuckle	2.1		3.4	1.3	4.5	1.7	4.8	2.0	4.0	1.7	3.3	1.9
Choke cherry	1.5				2.3		2.9		3.1	0.4	3.2	
Hawthorn sp.								0.7				
Lowbush cranberry						2.0		2.0		0.9		2.5
Mountain ash	4.3		5.1		10.0	1.8	11.1	3.0	12.7	2.5	29.0	5.2
Mountain maple	0.6	0.9	0.8	1.3	2.4	0.8	4.2	1.0	4.5	0.9	3.7	1.3
Paper birch	3.7	3.7	5.8	4.5	10.8	5.8	12.9	10.4	16.0	11.3	18.8	15.8
Pin cherry	2.3	1.4	3.4	2.0	4.8	2.3	7.1	3.1	8.7	3.2	5.4	3.8
Red-berried elder	3.0	3.2	4.0	2.2	5.6	3.7	5.6	4.1	4.9	3.3	6.4	5.0
Redosier dogwood	1.0		1.8									
Ribes sp.			0.6		1.0		1.0		0.9		1.5	
White-cedar	0.6		1.4		3.0		3.8		3.1	1.1	1.2	
White spruce								5.0		5.6		
Willow sp.	4.2		7.9		8.1		13.0	5.0	9.3	5.6	4.6	
All species	2.2	2.9	3.0	3.4	6.7	4.2	8.0	6.2	8.9	7.0	8.2	8.3

[1] 10 mil-acre plots.

Figure 39. This vegetation is within the Windigo exclosure on Isle Royale after 10 years of protection from moose browsing.

Table 28. Number and percentage of woody stems browsed in the Siskiwit Camp control plot on Isle Royale.[1]

Species	1950			1952			1956			1959			1961				
	No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Hare browsing		Moose browsing	
		No.	%		No.	%		No.	%		No.	%		No.	%	No.	%
Black spruce	1			1			1										
Canadian honeysuckle				2			2			2			5				
Choke cherry													2				
Elderberry	3	2	66	6	1	17	4	3	75	4	1	25	4			1	25
Fire cherry	10	7	70	10	7	70	8	7	87	12	9	75	9	5	55	4	45
Hawthorne sp.										2							
Lowbush cranberry							1			2	1	50	1	1	100		
Mountain ash							1	1	100	1	1	100	1			1	100
Mountain maple	1	1	100	1	1	100	4	1	25	5	2	40	4	4	100		
Paper birch	22	21	95	25	22	90	25	24	96	28	11	40	31	5	16	8	26
White-cedar													1	1	100		
White spruce										1			1				
Total	37	31	84	45	32	71	46	36	79	57	25	43	59	16	27	14	23

[1] 10 mil-acre plots randomly located.

mean height growth in the control among years also showed the differences were significant (P = .05). The mean of 1966 was significantly greater than the means of 1952 and 1956 (P = .05). Also, the mean of 1961 was significantly greater than the mean of 1950 (P = .05). The analysis of variance to compare number of stems in the control among years showed no significant differences.

For paper birch, the analysis of variance to compare mean height growth between plots showed the mean height was significantly greater in the exclosure than in the control (P = .05). The analysis of variance to compare differences in mean height growth among years in the exclosure showed that the differences were significant (P = .05). Also, the analysis of variance to compare mean height growth in the control among years also showed significant differences (P = .05). Analysis of variance to compare number of stems in the control among years showed no significant differences.

These results show moose browsing has had a significant effect on the height growth of paper birch and pin cherry. Browsing had no effect on the mean number of stems for these species. After 2 years of protection from moose browsing, the density of paper birch was 100 per acre; no control plot birch had reached the 10-foot level (table 21). By 1956, the growth was rapid since the density was 2,900

Table 29. Number of stems of woody vegetation in the Windigo exclosure and control plots on Isle Royale.[1]

Species	1949		1952		1956		1959		1961		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	119	37	116	31	102	17	87	16	31	13	21	12
Balsam fir	36	18	43	23	46	39	49	30	44	32	48	40
Black spruce	1		1		2		1					
Canadian honeysuckle	42	25	59	32	48	49	45	56	31	56	51	48
Ground hemlock	39	16	45	18	53	22	53	29	53	28	32	30
Juneberry sp.	1	6	1	9	1	10	1	8	1	10	4	18
Mountain ash	39	35	44	42	44	58	39	53	31	58	49	52
Mountain maple	39	62	45	91	40	86	43	101	38	94	65	95
Paper birch	39	31	45	40	46	44	38	51	28	49	51	53
Pin cherry	3	3	3	3	4	2	4	2		2	2	1
Red-berried elder	1	4	1	4	1	5	1	6	2	5		2
Redosier dogwood	14	3	17	3	18	8	20	10	6	10	7	12
Ribes sp.							3		9			
Sugar maple		1		1		1		1		1		1
White spruce	6	2	6	3	4	3	6	3	3	3	4	4
Total	379	243	426	300	409	344	390	366	277	361	344	368

[1] 25 mil-acre plots.

Table 30. Mean height of woody stems in the Windigo exclosure and control plots on Isle Royale.[1]

Species	1949		1952		1956		1959		1961		1966	
	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.	Exclo.	Cont.
Aspen	1.9	1.4	4.0	1.8	7.3	1.6	10.2	3.3	9.9	3.3	9.1	4.0
Balsam fir	1.3	0.6	2.3	0.6	3.8	1.0	5.6	1.3	6.8	1.5	9.8	2.0
Black spruce	10.0		16.0		12.2		23.0					
Canadian honeysuckle	1.3	1.8	2.4	2.2	3.1	1.6	3.9	2.2	3.6	2.3	4.5	2.9
Ground hemlock	0.6	0.7	0.9	0.8	1.5	0.7	2.2	1.1	2.4	1.2	3.5	1.9
Juneberry sp.	1.0	1.7	2.1	2.3	3.0	2.2	4.0	3.7	4.4	3.3	5.0	3.9
Mountain ash	1.7	1.3	2.9	1.2	5.5	1.5	7.6	2.8	6.8	2.8	8.3	3.4
Mountain maple	1.2	1.2	2.2	1.4	4.0	1.2	5.1	1.9	5.0	2.2	5.6	3.0
Paper birch	1.5	1.4	2.9	1.5	4.9	1.5	7.6	2.8	6.9	3.0	8.0	4.0
Pin cherry	1.3	1.8	2.8	1.2	5.4	2.1	3.9	3.2		3.4	4.5	3.5
Red-berried elder	1.4	1.5	3.9	1.9	4.3	1.2	3.5	1.7	2.9	1.9		3.8
Redosier dogwood	0.9	0.9	1.5	0.8	2.8	0.7	3.6	1.1	2.5	1.4	4.4	1.6
Ribes sp.							1.1		1.1			
Sugar maple		1.4		1.9		2.0		3.8		3.7		3.8
White spruce	2.4	5.2	4.0	5.9	8.3	9.9	9.9	13.1	13.5	14.9	15.8	15.6
All species	1.5	1.3	2.8	1.5	4.7	1.4	6.2	2.3	5.5	2.4	6.9	3.1

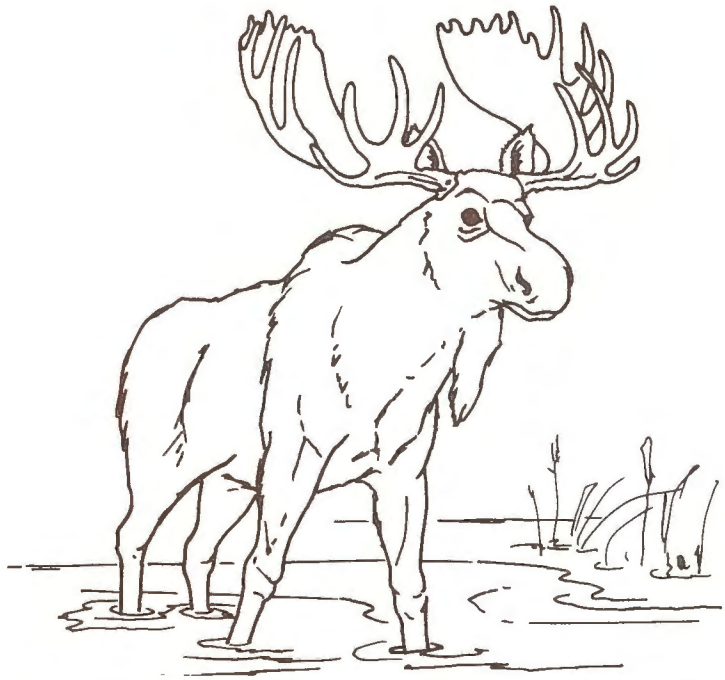
[1] 25 mil-acre plots.

per acre within the exclosure and 100 on the control area. And by 1959, the densities per acre were 1,500 on the control, and 3,100 in the exclosure.

