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MOOSE HABITAT SELECTION AND RELATIONSHIPS TO FOREST MANAGEMENT IN NORTHEASTERN MINNESOTA

by

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FRONTISPIECE. An aggregation of five moose occupying an area which had been recently logged within the Boundary Waters Canoe Area. This particular area was supporting nearly 2 moose per hectare at the time of the photograph, December 1969.

MOOSE HABITAT SELECTION AND RELATIONSHIPS TO FOREST MANAGEMENT IN NORTHEASTERN MINNESOTA[1]

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CONTENTS

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INTRODUCTION

Moose, *Alces alces andersoni* Peterson, have persisted in northeastern Minnesota since before settlement in the late 1800's (Carver 1956; Dewdney and Kidd 1962; Lukens 1963, unpublished doctoral dissertation, University of Minnesota, Minneapolis, Minnesota). Although they are of only cursory interest to most visitors to the area (Lime and Cushwa 1969, Lime 1971), interest in management of moose for recreational hunting has increased during the last decade, and the Minnesota Legislature authorized a limited harvest during 1 of 2 fall periods of the 1971–1972 biennium, and again in the 1973–1974 biennium.

Ecological data for moose in Minnesota are sparse. Except for a report by Surber (1932) and a brief undocumented report on moose food habits and natural history by Manweiler (1941), the literature deals primarily with diseases during the 1923–1950 period. The pertinent literature on moose diseases, summarized by Kurtz et al. (1966), extends from the initial studies by Thomas and Cahn (1932) and Fenstermacher and Jellison (1933), when a disease known as "moose sickness" was identified, until the nematode parasite, *Parelaphostrongylus tenuis* Dougherty, was identified and relationships between moose, white-tailed deer *Odocoileus virginianus,* and the parasite were studied (Karns 1967a).

Objectives of this study were initially to determine numbers, age and sex composition, and aggregation patterns of the moose population, its yearlong habitat use and forage use patterns, and subsequently to formulate habitat management recommendations which would effectively integrate management of this species into the major forest management efforts of the region. As activities associated with timber management and human recreational use of this area intensify, the need to understand influences upon this population also intensifies.

Human exploitation of this population since 1923 probably has been minimal. Although logging activities have profoundly influenced moose, as will be shown, the population provided an opportunity to investigate habitat selection and population dynamics without direct human influence on the moose population.

ACKNOWLEDGMENTS

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METHODS

Moose populations on the 1,958-km^2 study area (Fig. 1) were estimated by aerial census using the stratified quadrat technique of Siniff and Skoog (1964) as modified for moose by Evans et al. (1966). In 1967–1968, the study area was divided into high- and low-density strata based on previous observations of moose and moose sign. A total of 75 2.6-km^2 quadrats was randomly selected for counting within the 2 strata. To increase sampling efficiency with similar coverage, the census area was reduced in 1968–1969 to 632 km^2 in 8 sample units selected on a basis of vegetational charac-

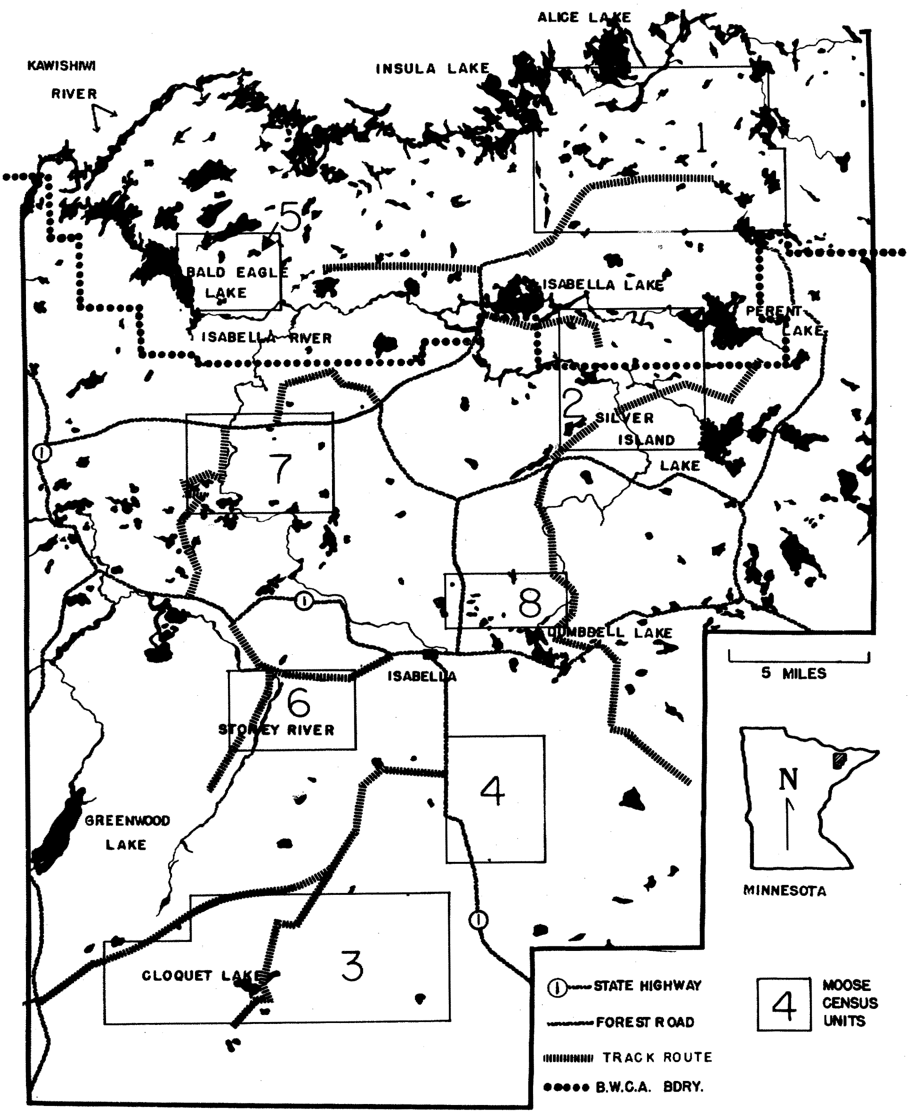

FIG. 1. The study area, showing boundary of Boundary Waters Canoe Area, moose census units, observation routes, and important lake and stream systems. Five-mile scale equals 8.05 km.

teristics typical of the study area (Fig. 2). Area 1, a cutover comprised of large brush fields interspersed with balsam fir *Abies balsamea,* black spruce *Picea mariana,* and jackpine *Pinus banksiana* stands, was considered the best moose habitat on the study area. Areas 2 and 3 also were in extensively cutover areas and were considered above-average moose habitats, but the former was more reforested to red pine *Pinus resinosa,* jackpine, and black spruce, while the latter contained more balsam fir and a taller shrub understory. The remaining areas were considered lower-than-average moose habitats and were comprised of lowland balsam fir–white cedar *Thuja occidentalis* swamps (Area 4), 90–100-year-old white pine *Pinus strobus*–red pine stands, aspen