Tallies of browsing by moose and nipping by hares on the control have been summarized by species and years (table 28). The percentage of stems browsed ranged from a low of 23 in 1961 to a high of 79 in 1956. Hares nipped 27 percent of the stems in 1961.

Windigo

The exclosure and control plots were established within the birch–fir–spruce type in October 1948 near Windigo in the southwestern area of the island (figure 39). The type covers 22,000 acres (16 percent) of the island, mostly in the southwestern area. Balsam fir, paper birch, and white spruce are the main overstory trees. The principal understory tree species include aspen, balsam fir, paper birch, and white spruce. Understory shrub species are Canadian honeysuckle, ground hemlock, juneberry, mountain ash, mountain maple, pin cherry, red-berried elder, and redosier dogwood. This cover type has been subjected to severe moose browsing for more than 40 years. The growth of balsam fir reproduction and ground hemlock has been curtailed by moose browsing.



For aspen, there were about three times more stems in the exclosure than in the control (tables 29 and 30); by 1966, the number of stems decreased. Since aspen is an intolerant species, some mortality may be attributed to natural shading. However in 1960, beaver entered the exclosure and cut down a variety of trees and shrubs, including aspen. The mean height of the aspen in 1949 was about the same both in the exclosure and control plot; by 1966, the mean height of the exclosure trees was more than twice the height of the control plot trees (P = .01).

The mean height of the balsam fir trees within the exclosure increased significantly from 1949 to 1966 (P = .01). Also, the mean height of the control trees increased significantly from 1959 to 1966 (P = .01).

The mean height of Canadian honeysuckle exclosure stems increased significantly from 1949 to 1955 (P = .01). Although the control plot stems increased in height, the difference was not significant.

For mountain ash, the number of stems and mean heights were about the same both within the exclosure and the control in 1949. By 1966, the number of stems was also about the same within the exclosure and control plots. However, the mean height of exclosure stems was significantly greater than was that of the control stems (P = .05).

Mountain maple, a medium-preference browse species, was influenced by moose browsing more than was anticipated. The mean heights were the same in 1949 (exclosure 1.2 feet; control 1.2 feet). By 1966, the exclosure stems averaged 5.6 feet in height and the control stems averaged 3 feet. The difference was significant (P = .05).

The number of stems of ground hemlock in the exclosure was: 39 in 1949; 45 in 1952; 53 in 1956, 1959, and 1961; and 32 in 1966. During the same period, the control plot stems increased from 16 to 30. While the mean height of the control plot stems was the same in 1949 (0.6 feet exclosure; 0.7 feet control), the exclosure mean height almost doubled by 1966 (3.5 feet exclosure; 1.9 feet control). The reduction in number of stems within the exclosure can be attributed to shading, even though hemlock is a fairly shade-tolerant species. The mean height of the exclosure stems was significantly greater than was that of the control plot stems (P = .05).

Paper birch, a highly preferred species, was influenced by moose browsing in a striking manner. Most years, the number of stems was about the same, both within the exclosure and control plots. While the mean heights were the same in 1949 (1.5 vs. 1.4), the exclosure trees had increased significantly in height by 1966 – from 4 feet to 8 feet (P = .05).

Redosier dogwood stems had the same mean height in 1949 (0.9 vs. 0.9), but by 1966, the exclosure stems increased significantly (P = .05). On the control, the increase from 0.9 to 1.6 feet was not significant.

In summary, the results show moose browsing has had a significant effect on the height growth of aspen, balsam fir, Canadian honeysuckle, mountain ash, mountain maple, paper birch, and redosier dogwood. Thirteen years of protection from moose browsing (1948-1961) were required for balsam fir to reach a density of 300 trees per acre; by 1966, the density was 800 per acre (table 21). Severe winter browsing prevented balsams on the control plot from reaching the 10-foot level. For paper birch, a future forest was established within the exclosure (500 trees per acre) by 1966; no control plot birch reached the 10-foot level. Unfortunately, beaver entered the exclosure in 1960 and cut down all the aspen. If this had not occurred, there would have been a satisfactory stocking of aspen by 1966.

Tallies of browsing by moose on the control have been summarized by species and years (table 31). The percentage of stems browsed was: 58 in 1949; 28 in 1952; 46 in 1956; 50 in 1959; and 44 in 1961 (figure 40).

The findings for the Daisy Farm, Siskiwit Camp, Siskiwit Lake, and Windigo study sites show that moose browsing has drastically reduced height and diameter growth. Moose browsing has had no effect on stem mortality, with the exception of redosier dogwood at the Siskiwit Lake site. Natural mortality of stems occurred within the exclosures as well as on the adjacent unfenced control plots. The time required for a future forest to become established with about 400 trees per acre that are 10 feet or more in height varied by tree species and the severity of browsing at each exclosure site. White spruce, a nonbrowse species, and white-cedar, sometimes browsed, increased significantly from 1945 to 1970 (P = .05).

Passage Island

This island lies about 3½ miles off the northeast tip of Isle Royale. Since there are no records of moose having

Table 31. Number and percentage of woody stems browsed in the Windigo control plot on Isle Royale.[1]

Species	1949			1952			1956			1959			1961		
	No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Moose browsing		No. Stems	Moose browsing	
		No.	%		No.	%		No.	%		No.	%		No.	%
Aspen	30	24	80	24	9	37	8	6	75	7	5	71	6	5	83
Balsam fir	7	2	28	8	4	50	20	3	15	7	4	57	8	5	62
Canadian honeysuckle	16			17			20			28			28		
Ground hemlock	10	1	10	9	3	33	9	7	78	14	5	36	14	3	21
Red-berried elder	2	2	100	2			1	1	100	2	1	50	1		
Fire cherry	2	2	100	2			1	1	100	1			1	1	100
Juneberry sp.	5	5	100	8	2	25	8	6	75	6	6	100	8	5	62
Mountain ash	19	16	84	20	10	50	29	11	37	24	20	83	28	19	67
Mountain maple	39	20	51	57	9	15	43	24	55	56	26	46	46	23	50
Sugar maple	1			1			1	1	100	1			1	1	100
Paper birch	15	14	93	19	11	57	15	12	80	22	19	86	23	12	52
White spruce	1			2			2			2			2		
Total	147	86	58	169	48	28	157	72	46	170	86	50	166	74	44

[1] 10 mil-acre plots randomly located.

Figure 40. Here is vegetation at Windigo subjected to browsing by moose for about 45 years. (Photo is by Aivars Zakis.)

Table 32. Average cover percentages on Passage Island and on Isle Royale.

Species	1945		1948		1965	
	Passage*	Isle** Royale	Passage*	Isle*** Royale	Passage*	Isle*** Royale
Balsam fir	34.1	5.3	31.5	3.5	32.0	4.7
Cherry sp.	3.9	2.3	3.7	1.7	4.1	1.1
Ground hemlock	32.4	1.7	28.5	1.0	29.8	0.7
Highbush cranberry	15.4	1.5	12.2	1.0	12.4	1.0
Juneberry sp.	0.2	3.1	0.1	1.7	0.1	1.5
Mountain alder	1.7	3.0	2.0	1.5	2.4	1.9
Mountain ash	8.5	8.8	8.5	3.7	7.0	2.1
Red-berried elder	0.5	1.0	0.3	1.0	0.5	0.7
Redosier dogwood	5.5	4.7	4.8	3.6	5.0	2.1
Speckled alder	0.3	1.5	0.3	1.6	0.2	1.5

* 27 1/100-acre plots.
** 592 1/100-acre plots.
*** 844 1/100-acre plots.

been on this island, it functions as a natural exclosure. The boreal climax forest on Passage Island has developed without moose browsing; on the main island, the vegetation has been subjected to moose browsing for about 60 years.

A comparison of the percent cover for 10 species on Passage Island and Isle Royale for 1945, 1948, and 1965 shows significantly higher amounts of cover on Passage Island (table 32). Balsam fir accounted for about one-third of the cover while, on Isle Royale, it made up 5 percent or less. Ground hemlock also made up about 30 percent of the cover on Passage Island; this is in contrast to less than 2 percent on the main island. On Isle Royale, highbush cranberry made up only 1½ percent of the cover while, on Passage Island, it amounted to 12 percent or more.

On Isle Royale, there is also a very striking absence of different sizes and age classes of balsam fir. Over most of the island, there still remains a noticeable browse line on the overstory balsams. This was formed by the die-off from about 1934 to 1935. Balsam reproduction is rather sparse over most of the main island, with the exception of the northeastern end. In contrast, on Passage Island, all age classes and sizes of balsams occur (figure 41). Stand density, as measured by basal area and tree numbers, is also much higher on Passage than it is on Isle Royale.

Figure 41. This balsam fir forest is on Passage Island near Isle Royale. Because Passage Island has no moose, this island has a variety of age classes of balsam fir not found on the main island. Ground hemlock and mountain ash also thrive on this island.