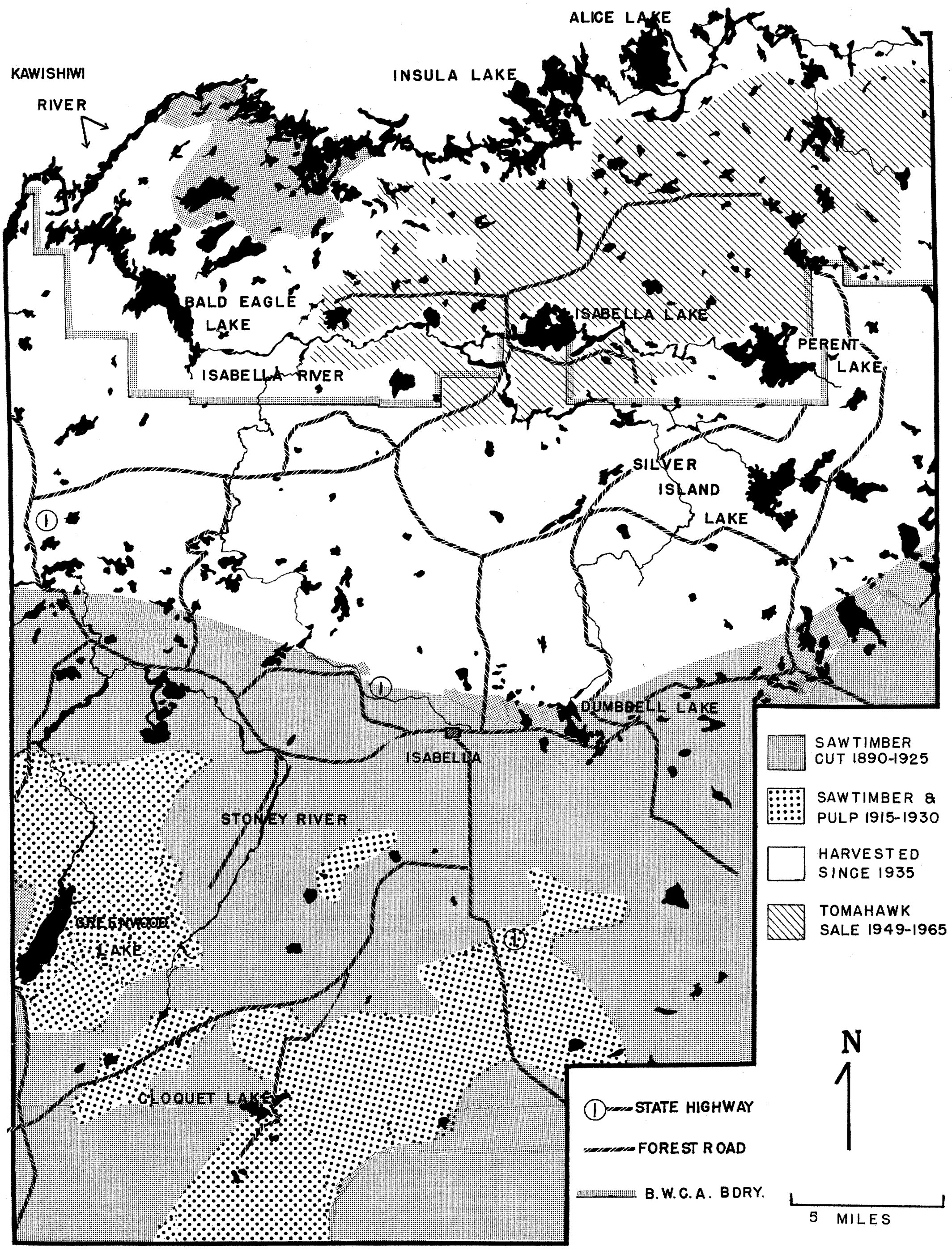

FIG. 2. Logging history of study area, after Heinselman (1969). Five-mile scale equals 8.05 km.

Populus tremuloides and *P. grandidentata*, and white birch *Betula papyrifera* stands (Areas 6 and 8), an extensively logged and replanted area (Area 7), and an uncut 100-year-old jackpine and black spruce stand (Area 5). Plant names follow Lakela (1965).

Quadrats were flown until pilot and observer were satisfied that as many moose as possible were observed. The same pilot and observer were used on all census flights to reduce bias between observers, as well as to take advantage of experience obtained from previous flights.

Quadrat boundaries were first located on a basis of recognizable topographic characteristics and then the quadrat was examined by at least 9 overlapping circular flights. In the very few cases where moose could not readily be determined to be in or out of a quadrat, the precise location was obtained from topographic maps and a decision made therefrom.

A Piper PA-18 Super-Cub, which Bergerud and Manuel (1969) and Evans et al. (1966) felt best suited for this work, was used for the census. Only observations of animals were tallied except for Area 3, censused in January 1969 after a fresh snow, when tracks were also recorded.

Animals were classified as to sex on the basis of presence or absence of antlers or, in some cases, the white vulvar hair patch characteristic of cows (Mitchell 1970). Calves were recognized by comparison of size with the adult cow and/or the short nose-to-ear distance characteristic of young animals. Moose with spikes, small forks or small palmated antlers were designated as yearlings following Peterson (1955). All classifications were completed in early December, before antler shedding occurred.

Since aerial observations may be subject to observational bias that influence sex and age classifications as well as enumeration, and this bias may be related to differential cover use by sex and age (Peek 1962), a system of classification of the vegetation within the vicinity of each aggregation was devised. The relative density of the overstory over 3 m tall within an area of approximately 30-m radius around a track or animal was recorded by class: (1) trees less than 3 m apart or 988/ha; (2) trees 3–9 m apart or 124–987/ha; (3) trees more than 9 m apart or fewer than 124/ha. The relative abundance of deciduous and coniferous cover was ranked according to which form was dominant or subordinate. Statistical differences between observed and expected numbers of each sex and age category in each cover class were determined using chi-square.

Food Habits

The feeding site examination method of Cole (1956) was used to determine food habits and to correlate plant usage with phenology and abundance. Each feeding site was arbitrarily confined to 1 reasonably homogenous habitat or cover type. If an animal fed in both a conifer swamp and adjacent upland, 2 feeding sites were recognized and examined individually. Sites examined included those where moose were observed feeding and, more frequently, where fresh tracks and browsing occurred.

Instances of use, or bites, were tallied separately by plant species. One freshly clipped twig (current annual growth) or, if leaves were taken, the current annual growth which was stripped, was considered one instance of use. Data were summarized monthly and seasonally using the aggregate percentage method (Martin et al. 1946).

At each feeding site, the overstory species and the composition, abundance, and height of species in the shrub understory were recorded. Abundance classes of shrubs were: (1) plants spaced less than 1 m, (2) 1–3 m, (3) 3–6 m, (4) 6–12 m, and (5) over 12 m apart. Average shrub heights were classified as: (1) less than 1 m, (2) 1–2 m, (3) 2–3 m, and (4) over 3 m tall.

Diameters of twigs at the point of browsing were measured at feeding sites and converted to weight of forage eaten using diameter–weight regression equations developed for each browse species on the study area (Peek et al. 1971). These data were used to compare percentage occurrence in the diet by weight with percentage occurrence by numbers of twigs eaten.

Preferences of individual species must be evaluated in terms of the abundance at each feeding site and frequency of occurrence in all sites examined over the month, as well as the actual utilization. An importance value, derived from the method of Cottam and Curtis (1956), was calculated by summarizing frequency of occurrence for each species within all feeding sites, plus the aggregate percentage relative abundance of each species, plus the aggregate percentage utilization for the month, and dividing by 3. This method was detailed by Peek (1971, unpublished doctoral dissertation, University of Minnesota, St. Paul, Minnesota).

Utilization of aquatic plants was difficult to observe directly, although grazed plants were common in lakes and ponds of the study area. Use of aquatic species was obtained by observing plants hanging from the mouths of feeding moose, and by examining for fresh use of plants at sites where moose were feeding immediately prior to examination.

Forage Utilization

Trends in forage utilization and condition were determined by: (1) estimating percentages of current annual growth browsed per plant, (2) recording the degree of hedging or removal of previous year's twig growth on each plant, and (3) measuring trends in species composition and coverage on selected range sites.

Measurements of utilization and condition of representative important browse species were modified from Cole (1959). Percentages of current growth browsed were estimated by class as follows: 0 = nonuse, 5 = 1–10 percent, 25 = 10–40 percent, 50 = 40–60 percent, 70 = 60–80 percent, and 90 = 80–100 percent use. Each plant was assigned to 1 of 3 form classes or condition categories based on appearance of the previous year's growth: Class 1 = lightly hedged = less than 25 percent of the previous year's growth browsed, Class 2 = moderately hedged = 25–50 percent of all previous year's twigs browsed, and Class 3 = heavily hedged = more than 50 percent of the previous year's twigs clipped. This method permitted condition classification of many species, especially trees such as pin cherry or fire cherry *Prunus pensylvanica*, mountain ash *Sorbus* spp., balsam fir, white birch, and aspen, which do not assume the typical hedged or clipped appearance illustrated by Cole (1959). Transects were randomly placed in upland areas of sparse overstory throughout the study area where moose sign was commonly observed. All plants were marked with numbered metal tags for individual recognition and remeasurement.

The line intercept method (Canfield 1941) was used to determine species compositional changes, coverage, plant condition, and utilization at 30 sites. The intercept of all woody species which bisected an assumed vertical plane above a 30-m line stretched between the 2 permanently marked stakes was recorded, including unoccupied space within that intercept. Leader use and condition were recorded as described above for each plant bisecting the line. Beaked hazel *Corylus cornuta*, a clonal species where the branches of rooted stems overlap each other considerably, was recorded as a single intercept except where obvious breaks in the canopy occurred, after Stephenson and Buell (1965). Plants 1–3 m tall, the typical browsing zone for moose, were arbitrarily assigned to Union 2 (tall shrub layer). Plants below and above those heights were assigned to Unions 1 (low shrub layer) and 3 (overstory), respectively. All measurements were made during early May of each year.

Habitat Use and Vegetational Analyses

Nine vehicular routes totaling 171.7 km were established along roads and trails on the study area (Fig. 1). They averaged 19.0 (range 7.6–31.9) km. Heavily traveled roads were avoided except in one case where the roadway was sufficiently wide to allow track observations along the margins. Three routes were within the Boundary Waters Canoe Area where roads frequently were unused by vehicles between observation trips.

The routes were traveled at intervals of a week or more from June through December to observe moose, track locations, and vegetational characteristics of sites used by moose. Routes were traveled in early morning when tracks made the previous night were most obvious, and only fresh tracks, with edges and marks still discernible, were recorded. Track locations were recorded where tracks entered or left the road. Those which left the road and continued down discernible trails were omitted; and at least 0.3-km intervals were maintained between recorded track locations to minimize recording of tracks of animals walking along or off and on the road.

The vegetation within a semicircle with a radius of 30 m from the point where tracks entered and/or left the road was described as indicative of the habitat selected by the moose. Immediate roadside vegetation such as dense stands of speckled alder *Alnus rugosa* in borrow pits or short balsam fir in cuts was ignored in these descriptions because it was not indicative of cover away from the roadway. Data recorded included designation as upland, lowland, or plantation type on the basis of dominant overstory and understory species or physiography of the site, stand type on the basis of dominant species, stand density and height, and tree–shrub species composition. Density and height classes were those described earlier for tree–shrub abundance and height at feeding sites.

For comparative purposes and to obtain a generalized description of the vegetation of the study area, similar vegetational data were obtained for 544 stands classified at 0.3-km intervals along 171.7 km of the forest road used as routes throughout the study area. In these analyses, a 60-m semicircular plot adjacent to the road comprised the stand, with immediate roadside vegetation ignored.

During midwinter, when vehicular routes were impassable, habitat use was recorded by following moose trails on showshoes and recording the same vegetational characteristics at 50-step intervals and at all bedding sites.

Aerial observations of moose and moose trails augmented observations made from the ground from late November through early April. Descriptions of overstory vegetation at observation sites were similar to those for ground observations except that species were classified as coniferous or deciduous and as dominant, codominant, or subordinate. Also, tree heights were not recorded.

Vegetational characteristics obtained along established trail routes were compared statistically with similar data for the study area as a whole using a chi-square test for independency. Data obtained by trailing moose in midwinter were similarly compared with vegetational data for the entire study area. Frequency distributions of moose in each overstory cover category from aerial observations were evaluated statistically by comparing observed with expected distributions in a chi-square contingency table analysis. In all tests, when use of a habitat category was not proportional to its occurrence or expected occurrence, the data were further inspected to determine which values contributed most to the calculated chi-square value. Statements concerning habitat preferences were made on this basis.

Use of aquatic habitats by moose on the study area was evaluated in special studies during the summers of 1968 and 1969. An aerial observation route covering 27 lakes and 103 km of stream was systematically flown at weekly intervals from June through August in 1968 and 1969. In addition, regular observations were made by canoe or from a vantage point on the shore of a lake commonly used by moose throughout the summer of 1969. The phenology of major aquatic and emergent plant species was examined weekly on this lake for correlation with observed use of water areas by moose.

Phenology of each species was estimated by classifying as vegetative, flowering, or fruiting according to the condition of at least 85 percent of each stand observed in the lake.

Nutrient analyses of current annual growth of 5 common understory species from 13 stands differing in age since disturbance, canopy closure, and soil moisture characteristics were determined to compare trends through time and between stands. Collections of current year's growth were made biweekly between July 1971 and June 1972 from plants distributed through the entire stand. An attempt was made to sample the entire stand each time and not to sample the same plants repeatedly. Current year's growth of leaves and twigs of beaked hazel and mountain maple *Acer spicatum* was analyzed separately. Peek et al. (1971) reported that browsing by deer and moose in northern Minnesota generally approximates removal of current year's growth. The terminal 8 cm of bush honeysuckle *Diervilla lonicera* and the leaves of large-leaf aster *Aster macrophyllus* and wild sarsaparilla *Aralia nudicaulis* were collected.

Plant samples were oven dried at 75–80 C for 24 hours as soon after collection as possible, ground, and stored in glass bottles. Crude protein, ether extract, NFE, and ash were determined according to the procedures of the American Association of Cereal Chemists (A.A.C.C. 1969). The ADF assay followed Van Soest (1963). Mineral determination was made by Jarrell–Ash Model 66-000 emission spectrograph at the University of Minnesota Agricultural Experiment Station, St. Paul, Minnesota.

Two soil samples were collected from the surface horizon of each stand in which vegetation was sampled for nutrient characteristics. The samples were crushed, air dried, and passed through a 2-mm sieve. Available soil moisture was measured at ⅓-bar minus 15-bar soil moisture (U.S. Department of Agriculture 1954). Stands were arbitrarily divided into 3 soil moisture categories based on available soil moisture, which ranged from 4.8 to 15.6 percent. Those stands falling within the top third of this range were grouped in the wet category. The dry category included stands in the lowest third of the soil moisture range and mesic stands fell in the middle third of the range.

Statistical procedures were used to determine significant differences in nutrient levels between stands to evaluate differences which may have been attributable to available soil moisture, overstory canopy coverage, overstory age, and overstory species composition.

A two-way analysis of variance with fixed model (Steel and Torrie 1960:109) was performed on each nutrient and each species separately. Data were first transformed using the inverse sine transformation. Sum of squares of the main effects of stands was partitioned into nonorthogonal subclasses to test differences between groups of stands for individual species (Steel and Torrie 1960:252).

Stands were selected on the basis of age and species composition as examples of the different stages of forest maturity. A total of 13 stands was sampled. Four quaking aspen *Populus tremuloides* stands, 15, 22, 54, and 80 years old; 3 jackpine stands, 23, 53, and 93 years old; 1 79-year-old red pine stand; 1 40-year-old balsam fir stand; 1 opening; 1 9-year-old pine plantation; and 2 burns were sampled. The slash burn stand, logged in the winter of 1970–1971, was mixed jackpine, aspen, and white birch. The slash was burned in the spring of 1971, a typical forest management technique in the area, resulting in incomplete burning of litter and dried slash. The wildfire burn occurred in a mixed balsam fir–white cedar stand during the spring of 1971. This fire, hotter than the slash burn, killed all aboveground woody stems and left a white ash layer over most of the burned area. The opening was a completely sodded clearing of approximately 2 ha with little shrub cover. The pine plantation was poorly stocked and dominated by shrubs, primarily beaked hazel and raspberry *Rubus* spp.

A list of plantations was compiled according to age and post-planting treatment from U.S. Forest Service records. Twenty-five stands representing various age–treatment categories were randomly selected for study. Tree and shrub composition, density, and importance values were determined for each plantation using the point-centered quarter method (Cottam and Curtis 1956). Eighty plants of each layer were measured. Canopy area, determined by measuring 2 diameters at right angles to each other across the width of each plant and converting to area, and plant height were recorded for all shrubs and trees less than 3 m tall, over 0.3 m tall, and under 3 cm DBH. Overstory canopy closure was estimated with a forest densiometer (Lemmon 1957). The importance value of each species in the shrub layer was derived from its density, frequency, and canopy area (substituted for dominance) after Cottam and Curtis (1956).

The terminal 8 cm of current year's growth of beaked hazel, aspen, and pussy willow *Salix discolor* were clipped for calcium, phosphorus, iron, magnesium, and potassium analyses in December 1969.

Soil samples from each horizon beneath each plant were analyzed for calcium, phosphorus, iron, magnesium, and potassium. Correlations between soil nutrient level, twig nutrient level, canopy area, stand age, and overstory canopy closure were examined by multiple regression analysis.

DESCRIPTION OF THE STUDY AREA

The study area, in the Superior National Forest in central Lake County, Minnesota (Fig. 1), encompassed 1,958 km^2 of high-density moose range (Ledin and Karns 1963). Approximately 30 percent of the study area was within the Portal Zone (open to logging) of the Boundary Waters Canoe Area. The Isabella and Halfway Ranger Districts of the Superior National Forest comprise about 90 percent of the study area.

Physiographically, the area may be characterized as gently rolling terrain ranging between 457 and 610 m in elevation. Precambrian bedrock underlies Pleistocene glacial drift over most of the area (Leverett and Sardeson 1932) with outcrops frequent on the northern half. Soils are coarse to fine texured, of the Ahmeek–Rock Outcrop Association (Arneman 1963). They range from clay loams to sandy loams (Grigal and Arneman 1970). Soils of the southern portion of the area are generally less well drained and deeper than those of the more northern portion, but considerable variation occurs.

Climate and Weather

Climate is cool temperate (Hovde 1941). Annual snowfall averages over 152 cm, with over 140 days of snow cover. The first persistent snowfall may be expected about late November, and about 50 percent of the ground will be bare by mid-April. Average annual precipitation at Isabella (U.S. Department of Commerce 1952–1970) is 72.5 cm, of which 38–51 cm falls during the growing season.

The growing season averages 118 days, with the mean first frost about September 20 and the last about May 30. Mean July temperature is 17.7 C and mean January temperature is –21.1 C. Temperatures between 27 C and 32 C in summer and below –29 C in winter are common on the area. Periods of up to 2 weeks of –17 C weather were not uncommon during January and February.

An index to relative severity of winters during the study period was derived by subtracting the mean monthly temperature from 32 F, multiplying the remainder by the corresponding monthly precipitation, and adding the monthly (December through March) products. Comparison with the 12-year average (89.15) shows that 1967–1968 was much less severe (45.76), the 1968–1969 winter considerably more severe (182.15), and the 1969–1970 winter about normal (76.93) in severity.