HOME RANGE OF MOOSE

Berg (1971) noted several definitions of home range. In his study on the Agassiz National Wildlife Refuge in northwestern Minnesota, he defined home range as "the area apparently traversed by an individual over a certain period of time." He considered the winter home range to be separate from the area traversed the rest of the year – it was distinctly different in terms of size. Berg's telemetry study showed the winter home range averaged 0.9 of a square mile and the summer home range 5.4 square miles. Phillips et al. (1973) reported the summer and fall home ranges averaged 6.9 square miles for cows and 5.6 for bulls. In winter, the home ranges averaged 1.2 square miles for bulls and 1.4 square miles for cows.

In northeastern Minnesota, the winter home range of moose was made up of a series of high use areas (Van Ballenberghe and Peek, 1971). The telemetry study showed the wanderings of moose in winter were confined to areas 0.25 x 3 miles in size. The summer range was 1.1 x 2.1 miles in size.

De Vos (1956) made observations on unmarked but recognizable moose in Ontario. His study showed that summer movements by moose were limited. The home range covered an area 0.5 by 4.7 miles in size. Goddard (1970) also determined the movements of tagged moose in a heavily hunted area of Ontario. On the basis of a total of 71 observations, he found that both sexes of all ages were quite sedentary in winter and summer. Movements between summer and winter range of the same year can extend over several miles. He concluded that moose have a rather well-defined and relatively small winter and summer home range. In addition, Macfie (1961) made winter observations on home range on Goddard's study area. He found one male and from one to four antlerless adults occupied a 600-acre area for 28 days. Other observations showed a single adult on 400 acres for 28 days and a cow and a calf on 1 square mile for 16 weeks.

In the western United States, McMillin (1953) concluded the summer home range of moose in Yellowstone National Park was about 0.6 x 3.3 miles in size. Houston (1968) in Wyoming reported 90 percent of the winter home ranges covered areas less than 1.5 square miles in size. Knowlton (1960) in Montana found the summer home range was 0.7 x 1.2 square miles in size.

Seasonal shifts occurred in northwestern Minnesota even though the terrain was extremely level (Berg, 1971). Similar shifts where the terrain was, for the most part, fairly level occurred in Ontario (Goddard, 1970) and in northeastern Minnesota (Van Ballenberghe and Peek, 1971).

In the mountainous west, definite seasonal shifts have also been reported by numerous investigators (Edwards and Ritcey, 1956; Houston, 1968; Knowlton, 1960; Nielson and Shaw, 1967; and Stevens, 1970). In Grand Teton National Park, Houston (1968) reported: 18 moose moved 5 to 10 miles between summer and winter home ranges; four moose moved at least 20 miles; and four moose used the same area winter and summer. Knowlton (1960) in Montana noted 0.5 of a mile maximum distances between locations on the summer range in 1958. The distance increased to 3 miles in 1959 and to 5 miles in 1960.

Edwards and Ritcey (1956) observed in Wells Gray Park, British Columbia, that annual migrations from the wintering areas in the valleys to the summer range in the high mountains were 40 miles and sometimes more.

And in the Hurdal Lake Region of southeastern Norway, Krafft (1964) noted that moose made regular migrations from winter to summer ranges. He reported the downward migration begins in early winter; in the spring, the moose begin a gradual return to the higher altitudes where they range in summer. The writer visited this part of Norway in the summers of 1968 and 1971. In 1968, he observed one wintering area had suffered severe and extensive browsing on Scotch pine (*Pinus sylvestris*) the past winter.

On Isle Royale, observations suggest the moose restricts its wanderings to a very limited area. Observations on unmarked but recognizable bulls suggested that moose occupy a small area in summer (Murie, 1934). Murie noted, "There may be some travel from summer to winter range, but it seems probable that many of the animals remain in the same general region the year round."

Hickie (1938) also concluded that the seasonal movements were short. He felt that the availability and palatability of the browse had more influence on movement than did topography. In late winter, the moose tended to congregate into moose "yards," but the yarding was not close. Mech (1966) reported the burns and the swamps had the highest concentrations of moose in summer and winter, but especially in winter. Spring observations by the writer indicate a noticeable seasonable movement of moose from the 1936 burn area into the northeastern area of the main island. Apparently, the aquatic plants in beaver ponds and particularly in Ojibway Lake are responsible for the movement.

MOOSE DISTRIBUTION AND HABITAT SELECTION

Habitat selection and snow relationships

Dodds (1973) reviewed the literature on climate and weather in relation to the distribution of moose and deer in Canada's Atlantic Provinces. He noted that, "Benson (1952) and Hawbolt and Benson (1953), and Benson (unpb. ms.) considered long term climatic changes as possible causes of changes in distribution of moose and deer and other animals in this region." Mercer and Kitchen (1968) reported that the extension of moose range into the Labrador Peninsula was probably limited by snow conditions, possible human predation, and habitat restrictions.

In western Canada and its adjacent regions, climate is probably the most important limiting factor (Kelsall and Telfer, 1973). Kelsall and Telfer noted that the depth, density, hardness, and duration of snow was one important climatic factor.

The first studies on the effects of snow on the movements of large ungulates were made in the U.S.S.R. (Formozov, 1946, and Nasimovich, 1955). These studies and later Canadian studies found "that moose can travel more or less freely through snow up to 60 cm." (23 inches) (Telfer, 1970b). Telfer noted, "Moose

are increasingly impeded and restricted to snow depths up to 100 cm." (40 inches, about the chest height of an adult animal).

In Norway, Lykke and Cowan (1968) reported: "The climate is indirectly one of the most important factors controlling moose populations through food production and availability, and imposing winter concentration." They noted, "Heavy snow for a certain period of time will probably give the same results as a long winter." They also pointed out that Scandinavia warmed up in the 1930's, which was beneficial to the moose, and that a more regular climate has prevailed since then.

Winter moose movements and habitat selection are directly affected by the quality and depth of the snow (Peek, 1971; Kelsall and Prescott, 1971). Also, studies in Quebec and New Brunswick have demonstrated that, as the winter advances, the moose moved from open stands of timber to denser cover (des Meules, 1964; and Telfer, 1970b). New Brunswick moose favored open stands of timber in January, and the white-tailed deer preferred the dense conifer belts. But by March, both moose and deer were confined to the dense conifer stands. Studies demonstrated that moose in Quebec shifted from cutover areas to small and medium openings at depths of 30 to 34 inches (des Meules, 1964). Des Mueles, too, noted that depths of 24 inches were preferred for bedding purposes. The maximum depth of snow for unimpeded movement was 40 inches. In New Brunswick, crusted snow over 36 inches in depth resulted in high moose use in softwood (conifer) cover types (Telfer, 1970b).

In northeastern Minnesota, the moose shifted from open to dense cover at much lower depths than reported for New Brunswick and Quebec (Peek, 1971). Few studies point out the importance of other snow quality factors such as compactness, density, and hardness as they relate to ungulate movement (Kelsall, 1969; Kelsall and Prescott, 1971; Ozoga, 1968; and Pruitt, 1959).

Recent studies on moose habitat selection in northeastern Minnesota suggest that extensively logged areas less than 20 years old were responsible for maintaining that area's high moose population (Peek, 1971). Peek found the logged areas were used in June, when the protein levels in key species were highest, and in late fall and early winter, when fat and carbohydrate levels were highest. The more mature aspen and white birch stands were favored in late summer; spruce–fir stands received their highest use in late winter. Aquatic communities were utilized most in June, together with the more open and poorly stocked stands. Upland stands of aspen and white birch were occupied throughout the summer. These relatively mature stands were, for the most part, sparsely to moderately stocked. Late summer and early winter use was centered on upland deciduous tree stands. From late November to April, the most significant changes in habitat use by moose occurred. The shifts that occurred from January to March were brought about mostly by snow quality and weather conditions. During moderate weather, the more open stands were used; in severe weather, use centered on the upland spruce–fir type. Peek's data also indicated that early winter forage selection may be more critical in midwinter. In early winter, cover requirements may also become important.

On Isle Royale, snow depths usually do not exceed 36 inches. With the exception of the northwest facing ridges, snow generally is not a hindrance to moose movement. In 1959, 1960, and 1961 (Mech, 1966), the depths did not exceed 26 inches in wind-protected areas. The depths in 1963 ranged from 18 to 36 inches. Snow depth records from 1966 to 1972 showed the depths exceeded 3 feet only for short periods in 1966, 1969, and 1972 (Park Service weather records). Peterson and Allen (1973) noted the increase in snow depths in recent years has resulted in more use of lakeshores by moose. These lakeshores are also the moose's primary travel routes. Peterson and Allen also reported, "In years of exceptionally deep snow wolves have generally increased their kill rate, chiefly due to increased vulnerability of calves and 'primeage' moose."