The 1967–1968 winter was one of the mildest of the 12 years of recorded weather at Isabella. Precipitation was much below normal until March, when higher than normal temperatures compensated for added

TABLE 1.—CHARACTERISTICS OF OVERSTORY VEGETATION OF STUDY AREA AS DETERMINED BY VISUAL CLASSIFICATION

Prominent Species in Stand	Percentage Composition			
	Lowlands	Plantations	Uplands	All
Balsam fir	33.8	2.2	40.5	33.9
White birch	6.0	12.9	16.8	14.2
Black spruce	47.4	5.4	5.1	13.4
Jack pine	0	32.3	5.3	8.0
Red pine and white pine	2.3	32.3	2.7	6.6
Aspen	2.3	14.0	21.7	16.8
Other species (Red maple, white spruce, white cedar, black ash, tamarack, balsam, poplar)	8.3	1.1	8.0	7.1
Stand Height				
A. Deciduous and coniferous trees similar, less than 9 m tall	17.7	55.9	6.7	21.5
B. Deciduous and coniferous dissimilar, less than 15 m tall	1.6	5.6	6.9	5.6
C. Deciduous and coniferous heights similar, over 9 but less than 15 m tall	72.6	14.2	44.8	42.4
D. Deciduous and coniferous heights over 15 m tall	8.1	24.2	41.5	30.5
Stand Densities				
Over 988 trees/ha	56.8	42.3	49.7	50.4
123–988 trees/ha	25.6	25.4	38.4	33.7
Less than 123 trees/ha	17.6	32.4	11.9	15.9

snowfall. No snow depths over 46 cm were recorded during this winter.

Precipitation in December 1968 and January 1969 was much above normal, with the monthly totals the highest recorded during the 12-year period. Conversely, precipitation in February and March 1969 was much below normal. Temperatures remained low enough so that the snowpack resulting from the previous 2 months was largely retained until the last week of March. Snow depths were over 102 cm in open areas from 1 January through 21 March 1969.

The 1969–1970 winter was the coldest of the 3 winters during the study. Snow depths ranged from 63 to 76 cm.

Growing season conditions during the study period tended to include near normal temperatures and to be wetter than average in early summer, especially in June 1968.

Vegetation

Plant communities on or adjacent to the study area have been described by Buell and Niering (1957), Butters and Abbe (1953), Flaccus and Ohmann (1964), LaRoi (1967), Maycock and Curtis (1960), and Ohmann and Ream (1971). The work of Cooper (1913) on forest succession on Isle Royale also appears applicable to the study area.

Lowlands

Lowland communities constituted 24 percent of the vegetation along roads on the study area (Table 1).

Treeless lowlands comprised 2 percent of the stands classified and consisted of sedge and shrub swamps, as well as lake- and riveredge communities. Usually, these stands were dominated by speckled alder, white spirea *Spiraea alba,* and sweet gale *Myrica gale.*

Conifer swamps comprised 10 percent of the stands classified. Black spruce dominated 80 percent of these while balsam fir dominated or codominated in 20 percent. Tamarack *Larix larcina,* jackpine, and white cedar were other common tree species. Trees were generally 9–15 m tall, and densities commonly ranged from 123 to 988 trees/ha (Table 1). Shrub understories were dominated by speckled alder (51%) or labrador tea *Ledum groenlandicum* (32%), with balsam fir, black spruce, mountain maple, tamarack, willows *Salix* spp., being other important species.

Mixed deciduous–coniferous swamps comprised 12 percent of the recorded vegetation. Balsam fir dominated or codominated 51 percent, black spruce 33 percent, and white birch 12 percent of these stands. Other species included black ash *Fraxinus nigra,* aspen, yellow birch *Betula lutea,* white pine, white cedar, and speckled alder.

Densities of over 988 trees/ha occurred in 57 percent of these stands. Tree heights of 9–15 m were recorded for 63 percent of the stands. Yellow birch was present only on the southerly portions of the area, while white spruce *Picea glauca,* and balsam fir were more common further south. Balsam poplar *Populus balsamifera,* and black ash occurred infrequently, being dominant or codominant on less than 1 percent of the lowland mixed swamp stands.

Speckled alder dominated the recorded shrub understory in 59 percent of the mixed swamp stands. Mountain ash, balsam fir, and labrador tea were other important species.

Uplands

Uplands (including plantations) constituted 76 percent of the vegetation (Table 1). Pure stands of natural upland conifer or upland aspen–birch communities constituted less than 3 percent of the stands observed. The aspen–birch stands were primarily over 15 m tall and moderately dense (123–988 trees/ha). Aspen, mountain maple, and green alder *Alnus crispa,* were dominant understory species. Upland coniferous communities were dominated by white spruce (45%), fir, jackpine, or red pine (each 18%), usually dense (over 988 trees/ha), and between 9 and 15 m tall.

Upland mixed coniferous–deciduous communities comprised 59 percent of the stands classified, attesting to the diversity of the vegetation of the area as well as to the broadness of this category. Balsam fir was the single most prevalent species, dominating 39 percent of these stands. Conifers dominated 49 percent, deciduous species 32 percent, and conifer–deciduous mixtures codominated 19 percent of these stands.

Balsam fir stands tended to be quite dense, usually over 988 trees/ha, and less than 15 m tall. Ages of representative trees in 42 balsam fir stands was 39.8 (27–82) years. Beaked hazel and mountain maple frequently dominated in the understory while balsam fir reproduction and green alder were common.

Aspen or white birch stands tended to be moderately dense (123–988 trees/ha) and over 15 m tall. Beaked hazel was the most important understory species while aspen, fir, juneberry *Amelanchier* spp., white birch, and willows were commonly present but seldom dominant.

Balsam fir and aspen–white birch stands covered a large percentage of the cutover area. Most of these have developed since 1950. In logging, northern boreal components of the original forest, especially balsam fir and white birch, were retained while the lake forest species, including red pine and white pine, were reduced in importance. Timber harvest records indicate that jackpine probably covered the majority of the upland sites prior to logging.

Stands dominated by red pine and white pine comprised 3 percent of all sites classified. Most were 90–100-year-old communities and occurred from Dumbell Lake west to the Stoney River in the center of the study area. This area was subjected to sawtimber harvest in 1890–1925, and these stands evidently were unmerchantable at that time. Existing stands usually were moderately stocked and over 15 m tall. Aspen and white birch were commonly interspersed among the pine, and a balsam fir understory was often present. Beaked hazel and mountain maple were the most common understory shrubs. White pine was currently being logged to salvage trees infested with blister rust.

White pine and red pine trees comprised a "super canopy" over much of the study area, often occurring as 1 or 2 individuals/ha or less. Also, some volunteer white pine reproduction was evident, though generally sparse and highly susceptible to blister rust with maturity.

Plantations comprised 14 percent of all stands classified. This estimate compared with a 10 percent estimate of plantation area for the Isabella and Halfway districts, suggesting that cutover and planted areas were slightly overrepresented in the sample. Trees in the majority of plantations were under 9 m tall. Heights greater than 9 m generally represented a residual overstory of aspen or white birch left after logging.

Plantations comprised 18 percent of the upland sites. Red pine and jackpine dominated or codominated 76 percent of these stands while aspen and white birch were dominant in 24 percent. Black spruce, white spruce, and white pine were other common species. Plantation records for the Isabella and Halfway districts show that red pine, jackpine, or combinations thereof comprised 47 percent of the total planted acreage, the 2 spruces 11 percent, and mixtures of 3–4 of the above species 22 percent, with an additional 20 percent in aspen, yellow birch, and white pine. Differences in survival between species when planted in mixtures probably account for much of the variation between planting records and the present classification.

Plantations on the Isabella District averaged 29 (1.6–202) ha, with little increase in size from 1933 to 1967. Halfway District plantations averaged about 25 ha during the 1933–1959 period, increasing to 69 ha during the 1960–1967 period. The larger acreages on this district occur primarily within the Boundary Waters Canoe Area, where aerial seeding of jackpine (included in the plantation classification) on inaccessible areas has been extensive.

Beaked hazel, juneberry, pin cherry, green alder, and aspen were common native dominant understory species in plantations.

Land Use Characteristics

The main land use was timber production and harvest (Fig. 2). The initial logging occurred between 1890 and 1925, primarily for red pine, white pine, and white spruce near the center of the study area. Logging was initiated north of Isabella about 1935. In recent years, all 3 species have been cut, depending upon market conditions. However, most logged-over area contained scattered uncut white birch, aspen, or balsam fir.

The influence of recent logging on vegetational characteristics of the area was revealed by timber sale records of the Isabella and Halfway districts. Over 370 km^2 (21%) of these districts were cut between 1948 and 1967.

Isabella District records show that jackpine accounted for 57 percent, black spruce 37 percent, and balsam fir, aspen, white birch, and red pine (mostly thinnings from 30-year-old plantations) 6 percent of the total cords cut for pulpwood. Fir, aspen, and birch increased from less than 1 percent of the pulpwood harvest in the 1950's to 9.1 percent of the harvest in the 1960's. Aspen accounted for 58 percent, white birch 27 percent, and white pine–red pine for 15 percent of the sawtimber sales.

Timber harvest and logging practices on the area have been greatly influenced by marketing problems including long distances to mills and a lack of demand for aspen, white birch, and balsam fir. Jackpine, then black spruce, have been preferred pulpwood species. Consequently, although clearcutting was the recommended silvicultural practice, residual stands of white birch and balsam fir were often left. Recent interest in fir, white birch, and aspen is perhaps indicative of the relative scarcity of the more economically desirable species.