Habitats on Isle Royale

The 210-square mile archipelago has a terrestrial community that has been subjected to moose browsing for about 60 years, but it has been relatively undisturbed by man. Major changes in the vegetation have resulted because of moose browsing, activities of the beaver, and forest fires. Fires over the past 125 years, and especially the 26,000-acre 1936 fire, have produced a good interspersion of types. A wide assortment of diverse high quality seral stage habitats have resulted for the moose.

Since the early airplane strip counts of moose were made Feb. 5, 1945, and Feb. 18, 1947, there have been some striking changes in the island's moose distribution (Krefting, 1947). These counts showed that, during much of each winter, most of the moose were concentrated on the 1936 burn area and the ridges (Aldous and Krefting, 1946, and Krefting, 1951). The browse surveys also indicated that the browsing pressure was centered in these areas. The northeastern third of the island had few moose.

Pellet group counts in different cover types in 1948 showed the density was 125 groups per acre in the Siskiwit Lake area of the 1936 burn. The next highest density was 98 groups per acre in the birch–fir–spruce habitat type. Other habitats had the following densities per acre: 83 in the Feldtmann area of the 1936 burn; 70 in the aspen–birch–fir–spruce; and 44 in the sugar maple–yellow birch habitat.

In February 1960, Mech (1966) also made airplane strip counts to obtain information on the number and distribution of moose. His distribution map (figure 83, p. 104) showed a concentration of moose in 1960 in a part of the burn area north of Lake Desor.

Jordan et al. (1967) prepared an approximate midwinter distribution map of moose on Isle Royale, based on a stratified sampling program. Different areas of the island supported the following moose densities per square mile: 0.5; 1.5; 3.8; and 11.8. The authors noted the moose density in the burn area north of Lake Desor had decreased since 1960. Also, moose densities apparently increased along the western and southern shores of the main island.

Peterson and Allen (1973) reported the midwinter densities of moose were highest in the spruce–fir type and in successional types having good conifer

cover. Apparently, deep snows in 1969, 1971, and 1972 also tended to force the moose to concentrate on lakeshore areas, resulting in fewer moose in the 1936 burn area in the central part of the island.

Information on Isle Royale winter habitat use is based on a total of 844 1/100-acre plots at 10 chain intervals (660 feet). The source of the material presented in the following habitat discussions was taken from Krefting (1973) and Hansen et al. (1973).

Maple–birch

This type is climax on certain sites because it is self-perpetuating under present conditions. It covers about 9,950 acres (7 percent) of the island. Most stands in this type have not been disturbed for 120 years or more. The yellow birch are over 150 years of age, and the sugar maples are over 220 years. The largest trees range from 25 to 30 inches in diameter; heights are from 70 to 80 feet. The square feet of basal area ranges from 140 to 160 per acre. Understory tree reproduction is mostly sugar maple and yellow birch. Shrub species are ground hemlock (small sprigs), mountain ash, mountain maple, juneberry, beaked hazelnut, and round-leafed dogwood (*Cornus rugosa*).

Pellet group counts (1948 to 1950) (figure 42) showed a significant downward trend ($P < .01$) and reflect the known die-off of the island's moose during that period. Pellet group densities were at a uniformly low level of about eight per acre. But from 1965 to 1970, there was a significant upward trend ($P < .01$). The low pellet count data for this type, the lowest of all the types, indicate that the type is unimportant to moose in winter. The type probably receives its greatest use in summer and early fall.

Birch–aspen–spruce (1936 burn)

The 26,000 acre burned-over area covers 19 percent of the island and contains two separate burns: the Feldtmann burn in the southwestern area (3,000 acres); and the Siskiwit Lake burn in the central area (23,000 acres).

In the burn area, paper birch is more widely distributed than aspen. The ages of both species are not uniform because of past moose browsing. Tree diameters are 3 to 5 inches for aspen and 1 to 7 inches for paper birch and white spruce. White-cedar, white pine, and white spruce are generally scattered. Balsam fir is largely absent. Understory shrubs are fire cherry, redosier dogwood, willow, juneberry, beaked hazelnut, rose, and mountain maple.

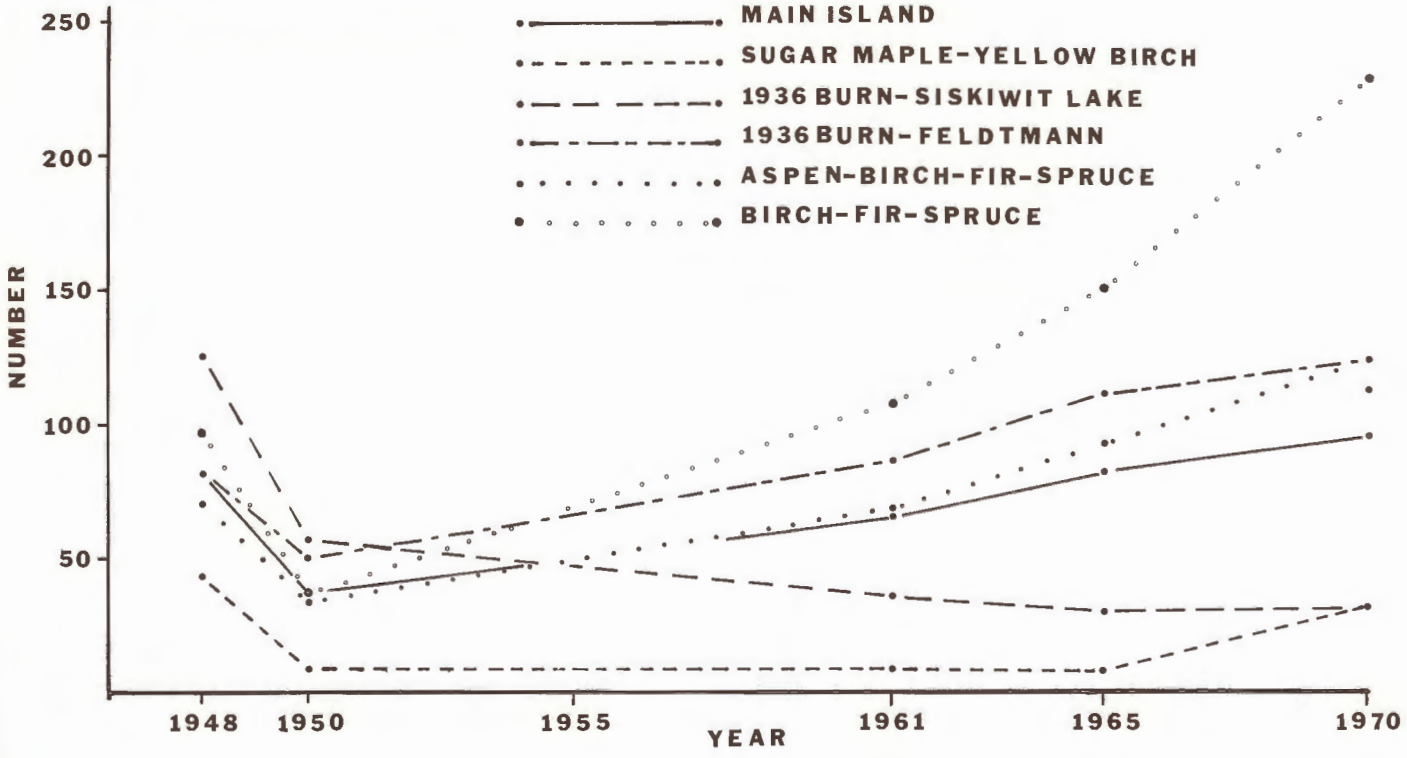
On the Feldtmann burn, the pellet counts showed a significant decrease from 1948 to 1950 ($P < .01$). A significant increase occurred from 1950 to 1970 ($P < .01$) (figure 41).

The Siskiwit Lake burn also showed a significant decrease from 1948 to 1950 ($P < .01$) (figure 42). The data also showed a significant decrease from 1950 to 1961 ($P < .01$), leveling off from 1965 to 1970. These population trends also relate to changes in the availability of browse from 1945 to 1970. During this period, the available browse supply decreased significantly in both burns. The Siskiwit Lake burn was attractive to the moose for about 14 years (1936 to 1950). Apparently, the smaller area burned, and the better interspersion of unburned patches of winter cover in the Feldtmann burn sustained longer use than did the Siskiwit Lake burn.

Birch–aspen–fir–spruce

Due to its fire origin, the type has extensive stands about 80 to 100 years of age. It's heavily invaded by white spruce and balsam fir. The type occurs mostly in the northeastern area of Isle Royale and occupies about 58,000 acres (43 percent) of the island.

Figure 42. These moose population trends are by habitat types and also for the main island of Isle Royale.



Species ages range from 43 to 83 years for aspen, 33 to 115 years for paper birch, 26 to 100 years for balsam fir, and 51 to 100 years for white spruce. Balsam fir reproduction has increased strikingly during the past 10 years. Aspen reproduction is scattered, but moose browsing is preventing its establishment. Common shrubs are beaked hazelnut, juneberry, mountain alder, mountain ash, redosier dogwood, and willow.

Pellet group counts (1948 to 1950) indicate a significant downward trend ($P < .01$). From 1950 to 1970, there was a significant upward trend ($P < .01$) (figure 42).

Birch–fir–spruce

Sixteen percent (about 22,000 acres) of the island is covered by this type. It consists mainly of three overstory species: balsam fir; paper birch; and white spruce. The type also has scattered large aspen. In the absence of fire, it represents the boreal climax stage toward which other plant communities evolve (Cooper, 1913). However, the forest classification by Halliday (1937) and Rowe (1959) suggests that Isle Royale is not typically boreal and it relates more to the Great Lakes-St. Lawrence Region (Rowe, 1959). Because of more than 60 years of moose browsing, much of the type has become open and parklike. Balsam firs 30 years old are less than 3 feet tall, and a distinct browse line on overstory trees still exists from the 1930's. The spruce budworm epidemic in the 1930's also killed off the older balsam fir. The openness of this type has encouraged shrub browse that is typical in the boreal region.

Pellet counts decreased significantly from 1948 to 1950 ($P < .01$) (figure 42). There was also a significant increase from 1950 to 1970 ($P < .01$). In 1948, the pellet density was 98 groups per acre – the second highest on the island. In 1970, the pellet density was 229 per acre – the highest on the main island. Apparently, the increased snow depths in recent years have attracted moose to this habitat because of the reduced snow under the denser balsam fir and white spruce cover.

MORTALITY OF THE MOOSE HERD

A history of the Isle Royale moose herd suggests a number of possible causes that led to moose mortality: malnutrition; parasites and diseases; accidents; and predation. Malnutrition and timber wolf predation are most important.

Malnutrition

A review of the literature shows the crash decline of the moose herd from several thousand to several hundred in the early 1930's was attributed to malnutrition. This conclusion was based on the autopsies of 24 dead and dying moose (Hickie, 1936). Hickie noted, "The ingestion of unsuitable food appeared to cause poisoning as evidenced by the abnormal formation of red blood cells in the bone marrow."

The mortality checks in 1934 and 1935 accounted for 60 dead moose. A similar, but less spectacular, die-off of the herd also occurred in the winters of 1948-49 and 1949-50 (Krefting, 1951). A minor search for moose carcasses produced 35 yearling and adult moose. Death was attributed to a food shortage, although bone marrow examinations were inconclusive. Peterson and Allen (1973) studied snow conditions in recent years as a parameter in moose-wolf relationships on Isle Royale. They reported: "As has been found in adult moose, the vigor of calves may be considerably lower during long periods of severe snow conditions, further increasing their vulnerability to wolves. Routine examination of bone marrow from calves has shown a great increase in the incidence of fat depleted marrow in recent years. Of 21 8- to 10-month-old calves examined from 1959 through 1964, 19 (90 percent) had undepleted fat reserves in the long leg bones. All of these calves died when snow depths were either medium or low. Since 1965, we have examined 33 calves of a similar age, and only 7 (21 percent) showed undepleted fat reserves (a significant difference at the 0.01 level, z test). The majority (79 percent) of these calves died during the severe winters of 1969, 1971, and 1972."

Parasites and diseases

The meager information on parasites, diseases, and miscellaneous causes of death has been reported by several investigators (Hickie, 1936; Mech, 1966; Murie, 1934; and Sweatman, 1952). Necrosis was found, and necrotic stomatitis was believed to be present, although the organism was not isolated (Murie, 1934). Also, 91 moose mandibles were examined. Fourteen had symptoms of "lumpy jaw," actinomycosis similar to that noted by Murie (Mech, 1966).

Hydatid cysts of the larvae of the tapeworm (*Echinococus granulosus*) were found in five of the eight Isle Royale moose Coburn originally examined in 1933 (Sweatman, 1952). The parasite was also found in three of four moose examined by Mech. Cysts of (*Taenia hydatidgena*) were also

present in two of four moose livers, and the lungworm (*Dictyocaulus*) was found in one moose (Mech, 1966).

Although the winter tick (*Dermacentor albipictus*) has not been shown to cause moose mortality, it definitely causes irritation when present in high numbers (Mech, 1966). Heavy infestations of the winter tick were noted on moose carcasses in the 1930's (Hickie, 1936), and they were common on the moose carcasses examined by Krefting in 1949 and 1950. Information on the ectoparasites of Isle Royale mammals has been summarized by Wilson and Johnson (1971).

"Moose disease" has been reported based on the larvae of *Paralaphostrongylus tenuis* found in fresh fecal samples collected on Isle Royale in 1965 and 1966 (Karns and Jordan, 1969). The finding is highly significant. The disease has been associated with the presence of the white-tailed deer, and no moose have been observed with the syndrome caused by this parasite. The authors report the disease at an area reported deer-free for 30 years. However, the time may have been closer to 40 years (Warren, 1926). Only nine deer were introduced in 1912, and they persisted until about 1925 (Warren, 1926). This report differs from that of Johnsson and Shelton (1960) who reported about six were released in the early 1900's.

Accidents

Losses of moose from other natural causes, such as accidents, have been reported by Murie (1934). He tallied 29 moose which apparently died for accidental reasons: their feet got caught in tree roots; they became mired in mud; and some drowned or were killed by man. More recent reports include a cow and calf that probably drowned and a bull that died from getting its antlers and neck tangled with an extension cord at one of the building sites (Mech, 1966).

Mortality survey results

To obtain information on past and present moose mortality, moose carcasses were tallied on the regular browse survey transects in May 1961 (personal communication, W.L. Robinette, July 7, 1961). Current winter loss was calculated to be 2.6 moose per square miles on transects supporting a winter moose population of 8.5 moose per square mile (pellet counts). This is a loss of 34 percent. However because the 2.6 moose that died lived only part of the winter, Feb. 15 was assumed to be the mean date of death. On that basis, 9.6 moose entered the winter, and the calculated loss rate accordingly amounts to 27 percent. The sight distances for 11 old carcasses averaged 35.5 feet compared to 34.0 for 3 current carcasses. Therefore, visibility was assumed to be the same for both old and new carcasses. An examination of the bone marrow from the five current carcasses examined showed: two were in poor condition; one was fair; and two were good. Two were adult males; one was an adult female; and two were calves. The ages of the carcasses were classified as follows: five calves (sex undetermined); four mature moose (two males, two females); nine males estimated to range from the 4-5 year class to the 14-15 year class; seven females from 6-7 to 13-14 year class; and one old carcass where sex and age could not be determined.

Predator-prey relationships

Red fox

This fox was not included on the list of mammals recorded for Isle Royale during the 1904-1905 biological survey (Adams, 1909). However, Johnson (1969) said that a commercial fisherman in the Rock Harbor area reported he saw a red fox in 1925. Murie (n.d.) reported no fox were seen during his stay on the island in 1929 and 1930, but one had been reported shot at Rock Harbor that winter. Apparently, there were very few fox on the island in the 1930's and 1940's since only occasional reports were received from fishermen. Gilbert (1943) said, "Reports received from residents living in the Hay Bay region persisted in claiming the presence of fox on the island. The two Park Service employees were unable to gather any definite proof of this animal being present other than these reports. At no time were tracks ever found that could be considered fox tracks." However on July 3, 1944, Gilbert's monthly report related, "A red fox was seen along the shore of Washington Creek near the mouth of the stream. The animal was seen during an apparent attempt to catch a group of American mergansers."

Mech (1966) reported, "Foxes seem to be common on Isle Royale but not abundant. A strong limitation on numbers probably is winter food supply, for mice are relatively unavailable, at least during the first year of the study (1959), hares were scarce." Mech also reported that the most foxes he observed from the air per day was 10 on Feb. 27, 1961, while a maximum of only four per day were seen the previous two winters. During the 1961 study period, he reported seeing 29 red fox. He said, "The most important relationship between the fox and the wolf involves the food gleaned by foxes from remains of wolf-killed moose." His analysis of 295 scats collected from trails during three summers (1958-1960) revealed the percentages of occurrence of major items were: snowshoe hare, 47; birds, 12; muskrat, 9; and moose, 6.

Some information on relative numbers was obtained during the winter study periods from 1961 to 1968 (Johnson, 1969). Shelton (1966) believed the increase in foxes seen per 100 flight hours (1961-1963) was because of the increased hare population. The numbers per 100 flight hours were: 21.5 in 1961; 37.2 in 1962; 51.9 in 1963; 23.2 in 1964; 32.1 in 1965; 17.5 in 1966; 42.1 in 1967; and 17.2 in 1968 (Johnson, 1969). He concluded that the fox had successfully colonized Isle Royale and that it was maintaining a healthy population. Johnson also examined 448 winter and summer fox scats for the 1966-1968 period. He found the percentages of occurrence of all were: mammals, 37.9; birds, 4.2; amphibians and reptiles, 1.4; fish, 3.6; insects, 5.8; and plant matter, 40. The major mammal food items included (percentages): snowshoe hare, 14.3; muskrat, 8.3; red squirrel, 7.9; and deer mouse, 7.1.