Logging on the Halfway District consisted primarily of the large sale within the Boundary Waters Canoe Area of about 26,200 ha, to the Tomahawk Timber Company beginning in the 1940's and continuing through 1964. The average timber sale size on the Isabella District was 314 ha during the 1950's decreasing to 61 ha during the 1960's, and involving several small operators. The high percentage of both districts which were cutover during the last 20 years reflected the even-age character of the forest, which Heinselman (1969) reported to originate primarily from an 1864 fire (Fig. 2).

MOOSE POPULATIONS

Historical Trends

Historical trends of moose in Minnesota have been reported by Herrick (1892), Surber (1932), and Swanson et al. (1945). The records may be characterized by a statement by Herrick: "A few specimens of this noble animal may still remain in the inaccessible regions of northern Minnesota but the time is not far distant when it will have deserted the territory of the U.S. forever." Swanson et al. (1945) considered moose scarce in Lake and Cook counties and caribou *Rangifer tarandus* common about 1885. Moose were common in northern Lake County in 1912 and 1915 (Johnson 1922). Indians were accused of killing moose, caribou, and deer in northern Lake County in 1891 and 1895 (Swanson 1940, unpublished doctoral dissertation, University of Minnesota, St. Paul, Minnesota).

Moose were scarce, rather than absent, in Cook and Lake counties in the latter part of the 1870's and early 1880's, but became common about the time caribou disappeared in 1890 (Surber 1932). Caribou were said to be still comparatively common in the upper part of Lake County until 1885. Thus, Surber (1932) suggested the presence but scarcity of moose in Lake and Cook counties in 1885, through reports of "old settlers." It is reasonable to assume that presence or absence of moose in this area would be more reliably reported than relative abundance. Even though animals might not be seen, evidence of their presence through tracks and signs of browsing is readily noticed. John Tanner (James 1956) noted that "the Indians consider the moose shyer and more difficult to take than any other animal. He is more vigilant, and his senses more acute than those of the buffalo or caribou."

From this, we conclude that Peterson's (1955) map of moose distribution in North America in 1875, which includes northeastern Minnesota, more accurately depicts the distribution than the map drawn by Idstrom (1965). Additional evidence that moose were present in this area in the 1800's is given by Nute (1951), who reported an incident concerning moose in the Little Vermillion Lake area 40 km west of the study area during the 1807–1823 period. Moose were reportedly common in the forested regions of northern Minnesota at settlement time (about 1900) as indicated by historical records and by references made to the animal in Minnesota place names in the region (White 1967). There are Moose Lakes at Ely, 11 km northwest of Taconite Harbor, on the Pigeon River, a Moose Portage on the Pigeon River, a Moose Mountain near Lutsen, a Moose River, Nina Moose, and Big Moose Lakes near Ely. There is also a Hog Creek 29 km northwest of Tofte.

Although the presence of moose in northeastern Minnesota seems certain from the early 1800's up through the present, questions still arise: when did moose originally occupy the area, and what were the relative abundances of moose?

Presence of moose in prehistoric times may be indicated by fossil records, Indian records, and the prehistoric vegetational record. Vegetational records have been used to indicate presence of elk *Cervus canadensis* habitat in the Yukon (Guthrie 1966) and of moose habitat on the Kenai (Lutz 1960), prior to the arrival of civilized man.

The pattern of postglacial occupation of habitat and subsequent dispersal of moose was extensively investigated by Kelsall and Telfer (1973). Moose which occupy Minnesota were considered descendants of populations which occurred immediately south of their present range during the greatest extent of Wisconsin glaciation. Moose were not considered present in the area immediately north of Lake Superior in Ontario until 1900 (Peterson 1955). Subsequent to Peterson's work, Churcher (1965) reported the remains of moose at the Fishing Creek archaeological site on James Bay, near Fort Albany, which date back to 1700 AD. It is possible that these remains were transferred into the area from further west, since there were also many furbearing species at the site which were trapped elsewhere. This suggests that moose were present somewhere north of northeastern Minnesota in 1700.

At least the west half of Lake County is in a direct line of the postglacial dispersion of moose as indicated by Peterson (1955). Also, moose were present in the Rainy Lake area, 80 km northwest of Ely, in the 1700's (Carver 1956). John Tanner (James 1956) killed moose at Rainy Lake in the 1800's. Moose, deer, and bear (*Ursus* spp.) were the main quarry of the Ojibway in the Quetico region, immediately north of the study area, during this period (Coatsworth 1957).

The most interesting evidence of moose distribution in the Great Lakes area may be Indian pictographs (Dewdney and Kidd 1962). These probably were the work of late woodland culture peoples (1000–1650 AD) or eastern woodland culture peoples (1650–1750 AD). The greatest occurrence of these pictographs is between Lake Superior and the Manitoba border, where natural waterways are most abundant. Pictographs showing moose occur in the Quetico–Superior area, Rainy Lake area, Ontario north of Rainy Lake, and the area east of Lake Superior. The distribution of moose pictographs is surprisingly similar to the 1875 distribution of moose (Peterson 1955). They are noticeably absent from the Nipigon area north of Lake Superior, where caribou pictographs occur. These Indians were nomadic (Coatsworth 1957), and the moose pictograph distribution and the 1875 moose distribution may coincide purely by chance.

Perhaps the best evidence of prehistoric occurrence of moose in the region is the record from archaeological sites, representing Indian campgrounds and burial sites. The Pikes Bay site, 56 km west of the study area, and Nett Lake site 106 km west and the McKinistry sites 169 km northwest, all contain the remains of moose (Lukens unpublished doctoral dissertation). There were enough remains of moose to indicate the presence of a high population during the woodland cultural period (500 BC–100 AD). The pictographs and archaeological sites tend to corroborate each other as to the presence of moose in the region back to about 2000 BP.

The paleobotanical record, tied into the glacial record for the region, provided some clues to when suitable moose habitat might first have become available after the last glacial recession. Identification of pollen which accumulated in sediments at Weber Lake, on the study area, by Fries (1962), indicates which plant species were present adjacent to the lake, that may also be identified according to age of sediment. Moose habitat may be represented by the presence of spruce–fir pollen, plus charcoal which indicated the presence of fire, and thus seral vegetation as well. Currently, the ranges of spruce–fir communities and moose generally coincide in eastern North America (U.S. Forest Service 1965, Peterson 1955). Apparently little question exists about the validity of a spruce–fir zone following the glacial recession (Deevey 1949). This occurred 10,000 to 10,500 years ago in northern Minnesota (Wright 1964). Spruce and birch pollen dominate the lowest sediments of Weber Lake (Fries 1962). However, since then, a postglacial hypsithermal interval (Deevey and Flint 1957) occurred, when pines greatly increased in the pollen rain. A cooling trend occurred somewhere around 2000 BP and brought with it spruce, fir, and larch pollen.

Charcoal occurs throughout pollen profiles from lakes of the region indicating that fire was an important ecological influence in the past (Heinselman 1970). The presence of charcoal, plus such species as hazel, aspen, birch, and willow in the pollen diagrams indicated that such factors as fire, insect infestation, windthrow and the qali effect (Pruitt 1958) created seral boreal forest communities which are characteristic of present moose habitat. Approximately 80–90 percent of the forest of the Boundary Waters Canoe Area was burned over one or several times during the last 300–400 years (Heinselman 1969), but the quantity of fire is still in doubt (Heinselman 1970). However, the 13 fire dates reported by Heinselman (1969) averaged 25 years apart. This suggested that habitat favorable to moose developed frequently.

The original land survey records of the study area (Trygg 1966) show that the 1890–1900 forest was comprised of aspen, spruce, birch, and jackpine with scattered red pine and white pine stands, as indicated also by Sargeant (1884) and others. Aspen, birch, pin cherry, juneberries, mountain maple, beaked hazel, and willows, all palatable to moose commonly occur on burned sites (Ahlgren 1959). Fires were a part of the normal presettlement scene of the Itasca region west of the study area, and the present forests there were also a product of fires (Spurr 1954).

The vegetational and fire history suggests that northeastern Minnesota probably was a vegetational mosaic, wherein the older stands of aspen–birch, spruce–fir, or jackpine were interspersed with the seral brush and sapling stages characteristic of moose habitat. Abundance and scarcity of moose probably was dependent upon the time since the last disturbance took place, with high populations probably occurring the 15–20 years following each fire. Similar conclusions were reported for Alaska (Lutz 1960) and Ontario (deVos 1962).

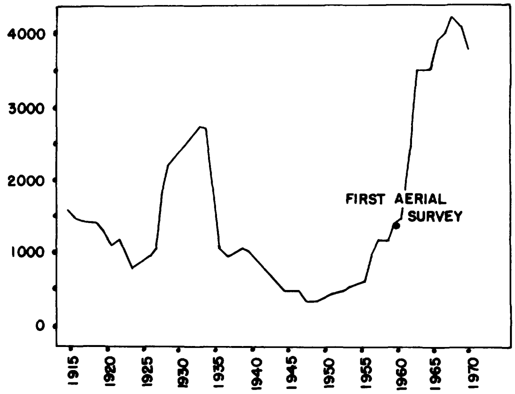

FIG. 3. Estimates of moose populations for northeastern Minnesota, including the study area, based on Superior National Forest records.