The wolves on Isle Royale apparently kill red foxes on occasion. Mech (1966) observed a red fox being killed by a wolf near Halloran Lake on March 15, 1960. And on field trips to the island in 1972, Park Service personnel reported a fox killed by a pack of wolves in the Malone Bay area.

Coyote

Although Dustin (1946) speculated that the coyote probably arrived on

the island in the winter of 1912-13, together with the moose, coyotes may have arrived as early as 1906 (Krefting, 1969). Coyotes reached a peak of around 150 animals at about 1948. They gradually decreased the next 10 years (Krefting, 1969). The decline after 1950 was associated with the moose die-off (1948-1950), a low snowshoe hare population in 1950, and a die-off of the beaver about the same time. No evidence was found of coyotes after 1958.

The Michigan Department of Conservation trapped coyotes because they were regarded as an effective predator on the moose, particularly on calves. Coyote predation on moose was regarded minor in the 1930's. One case was reported where two coyotes attacked a moose calf but were unable to kill it (Hickie ca., 1943).

The frequency of occurrence of food items in 92 scats in winter and spring scats were (percentages): moose, 55; beavers, 52; snowshoe hares, 27; thimbleberry seeds, 9; redosier dogwood, 1; insects, 3; and fish, 1 (Krefting, 1969). The moose remains found in the scats must have been from carrion since the coyotes survive best when the carrion supply is abundant. Soon after the timber wolf arrived, moose carrion in large amounts was no longer available. Apparently, a reduced food supply and possible direct killing by wolves were factors responsible for the disappearance of the coyote. An undesirable habitat resulting from changes in the vegetation plus social stress may have also resulted in emigration back to Canada. These data suggest that the coyote was not an effective moose predator – even on moose calves.

Timber wolf

The arrival of the timber wolf on Isle Royale can be dated fairly accurately. Wolves were seen on the ice between Sibley Peninsula, Ontario, in the late 1940's (de Vos, 1950). In September 1949, scats unusually large for a coyote were found in the Crow Point area. The scats were probably made by a wolf (Krefting, 1949). In November 1950, tracks were definitely identified as those of the timber wolf (Hakala, 1954). In 1952, Hakala sighted one large and one small wolf on the trail between Siskiwit Camp and Feldtmann Tower in the southwestern area of the island. One year later, Hakala and Cole saw a pack of four wolves on Siskiwit Bay. By 1956, the island was reported to have at least 14 wolves; a year later, 25 wolves were reported (Cole, 1957). The author prepared the following discussion on moose-wolf relationships and reported it in the publication by Hansen et al., 1973.

Mech (1966) studied the timber wolf-moose relationship from 1958 to 1961. He reported a large pack of 15 wolves plus a small pack of three. The number remained about the same each year. His findings showed the wolf pack killed an average of one moose per 3 days, stabilizing the moose herd by culling undesirable animals. He concluded: "Indeed, the Isle Royale moose population is one of the best 'managed' big game herds in North America ... Apparently the Isle Royale wolf and moose populations have reached a state of dynamic equilibrium ... Each is relatively stable, so any substantial fluctuation would be absorbed by the other until another equilibrium is reached."

Subsequently, Jordan et al. (1971) reported the moose population remained stable from 1959 to 1969 and that no evidence showed any major fluctuations had occurred. However, pellet count data previously discussed have shown a significant upward population trend from 1950 to 1970. Mech justified his conclusion that wolves were removing the annual increment of moose by assuming there were 600 animals in the late winter of 1960. He extrapolated data taken over a 2-month winter period to the whole year (Pimlott et al., 1969). If the base population was closer to 1,000, as the more intensive surveys of Jordan et al. (1971) indicate, then the pellet group data and the Jordan data do not suggest that wolves were "managing" the moose herd. More recently, Mech (1974) concurred with Hansen et al (1973) that the moose herd had increased from 1961 to 1970. The wolf had only a dampening effect on the moose population. He noted: "Thus it appears that, at present, the Isle Royale wolves are not regulating the moose herd; they are only cropping off part of the available surplus production." The wolf population has also increased from 18 in 1961 (Mech, 1966) to a high of 31 in 1974, the most in 15 years (Rolf Peterson, Duluth News-Tribune, March 28, 1974).

More recently, research by Schaller (1972) on predator-prey relations of the Serengetti lion noted: "The most important influence of predation is this dampening of the tendency of populations to increase beyond the carrying capacity of their range, an effect that prevents serious oscillations ... While predation may be a major factor limiting the size of the populations, the primary factor which ultimately exercises control is the habitat."

The habitat has changed substantially since the wolf pack arrived on the island about 24 years ago. Possibly the most significant habitat change has occurred in the 1936 burn area. This covers about one-fifth of the island. It has furnished the bulk of the browse supply for the moose. Therefore, it seems apparent that the future moose-wolf relationship is dependent on a major habitat disturbance – such as fire – to increase the browse supply for the moose.

Rutter and Pimlott (1968) summed up their ideas regarding the future of the Isle Royale wolf when they noted: "They are protected. This does not, however, assure their future, since the environment is gradually changing. It is most likely that the end result of the change will be a small moose herd that can support fewer wolves or none. Emigration over the ice in winter, disease, or other problems may also eliminate wolves on the island."

PRODUCTIVITY OF THE HERD

Since moose hunting is prohibited by law on Isle Royale, it has not been possible to obtain information on the productivity of the herd based on kill studies. During the past 40 years (1930-1970), several investigators have made sight observations on calves and yearlings throughout the year. Although data on percentages of yearlings in the population probably represent the best measure of productivity, only a small amount of data has been gathered. The number of sight observations has been too small, in most instances, to permit making reliable predictions on productivity.

Yearling – total population ratios reported for Isle Royale[a]

Year	Months	Sample size	Percent of yearlings in populations[a]	Source
1930	May-June	128[c]	21.0[d]	Murie (1934)
1953	Feb.-Mar.	66	20.0	Hakala (1953)
1957	Feb.	252	15-23.0	Cole (1957)
1959	Mar.	176	17.0	Mech (1966)
1960	Feb.	529	17.0	Mech (1966)
1961	Feb.-Mar.	133	10.5	Mech (1966)

[a]Table 13 from Mech (1966), p. 105.

[b]Excluding newborn calves.

[c]Cows and yearlings only.

[d]Calculated from Murie's cow-calf ratio, with assumption that sex ratio was equal.

Mech (1966) has summarized yearling-total population ratio data gathered by himself and others. His summary is tabulated above.

These data show the percentage of yearlings in the population was probably about 17; the twinning rate was 38 in 1959 and 15 in 1960. In 1930, the twinning rate was less than 5 percent (Murie, 1934).

Moose observation records were kept at intervals during this study (1945-1970) – mostly in the spring – together with browse and pellet count surveys (table 33). Since the survey transects sampled all parts of the island within 3 to 4 weeks, the chances of seeing the same moose more than once were remote. Sight sample sizes ranged from 19 to 75 moose. The findings showed the percentage of yearlings in the population ranged from 9 to 20 percent and averaged 15 percent. This is lower than reported by Mech (1966).

The Isle Royale information also compares favorably with that of other studies. Northwestern Ontario reported 25 percent calves (Simkin, 1965); British Columbia reported 22 percent calves; and 12 percent twins were reported for Newfoundland (Pimlott, 1953). In Norway, a study reported 26 percent calves and 6 percent twins (Krafft, 1964), and Sweden had 32 percent calves (Stalfelt, 1969).

Fluctuations in the Isle Royale moose population over the past 60 years also suggest the Isle Royale herd has been productive. The moose herd increased by several thousand from the early 1900's to 1934, clearly demonstrating what happens when there is a shortage of winter browse. The increase in the moose herd by several thousand from the early 1900's to 1934, in the absence of an effective predator, clearly demonstrates the result of a super abundance of "stored" browse – an "introduction boom" phenomenon. The die-off, followed by the 1936 burn, also demonstrates the importance of such a disturbance which led to the increase in the moose population. A second die-off occurred in the 1948-1949 winter and continued through 1949-1950; it was attributed to a depleted food supply in the absence of an effective predator (Krefting, 1951). Since an apparent wolf scat was found in September 1949 and tracks positively identified as a wolf's were discovered in November 1950, the decrease occurred while the wolf was present. Although the browse supply has gradually decreased from 1950 to 1970, with the exception of balsam fir, the moose herd has increased in spite of wolf depredations. This suggests that the summer and fall range is still adequate and the moose are in good physical condition before winter starts. Rarely are possible future die-offs of ungulates predicted in advance, but W.T. Hornaday of the New York Zoological Park sounded a warning in 1922. He wrote "... There is always a chief drawback to an island as a game preserve and that is that the surplus game is unable to migrate into contiguous territory ... the surplus game might become embarrassing."