Moose populations have been "estimated" annually since 1923. These data indicate that populations on the Superior National Forest generally increased from 1923 through 1933, declined until the 1950's and increased in the 1960's (Fig. 3). Efforts to census moose were initiated in 1949 by the Minnesota Department of Natural Resources (U.S. Fish and Wildlife Service 1949) in the Red Lakes region of northwestern Minnesota. Although these efforts were not extended to northeastern Minnesota until 1959, incidental moose observations were obtained by Bue (1951) during an aerial census of white-tailed deer, and Magnus (1952) reported a postcard survey of Department personnel which gave opinions on habitat use, herd condition, and distribution in the state. Aerial censuses have been conducted in northeastern Minnesota since 1959 (Karns 1967b). Surveys by the U.S. Forest Service and Minnesota Department of Natural Resources indicated 0.5 to 0.66 moose/km² "low-density" range in northeastern Minnesota. Reproductive data from these surveys indicated decreasing productivity attributed to deterioration of forage supplies through heavy browsing (Karns 1967b).

TABLE 2.—WEATHER CONDITIONS DURING THE MOOSE CENSUSES

Year	Total Hours Census	Minutes Per Quadrat Mean (Range)	Census Dates	Snow Depth	Temperature Range (C)
1967–1968[1]	18.0	9.2 (5–15)	15, 16, 17, 19 Jan	15 cm	−23 to +4
1968–1969[2]	19.9	9.8 (6–34)	14, 15, 16, 17 Dec 1 Jan	12 Dec, 46 cm 1 Jan, 76 cm	−29 to −7
1969–1970	20.5	10.8 (7–17)	5, 15, 16, 17, 19 Dec	5 Dec, 10 cm 15–19 Dec, 36 cm	−23 to −7

[1] Snowfall 13 Jan; fog on 18 Jan.
[2] High wind on 1 Jan.

Population Characteristics 1967–1972

Density

Conditions for moose census were most ideal in 1969–1970 and least ideal in 1967–1968 (Table 2). Those for 1968–1969 were generally ideal except the final day when Area 3 was flown in a 17–32 km/hour wind with 1 m of fresh snow on the ground.

The increased population estimates for succeeding years (Table 3) probably reflected increased sampling efficiency. Observer and pilot experience, time of sampling, concentration of sampling effort, amount of time spent over each quadrat, weather and snow conditions, and moose distributional patterns all affect census results. The 1967–1968 estimate of 0.43 ± 0.11 moose/km^2 was 55 percent of the 1969–1970 estimate of 0.78 ± 0.18; and the 1968–1969 estimate of 0.62 ± 0.14 was 79 percent of the 1969–1970 estimate. Confidence intervals for the population estimates ranged from 22 to 26 percent of the estimate at the .90 level of significance for all 3 years, which was not precise enough to detect a population trend.

Population estimates in Area 1, consisting of 140 km^2 of high density moose range of which 78 km^2 were censused from 1968–1972, provide a more accurate index to population trend (Table 4). The population in this area declined from a high of 1.96 moose/km^2 in 1969 to 0.88 moose/km^2 in 1972. Census conditions during the last 3 years were about equal.

Sex and Age Composition

Chi-square analyses of sex ratio, adults and yearlings combined, indicated no significant deviation from equality over the 1967–1972 period (Table 5). Also, the proportion

TABLE 3.—MOOSE CENSUS DATA FOR 1967–1968, 1968–1969, AND 1969–1970, NORTHEASTERN MINNESOTA

Year	Stratum	Total Square Kilometers in Stratum	No. Quadrats Sampled	Total Moose Observed	Mean Moose Per km² Quadrat	0.90 Confidence Interval	Variance
1967–1968	high	1119	51	79	0.60		1.568
	low	839	24	13	0.21		0.608
	total	1958	75	92	0.43	± 0.11	0.125
1968–1969	high	373	54	124[1]	0.94		3.539
	low	259	17	8	0.18		0.291
	total	632	71	132	0.62	± 0.14	0.017
1969–1970	high	373	65	209	1.05		8.693
	low	259	17	18	0.41		0.990
	total	632	82	227	0.78	± 0.18	0.033

[1] Includes 2 sets of tracks.

TABLE 4.—MOOSE POPULATION ESTIMATES FOR A 140-KM^2 HIGH-DENSITY STRATUM (AREA 1), 1968–1972. THIRTY 2.5-KM^2 PLOTS WERE COUNTED EACH YEAR. VARIANCE IS BASED ON MOOSE/KM^2

Year	Number 2.5-km^2 Quadrats with Moose	No. Moose Seen	Mean No. Moose/km^2	S^2	Population Estimates 140-km^2 Unit	
					Mean	.90 C.I.
1968	22	90	1.15	4.48	161	115–231
1969	24	153	1.96	12.49	274	163–386
1970	24	106	1.34	3.64	188	133–243
1972	19	68	0.88	3.26	123	52–175

of calves did not change appreciably, averaging 20 percent of the fall population. The percentage of yearling males was weakly but significantly correlated with the previous year's percentage of calves ($r^2 = 0.34$) and better with the previous year's percentage of twin calves in fall ($r^2 = 0.76$). There were no significant correlations between the percentage of calves and percentage yearling males in the population for the same year, or between percentage of twin calves or percentage of calves and the previous year's percentage of yearlings. This indicated that overwinter survival of calves influenced the percentage of yearlings in the population, but that the yearling complement probably was not contributing significantly to calf production, as the percentage of calves did not change appreciably. The fluctuations in percentage of yearling males, probably reflecting overwinter survival of calves, was lowest following the severe winter of 1968–1969 and highest following the milder winters during the study.

Sex ratios were subject to bias because of differential habitat selection and misidentification of males and females, and group size differences between sexes. Eight bulls were observed with only one antler and 5 antlerless moose were recognized as bulls during fall classifications. Earliest observations of bulls with shed antlers occurred on 22 November 1968 and 3 December 1969.

The percentage of bulls with 1 or no antlers was 4 percent of the total of 318 males observed during the classification flights, which indicates that the possible bias involved in classifying antlerless bulls as cows probably was negligible. However, 9 of the 13 observations occurred in 1970, the year the sex ratio was most heavily weighted towards females, which indicated that this bias may be more important in some years than in others. This further suggested that timing of the antler drop varied between years in the area.

Habitats selected by bulls, cows, and cows with calves in fall were different (Table 6). In all years, selection for areas dominated by aspen or white birch was evident for all sexes/classes during the classifications. However, bulls were ob-

TABLE 5.—AERIAL OBSERVATIONS OF SEX AND AGE OF MOOSE ON THE STUDY AREA, 1967–1972. PERCENTAGE OF TWINS IS THE NUMBER OF TWINS DIVIDED BY THE TOTAL NUMBER OF CALVES

Year	% Adult ♂♂	% Yearling ♂♂	% ♀♀	% Calves	% Twins	Total seen
1967	39	7	37	17	18	196
1968	33	7	42	18	11	348
1969	31	4	46	19	14	370
1970	27	6	48	19	22	188
1971	28	10	39	23	12	138
1972	31	8	41	22	22	166

TABLE 6.—ANALYSIS OF FREQUENCY DISTRIBUTIONS OF MOOSE ACCORDING TO SEX AND WHETHER WITH OR WITHOUT CALVES, WITHIN VARIOUS COVER COMBINATIONS AS OBSERVED BY AERIAL SEARCH IN FALL AND EARLY WINTER 1967, 1968, AND 1969

Overstory Conifer		Character[1] Deciduous		1967						1968						1969					
				Bulls		Cows		Cows & Calves		Bulls		Cows		Cows & Calves		Bulls		Cows		Cows & Calves	
ABD	DEN	ABD	DEN	#	χ^2	#	χ^2	#	χ^2	#	χ^2	#	χ^2	#	χ^2	#	χ^2	#	χ^2	#	χ^2
+	+	—	—	12	0.43	8	0.46	6	0.12	28	0.82	14	0.13	7	0.85	15	0.09	12	0.56	13	1.89
+/=	=/+	—/=	=/—	12	0.66	5	0.20	0	3.40	11	0.08	6	0.46	8	1.65	42[2]	+5.61	18	—2.88	12	—1.00
=	=	=	=	6	0.07	2	0.28	4	1.07	22	0.00	12	0.43	12	0.72	60	0.51	49	0.03	26	0.56
—/=	=/—	+/=	=/=	12	0.66	3	0.29	2	0.58	34	0.53	34	3.07	12	1.13	42	—1.89	58	+2.27	28	0.01
—	—	+	+	25	0.12	11	0.31	12	0.60	35	0.05	19	0.41	16	0.20	23	—1.59	30	0.22	21	+1.23
Totals				67		29		24		130		85		55		182		167		100	
Total for year				120						270						449					
χ^2 value for year					9.25						10.53						20.34				
χ^2 .05, 12 DF					15.51																

[1] ABD indicates whether deciduous or coniferous trees dominated (+), codominated (=), or were subordinate (—) in the overstory canopy within a 30-m radius about the moose.

DEN indicates whether deciduous or coniferous trees were more dense (+), of similar density (=), or were subordinate (—) in the overstory.

[2] Indicates whether the observed value was more (+) or less (—) than expected value in cases which comprised a major share of the calculated chi-square value.

TABLE 7.—FREQUENCY DISTRIBUTIONS OF ADULT AND YEARLING BULL MOOSE WITHIN VARIOUS COVER COMBINATIONS AS OBSERVED BY AERIAL SEARCH IN FALL AND EARLY WINTER 1967, 1968, AND 1969

Overstory Conifer		Character[1] Deciduous		1967				1968				1969			
				Adults		Yearlings		Adults		Yearlings		Adults		Yearlings	
ABD	DEN	ABD	DEN	#	χ^2	#	χ^2	#	χ^2	#	χ^2	#	χ^2	#	χ^2
+	+	-	-	11	0.31	1	1.07	26	0.31	2	1.55	14	0.01	1	0.01
+	=	-	=	5	0.31	0	1.10	3	0.03	1	0.13	30	0.03	1	0.09
=	=	=	=	5	0.02	1	0.07	20	0.16	2	0.78	57	0.63	3	0.11
=	+	=	-	5	0.03	2	0.10	6	0.01	1	0.03	10	0.09	1	0.18
-	=	+	=	4	1.85	6	3.80	22	0.07	5	0.03	32	0.03	3	0.37
-	-	+	+	20	0.02	5	0.06	25	0.58	10	2.85	21	0.02	2	0.27
=	-	=	+	2	0.10	0	0.40	6	0.01	1	0.03	7	0.02	0	0.42
Totals				52		15		108		22		171		11	
Total for year				67				130				182			
Calculated χ^2					9.24				6.57				2.28		
χ^2 .05, 6 DF					12.59										

[1] See footnotes on Table 6 for overstory characterization.

served more often in conifer dominated areas while cows without calves used cover in the opposite manner. Cows with calves selected predominantly conifer cover more often than expected during 1969–1970 as compared to the previous 2 years, but this did not appear to affect the percentage of calves observed. No differential habitat use was observed between adult and yearling males (Table 7).

Two behavioral patterns may also have influenced the relative proportion of sex and age groups observed. Bulls occurred more frequently in larger groups than cows in late fall (Peek et al. 1974) which made them easier to locate. However, in 1968, bulls and cows with calves were observed more often in dense cover than expected, which would make them more difficult to locate. These 2 biases appear compensatory, but the larger group size may be most important because at least 30 percent of the adult cows (those with calves) were also using the denser cover more than expected.

The percentage of yearlings provides the best estimate of recruitment into the adult population since mortality of the younger age groups through their second summer of life has occurred. If the fall calf percentage of one year is compared with the fall yearling percentage of the following year, an estimated mortality from 6 months of age to 18 months of age is obtained. The estimated mortality of the 1967 cohort during the 5–17 month period after it was born was 24 percent, while for the 1968 cohort it was 61 percent. Such figures may be compared with a 57–81 percent calf mortality through 11–13 months following parturition in 2 areas of Alaska (Rausch and Bratlie 1965), and with a "normal" mortality of 3–50 percent and sometimes up to 80 percent for some areas in the U.S.S.R. (Heptner and Nasimowitsch 1967).

Mortality

Age-specific mortality patterns were determined from examination of 61 moose jaws collected on an opportunistic basis (Table 8). Natural causes accounted for the deaths of at least 34, of which 26 (77 %) were 2 years old or less. Ten (29 %) were attributed to predation by the wolf *Canis lupus*, including 2 2–3-month-old calves killed during the summer of 1969.

All deaths attributable to cerebrospinal nematodiasis were animals under 5 years of age. The presence of diseased moose in this population may alter the age structure of the wolf kills by causing yearling and 2-

TABLE 8.—AGE STRUCTURE OF MOOSE ACCORDING TO CAUSE OF DEATH IN NORTHEASTERN MINNESOTA[1]

			Natural Causes				
Age	Humans[2] %	Unknown %	Malnutrition %	Wolf[3] %	Cerebrospinal[4] nematodiasis %	All %	Totals %
Calf	10	6	100	30	4	15	13
1	40	–	–	–	78	53	36
2	10	–	–	20	4	9	7
3	–	12	–	–	–	–	3
4	30	–	–	–	13	9	10
5	–	12	–	10	–	3	5
6	–	6	–	10	–	3	3
7	–	25	–	–	–	–	7
8	–	–	–	10	–	3	2
9	–	–	–	10	–	3	2
10	–	6	–	–	–	–	2
11–15	10	31	–	10	–	3	12
Total	10	16	2	10	23	34	61

[1] Based on incisor cementum examination. Included collections of L. D. Mech and P. D. Karns; data on file U.S. Bureau of Sport Fisheries and Wildlife, Minneapolis, and Carlos Avery Research Center, Minnesota, respectively.
[2] Includes illegal kills, warden kills, and collections.
[3] Includes cases considered probably wolf predation.
[4] Includes some diseased animals killed by wardens. Diagnosis procedures follow Karns (1967).

year-old moose to be vulnerable to predation. One 2-year-old cow listed as a wolf kill when a wolf was observed feeding on its carcass had been observed for over a week by L. D. Mech (pers. comm.) during which time its behavior was symptomatic of nematodiasis. These wolf killed moose may be considered mortality attributable primarily to the nematode *Parelaphostrongylus tenuis* infestation which predisposed them to predation. Also, diseased animals may be products of unknown factors ultimately predisposing them to infestation, including the presence of white-tailed deer and abundant gastropods which host different stages of the parasite.

The relative proportion of deaths attributed to each mortality factor probably was not representative. Special searches for cases of disease and predation were being conducted in the area (Mech and Frenzel 1971, Karns 1967a), and may be overrepresented in the collection. However, the data, together with aerial classifications, did suggest that the major mortality factors operated upon younger age groups in the population and that life expectancy of a moose, once it reached 2 years of age, may be high until past 10 years of age. Similar mortality patterns were observed in the unhunted moose populations on Isle Royale (Mech 1966).

Natural mortality in the unexploited population was not concentrated at one season. Predation by wolves may be more or less continuous throughout the year on the study area. Moose occurred in an average of 30.3 percent of all wolf scats collected in spring, summer, and fall on the northern part of the study area (Frenzel 1974). Spring collections represented scats deposited since the previous fall. While 142 deer known or suspected to have been killed by wolves were collected during the winters of 1967–1969, only 6 moose were located that probably were wolf kills (Mech and Frenzel 1971). These data suggest that wolf predation on moose may be somewhat more common during the snow-free period.

While wolves were thought to kill moose on the Superior National Forest in the 1940's and the early 1950's, examination of 57 wolf stomachs revealed no evidence of moose (Stenlund 1955). Apparently, wolf predation on moose has increased in the study area, and may be related to an increase in moose populations. Moose constituted from 8 to 17 percent of the summer diet and less than 6 percent of the winter diet in Algonquin Park, Ontario (Pimlott et al. 1969), again suggesting that wolf predation on moose was more prevalent in summer when the alternative ungulate prey species is the white-tailed deer.

Mortality due to cerebrospinal nematodiasis was concentrated during January–April (Fenstermacher and Jellison 1933, Karns pers. comm.). Karns reported that 30 of 41 diseased moose were recovered during January–April similar to that recorded by Benson (1958) in Nova Scotia, and Lamson (1941, unpublished master's thesis, University of Maine, Orono, Maine) in Maine.

Winter mortality due to malnutrition might be expected to occur most frequently in late winter and early April, as Krefting (1951) suggested for the Isle Royale die-offs of the 1940's. However, some losses related to malnutrition apparently occur in midwinter on the study area, since the 2 calves found dead from this apparent cause were found in January and February.

Predation and disease appear more prevalent than malnutrition as natural mortality factors in this population, although poor nutritional status may predispose moose to other mortality factors. Predation may be more prevalent during summer, and disease and malnutrition during winter. Accidents, and drownings, probably most important in calves and yearlings, probably occur most frequently in early summer when calves are weakest and least experienced. All mortality appears concentrated on calves, yearlings, and the oldest animals.

Dead moose were not readily observed in this area because of the dense vegetation and the dispersed nature of the moose populations. Assuming a density of 0.8 moose/km^2, 10–26 percent net productivity, and a relatively stable population, then approximately 1 moose every 5–13 km^2 would disappear each year from all causes which would include an unknown amount of dispersal to other areas, as well as direct mortality.