The 1936 burn provided sufficient browse to permit the herd to reach a peak of about 800 by 1948, before a second die-off occurred. This comeback also indicates the herd was productive. The increase from an estimated low of about 500 moose in 1950 to a peak of about 1,000 in 1970 also suggests a healthy herd response. Although the upward population trend was only gradual during the 20-year period (1950-1970), the increase has occurred in spite of mortality caused by the timber wolf and a significant decrease in the browse supply for all species, with the exception of balsam fir.

Table 33. Spring observations of moose on Isle Royale.

Period	Cow	Yearling	Bull	Sex undetermined	Total
May 5-28, 1945	17	6	14	2	39
May 7-June 5, 1946	14	5	3	3	25
May 18-20, 1947	10	3	7	5	25
May 2-23, 1948	39	13	18	5	75
May 16-June 5, 1949	10	3	3	3	19
May 19-June 2, 1950	14	4	7	3	28
May 10-24, 1961	12	3	12	8	35
May 13-27, 1965	16	5	8	3	32
May 8-21, 1970	16	5	9	2	32

The concept and use of the term ecosystem was first coined by Tansley (1935). He reported that, "The fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment is the ecosystem, which is a particular category among the physical systems that make up the universe. In an ecosystem the organisms and the inorganic factors alike are components which are in relatively stable dynamic equilibrium. Succession and development are instances of the universal processes tending towards the creation of such equilibrated systems."

More recently, Clapham Jr. (1973) also reported that, "An ecosystem includes not only the organisms, but also the several nonliving components of the environment within which the organisms are found." He noted that the system includes all the interactions that bind the living and nonliving components together into a stable system.

Islands, because they are well-delineated geographic entities and because they have a degree of biological isolation provided by water around them, constitute ideal objects of ecosystem study. Islands are particularly advantageous sites for studies involving vegetation and animal interrelationships – the animals' normal facility to move into or out of the ecosystem is curtailed by the water barrier. Udvardy (1969) reported fauna barriers may be ecological, physical, or water. He noted the faunas on small islands are simple but become more diverse on larger islands. Hesse et al. (1937) also reported, "Other conditions being equal, an insular area must accordingly have a smaller fauna than an equal or even much smaller area on the mainland. Even when the area is large enough for individuals of a species of a given size, it may not suffice for breeding and other activities of the species."

The dominant population regulatory mechanisms on islands are the food supply and climatic factors (Klein, 1968). Therefore since the food chain of nature starts with the plant life, a knowledge of the consumer animals and their predators is essential. Environments having several diverse population regulatory mechanisms – such as food, predators, and interspecific competition – are much more stable than those with only one limiting factor, such as a food supply (Klein, 1968). The more complex the environment is in terms of flora and fauna, the more graded would be the response of the species (Klein, 1968). Klein also reported that island ecosystems tend to be less complex than are continental ones and that, although sparse from a species standpoint because of their restricted access, island ecosystems tend to be younger since there has been less time for the development of less complex interrelationships. He said there was an apparent relationship between the self-regulatory ability of animal populations and the relative stability of the environments in which they have evolved.

Crowell (1963) also noted that insular habitats support fewer fauna species than do their mainland counterparts. He observed that, of the species reaching an island, those which succeed do so because they find their habitat preferences fully satisfied.

Dunbar (1960) compared the stability in marine environments between the lower and higher latitudes. He concluded there is a striking contrast . . . "of warm adapted floras and faunas and the instability of the ecosystems of the cooler parts of the world." Dunbar noted that simplicity is found as a rule only in cool climates with marked seasonal variation. Oscillations are absent in tropical or subtropical environments which foster more complex ecosystems.

Faunal populations on other islands

Crowell (1963) observed that, of the species reaching an island, those succeeding do so because they find their habitat preferences fully satisfied. He reported on 14 bird species introduced into Bermuda the past 100 years. Three species maintained stable populations for more than 50 years, and two species recently introduced were doing well. Five species were limited or unstable, and four became extinct.

A review of the mammals found on the islands in eastern Lake Superior shows that the number of species is low (Hatt et al., 1948). On Beaver Island (58 square miles), there were 12 species; on South Fox Island (5 square miles), there were only 10 species. Also, North Manitou (20 square miles) had 13 species, and South Manitou (8 square miles) had 12 species. In the Gulf of St. Lawrence, the number of mammal species found on islands (Cameron, 1958) was: Cape Breton – 35 recorded, 2 introduced, 5 extirpated, and 2 reintroduced and surviving; Prince Edward – 32 recorded, 4 extinct, and 5 introduced; Anticosti – 5 species which are indigenous; Magdalen Islands – 4 species that may be native; and Newfoundland (42,700 square miles) – 14 species belonging to five orders which are native and five species introduced (Cameron, 1958). Hesse et al. (1937) listed 22 species for Iceland, 40 for Britain, and 60 on the Scandinavian Peninsula. Currently, St. Matthew Island in the Bering Sea has only two species of mammals (Klein, 1968).

In the absence of effective predators on islands, the food supply and climatic factors become the dominant population regulatory mechanism. For example on St. Matthew Island in the Bering Sea, 29 reindeer (*Rangifer tarandus*) were introduced in 1944 (Klein, 1968). The native mammals included the arctic fox (*Alopex lagopos*) and the vole (*Microtus abreviatus*). The polar bear (*Thalarctos moritimus*) inhabited the island in recent times, but is now extinct. Without an effective predator, the population increased to 6,000 by 1963. A crash decline occurred the following winter, and less than 50 reindeer were left by 1964. The ground lichens were eliminated as a significant part of the diet, and grasses and sedges expanded to areas once occupied by lichens. Starvation in association with an extreme snow accumulation brought on the crash decline. In 1966, one male and 42 female reindeer had survived.

MacArthur (1972) pointed out that islands are areas where extinctions of species are greatly accelerated. He also noted that the number of species on an island reaches an equilibrium when extinction balances immigration. MacArthur felt that such an equilibrium was no accident and it is reasonable to assume that each island is approaching some sort of equilibrium.

Faunal populations on Isle Royale

Sixteen species of mammals representing five orders are known to currently inhabit Isle Royale. There are only 12 mammalian species, excluding the four species of bats. In the nearby Thunder Bay District of Ontario, the area list contains 56 species representing six orders (Denis, 1959). These data demonstrate that the mainland area of Ontario supports 3½ times more species than are found on nearby Isle Royale.

A total of 197 bird species have been reported on Isle Royale (Krefting et al., 1966) compared to 267 species on the nearby Canadian Lakehead of Ontario (Denis, 1961). The comparison also showed that Isle Royale also had fewer permanent, summer, and winter residents (table 34).

On Isle Royale, the food supply and climatic factors were the dominant population regulatory mechanisms controlling the crash declines of moose in the early 1930's and late 1940's. Although the population trend of moose has been upward since 1950, the timber wolf has had a dampening effect on the population, and there have been no major die-offs during the past 23 years.

Dodds (1960) in Newfoundland reported that good moose range is also good range for snowshoe hares; marginal range for hares is also marginal for moose. On Isle Royale, the impact of moose browsing on the woody vegetation probably influenced snowshoe hare abundance, especially food and cover to some extent. The snowshoe hare also competed with the moose for food on most of the woody plants, with the exception of white-cedar and white spruce. Dodds noted hares fed on 27 of the 30 species browsed by moose. At four exclosure sites on the main island of Isle Royale, the impact of hares on the vegetation was negligible (1948-1970); very few white-cedar and spruce were clipped. Observations suggest that the moose die-offs (early 1930's and 1948-1950) also coincided with hare abundance, but this apparently was only a coincidence. However, it seems apparent that the food supply of the coyote, marten, and lynx was influenced by hare abundance.

The predator-prey relationships of the coyote and red fox represent examples of instability. About 8 years after the wolf arrived, the coyote became extinct. This was followed by the increase in red fox abundance. The snowshoe hare is the most important mammalian prey on the island, and the fox increases are influenced by the hare abundance. Also, the low number of prey species compared to other mainland areas apparently accounts for the lower fox density. Some of the most preferred prey species, such as the meadow vole (*Microtus* sp.) and the cottontail rabbit (*Sylvilagus floridanus*), are not present. Therefore, food will always be a limiting factor in future population growth of foxes (Johnson, 1969).

Extinct mammals on Isle Royale

The redbacked vole (*Clethrionomys gapperi*) was listed present on Isle Royale in 1877 (Coues and Allen, 1877), and it may have been present in 1904 and 1905 (Adams, 1909). However, it appears unlikely that this vole now exists on the island (Johnson, 1969).

The coyote probably reached the island during the winter of 1912-13, together with some of the moose (Dustin, 1946). The species built up to an estimated 150 animals about 1948 (Krefting, 1969). After that, the population decreased, and the species apparently disappeared in 1957 or 1958. No evidence of them was found after 1958 (Krefting, 1969). Krefting noted the factors that may have contributed to its increase and final disappearance were: food shortage; destruction of the habitat; killing by wolves; and social stress. Even at its best, the island habitat was probably of low quality for coyotes. With fire protection, the changes in plant succession gradually produced an even less favorable habitat. Factors that contributed most to its disappearance were the reduced food supply and possible direct killing by wolves. A combination of these factors, plus the island situation, probably was necessary to cause extinction. Social stress at peaks of abundance may also have led to some emigration across the ice bridge to Canada.

The marten was abundant in 1904-1905 (Adams, 1909). "But a rapid decline in numbers, due perhaps to trapping and burning soon occurred." (Johnson, 1969). Johnson also reported that Murie (n.d.) "talked to trappers who said it was then (1929) extinct."

The lynx (*Lynx canadensis*) were trapped in large numbers in the early 1900's (Adams, 1909). Johnson (1969 in Murie n.d.) said the marten was extinct in the middle 1930's. In May 1963 and later, sight observations suggest that either lynx or bobcat were present.

The white-tailed deer was introduced about 1912. It then disappeared in 1925 for unknown reasons (Warren, 1926). In spite of the abundance of nutritious browse species, it appears that poaching kept the population at a low level and finally resulted in extirpation.

The woodland caribou probably was the first ungulate to reside on Isle Royale. Two animals were killed in the early 1800's (James, 1830), a solitary herd was reported in 1840 (U.S. Indian Bureau Ann. Rept., 1840), a number of observations were made in 1904-1905 (Adams, 1909), two large herds were reported in 1911 (Woods, 1917), and the woodland caribou apparently became extirpated in 1926 (Dustin, 1946).

Shelton (1966) reviewed the literature and concluded that island faunas have two characteristics: simplicity; and instability. "Both of these have been shown by Isle Royale's fauna." He reported that, "The instability frequently results in the extinction of species, which maintains or insures simplicity. The ultimate cause of both the instability and simplicity is thus insularity."

Table 34. Comparison of bird species on the Canadian Lakehead and on Isle Royale.

Area	Residents			Total species
	Summer	Permanent	Winter	
Canadian Lakehead	110	19	10	267
Isle Royale	106	14	4	197

MANAGEMENT IMPLICATIONS FOR WILDLIFE

The general patterns of forest succession on Isle Royale and the role of fire and other secondary successional factors have been summarized by Hansen et al. (1973) with respect to their wildlife implications. Factors initiating secondary succession – such as insects, wind, logging, and fire – have been discussed previously in this report. In the historic past, fire has been the major agent for bringing about secondary successions. It has induced second-growth stands that many species of wildlife – including moose, beaver, snowshoe hare, and sharp-tailed grouse – prefer. On the island, the most dynamic forest types are those which have been burned over and on which postfire successional processes are underway. The more recent the fire, the more fluid is the stand's development. The primary succession leading to the sugar maple–yellow birch climax, or the swamp succession, are of lesser importance to the major wildlife species. A second major line of succession leads to the paper birch–balsam fir–white spruce climax association through various preclimax successional stages. These seral stages are generally the habitats preferred by moose, beaver, snowshoe hare, and some bird species. Because these habitats are constantly changing, the moose populations vary accordingly. Normally, the subclimax types have the highest moose densities; the populations decrease as the forest reaches maturity. Aspen is the most preferred and nutritious browsing species for moose. But as succession advances, aspen will be eliminated on large areas of the island. It will be replaced by balsam fir and white spruce as the stands reach maturity. Gradually, the overstory species will also shade out the reproduction and shrubs needed for food. Snowshoe hares also thrive best during the early stages of plant succession, especially when there is an abundance of aspen, willow, and white-cedar. Along with the moose and beaver, the snowshoe hare is best adapted to a fire-induced ecosystem. It is not a climax forest species. To maintain the present moose-wolf relationship at a satisfactory level, the seral stages must cover larger areas of the island than now exist.

We need to evaluate the impact of fire on Isle Royale's ecosystem and how to use fire to obtain the most desired results with the least amount of undesirable impact. Unfortunately, very few prescribed burning studies have been made in the Lake States. Ahlgren (1973) reported on the use of fire in the North Central States. He noted that . . . "prescribed burning is a more recent and less extensively practiced procedure than in the south. Hazards and inconsistencies of desirable results when burning remote forests without suitable site preparation and logging, and the need to preserve the non-fire adapted ecological niches within such natural environment make extreme caution advisable in the application of prescribed burning for this purpose."

Sando and Dobbs (1970) have outlined the precautions and procedures to execute prescribed burns to regenerate jack pine on logged areas in Manitoba and Saskatchewan. Sando (1972) has also carried on a prescribed burning study in northern Minnesota in the aspen-birch type. The study is designed specifically to learn to improve the habitat for white-tailed deer and other wildlife.

Currently, National Park Service biologists are documenting the role of fire in 18 National Parks and Monuments (Hendrickson, 1973). The majority of these study areas are located in the western United States (Houston, 1971; Kilgore, 1971 and 1973; Loope, 1971; Loope and Gruell, 1973; McLaughlin, 1973; and Shuft, 1973).

Kilgore (1973) reported the impact of prescribed burning on a sequoia-mixed conifer forest and the ecological role of fire in Sierran conifer forests. He reported that: "At the same time, research must determine more precisely the ecological role of fire so that the management techniques can be guided by the best knowledge we can provide." Kilgore posed the following questions:

1. How often should an area be burned?
2. What prescription is appropriate?
3. How much fuel accumulation indicates the need to prescribe burn again?
4. What amount of habitat diversity is optimum for wildlife and what actions can best simulate "naturalness"?

Shuft (1973) reported on a prescribed burning program for Sequoia and Kings Canyon National Parks, both in California. He stated that burning under prescribed conditions has been carried out in a number of units and that additional work is planned. Since 1968, all lightning fires above 8,000 feet elevation were allowed to burn in some areas of the parks.

Realistically, we want to maintain the natural ecosystem of Isle Royale and especially its dynamics aspects. Theoretically, the wolf has maintained a moose balance in numbers of moose killed, since there have been no major moose die-offs since 1950. While wolf predation has been a major factor limiting the size of the population, the most important factor ultimately exercising control is the habitat. The moose population trend has been upward despite the timber wolf. There has been a gradual decrease in the browse supply, with the exception of balsam fir which is a primary winter browse species.

Figure 43. Thirty-one wolves are on Isle Royale — the most in 15 years. Wolves have been a major factor limiting the size of the moose herd which, however, has been increasing in spite of the wolf. (Photo is by the National Park Service.)

LEFT: Figure 44. For many years, this osprey nested on Monument Rock which is a landmark near Tobin Harbor. (Photo is by F.B. Lee, Fish and Wildlife Service, USDI.) RIGHT: Figure 45. The snowshoe hare is the third most important consumer of Isle Royale vegetation. For protection from its enemies, it changes colors with the seasons. (Photo is by O.J. Murie, Fish and Wildlife Service, USDI.)

LEFT: Figure 46. The raven is a permanent resident on Isle Royale, occurring in small numbers throughout the island. (Photo is by Karl Gilbert, National Park Service.) RIGHT: Figure 47. The woodcock breeds on Isle Royale. (Photo is by Karl Gilbert, National Park Service.)

TOP LEFT: Figure 48. The red squirrel has always been abundant on Isle Royale. It can be readily seen and heard by tourists to the island. (Photo is by the National Park Service.) TOP RIGHT: Figure 49. The red fox is a fairly common resident on Isle Royale. Apparently on occasion, wolves kill red fox. (Photo is by the National Park Service.) MIDDLE LEFT: Figure 50. Herring gulls nest by the hundreds on long, narrow reefs near Isle Royale. This is a colony on Long Island where 290 nests were counted in 1948. At the left on the photo is a blue heron. MIDDLE RIGHT: Figure 51. This is a herring gull nest. Both early and recent bird expeditions reported that the herring gull was probably the most common bird. (Photo is by F.B. Lee, Fish and Wildlife Service, USDI.) BOTTOM LEFT: Figure 52. Beaver, currently abundant, prefer to feed on aspen. Both beaver and moose often feed on trees cut down by the beaver. BOTTOM RIGHT: Figure 53. This bald eagle nest is in an old white pine tree at Siskiwit Lake. The bald eagle was quite common before 1958. Since then, it has been observed on rare occasions.

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Figure 54. The lighthouse at Menagerie Island on Siskiwit Bay has warned 19th and 20th century vessels of the dangerous reefs. Isle Royale is a 210 square mile island in Lake Superior. Moose on the island have received worldwide attention. This publication discusses the ecology of the Isle Royale moose, with special reference to the habitat.

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