FOOD HABITS

Monthly and Seasonal Trends

A summary of seasonal and yearlong browse use is presented in Table 9. A total of 26 feeding sites comprising 3,766 instances of use on 13 browse species was examined during June. Quaking aspen accounted for over 70 percent of the total, 7 times more than willows, the next most important plant. Because of its high relative abundance, the importance value of aspen was lower than its percentage occurrence in the diet. Collectively, upland willows (*Salix discolor, S. bebbiana, S. humilis*) were the only commonly used species with importance value rankings higher than recorded use rankings. This may imply that willows were more palatable than aspen.

Moose fed mainly on leaves during June. Use of twigs rarely occurred and appeared to be incidental to leaf stripping.

Aquatic vegetation may provide most of the moose diet in June, at least during some years. It was extremely difficult to locate evidence of feeding on land during June 1968, though moose tracks were common. This, plus the fact that feeding was primarily on aspen, suggested that aquatic habitats were more heavily used. In June 1969, more terrestrial feeding sites were found.

Evidence of plant species used by moose feeding in ponds and streams was obtained at 14 locations (Table 10) including 8 during June. Yellow pond lily *Nuphar variegatum* was most commonly eaten (4 locations), while wild rice *Zizania aquatica,* burreed *Sparganium angustifolium,* bladderwort *Utricularia vulgaris,* pondweeds *Potamogeton* spp., sedges *Carex* spp., and water milfoil *Myriophyllum* spp. were also observed to be used. Examination of favored moose feeding areas further indicated that yellow pond lily and wild rice (less widely distributed than the lily) were favored aquatic food plants.

Use of 14 browse species at 58 feeding sites, comprising 8,437 instances of use, was

TABLE 9.—SUMMARY OF BROWSE SPECIES AGGREGATE PERCENTAGE USE AND IMPORTANCE VALUES (IV) WITH RANKINGS FOR TOP 10 BROWSE SPECIES THROUGHOUT THE YEAR, OBTAINED BY EXAMINATION OF MOOSE FEEDING SITES IN NORTHEASTERN MINNESOTA

	Jun–Sep				Oct–Dec				Jan–Apr				Yearlong				
	Agg. % Use	Rank	IV	Rank	Agg. % Use	Rank	IV	Rank	Agg. % Use	Rank	IV	Rank	Agg. % Use	Rank	IV	Rank	Season of Highest Use
Balsam fir	–	–	–	–	1.6	9	.056	7	10.8	3	.103	4	4.8	7	.052	9	winter
Red maple	–	–	–	–	–	–	–	–	–	–	–	–	0.8	–	.009	–	winter
Mountain maple	6.1	5	.046	6	1.2	–	.023	–	5.2	7	.052	9	4.3	8	.043	10	summer
Alders	–	–	–	–	1.5	10	.046	10	–	–	–	–	2.1	–	.039	–	fall
Juneberries	1.6	9	.037	7	4.3	6	.049	8	5.0	8	.080	7	3.8	9	.058	7	winter
Yellow birch	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	winter
White birch	12.3	3	.133	4	2.6	8	.084	4	8.1	6	.083	6	7.7	5	.098	3	yearlong
Leatherleaf	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	winter
Beaked hazel	0.3	10	.008	10	15.5	3	.098	3	19.7	2	.132	2	12.6	3	.085	4	winter
Round-leaved dogwood	–	–	–	–	–	–	–	–	–	–	–	–	1.0	–	.008	–	winter
Red osier	2.4	8	.030	9	17.6	2	.143	2	8.3	5	.086	5	8.6	4	.078	6	fall
Bush honeysuckle	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.002	–	summer
Labrador tea	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	fall
Black spruce	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	winter
Jack pine	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	.008	–	fall, winter
Red pine, white pine	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	.004	–	winter
Balsam poplar	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.014	–	winter
Quaking aspen	32.1	1	.228	2	6.5	4	.065	4	10.6	4	.104	3	15.8	2	.133	2	summer
Fire cherry	10.9	4	.144	3	6.1	5	.074	5	3.2	10	.046	10	6.4	6	.084	5	summer
Chokecherry	–	–	–	–	–	–	–	–	–	–	–	–	1.2	–	.023	–	
Mountain ash	2.9	7	.055	5	3.6	7	.046	9	3.9	9	.058	8	3.5	10	.053	8	
Roses	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	fall
Raspberries	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	
Willows	26.2	2	.236	1	32.9	1	.237	1	20.6	1	.145	1	26.0	1	.200	1	yearlong
Red-berried elder	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	winter
White cedar	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	.001	–	winter

TABLE 10.—FREQUENCY OF USE OF VARIOUS AQUATIC PLANTS AT 14 SITES WHERE MOOSE WERE OBSERVED FEEDING

Number of Sites	1	2	1	2	2	2	1	1	1	1	14
Date	15 Aug	26 Jun	2 Jul	8 Jun	20 Jun	22 Jun	2 Jul	4 Jul	28 Jul	20 Aug	Totals
Species Used	67	68	68	69	69	69	69	69	69	69	
Pondweed	1	1	–	–	–	–	–	–	1	–	3
Yellow pond lily	–	2	1	1	–	1	1	–	–	–	6
Wild rice	–	–	–	1	2	–	–	–	–	–	3
Horsetail	–	–	–	–	–	–	–	–	–	1	1
Bladderwort	–	–	–	1	–	1	–	–	–	–	2
Sedge	–	–	–	1	–	–	–	–	–	–	1
Water milfoil	–	–	–	1	–	–	–	–	–	–	1
Burreed	–	–	–	–	1	1	–	–	–	1	3
Calla	–	–	–	–	–	–	1	1	1	–	3
Crowfoot	–	–	–	–	–	–	–	1	–	–	1

recorded in July and August. Upland willows, aspen, mountain maple, white birch, and pin cherry were the most frequently used plants. Importance values indicated that, in order of descending palatability, the preference was: willow, pin cherry, white birch, aspen, and mountain maple.

Both leaves and twigs were used, with a transition from predominantly leaves in July to both in August. Although each feeding site was examined for evidence of forb and grass use, herbaceous species appeared to contribute little to the diet of the moose, accounting for about 1 percent of the recorded plant use. Fireweed *Epilobium angustifolium* was the most commonly used forb.

Use of aquatic plants was recorded at 4 sites during July and at 2 sites in August (Table 10). Yellow pond lily, caltha *Caltha palustris,* pondweed, and crowfoot *Ranunculus septentrionalis* were used during July. Use of pondweed, burreed, and horsetail *Equisetum* spp. was recorded in August.

Data were obtained at 24 feeding sites totaling 5,008 instances of use in September and at 39 feeding sites totaling 7,208 instances of use in October. Upland willows increased in the diet, while aspen decreased during September. Upland willows, pin cherry, and white birch together comprised over 70 percent of the recorded use. Red osier *Cornus stolonifera,* green alder, and mountain ash became important items in the diet for the first time. Upland willows were again important in October, but red osier ranked second. Willows, red osier, and pin cherry combined received 81 percent of the use. Jackpine and red pine received limited use during the fall. Jackpine plants 1–2 m tall, commonly established along logging trails, often had a portion of the terminal leader browsed.

Thirty-one feeding sites comprising 7,637 instances of use were examined during November. Beaked hazel became the most common item in the diet, although willows retained the highest importance value because of more limited availability. Use of red osier declined, and pin cherry became unimportant. Balsam fir and red maple *Acer rubrum* were used for the first time during the fall–winter period, and use of jackpine increased slightly over October.

In December, 15 feeding sites were examined, totaling 3,733 instances of use. Willows were the most important food item, while beaked hazel, red osier, and aspen were commonly used. Use of balsam fir continued to increase and use of red osier continued to decrease. Juneberries, mountain ash, and chokecherry *Prunus virginiana* were eaten consistently but never in large amounts.

Trends in food habits reported for earlier winter continued through January, based on 9,657 instances of use at 34 feeding sites. Willows and beaked hazel together ac-

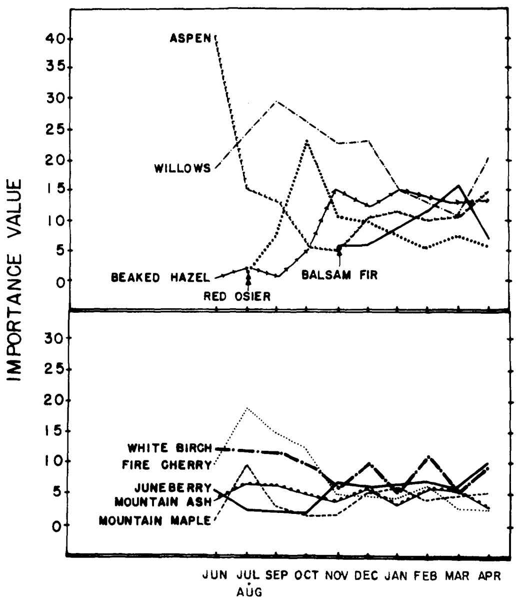

FIG. 4. Importance values of the 10 browse species most commonly found in the moose diet. The importance value is the sum of instances of use, aggregate abundance of species in all sites for period, plus frequency of occurrence in feeding sites for period divided by 3 and multiplied by 100.

counted for 42 percent of the diet, while red osier and aspen accounted for 20 percent. Juneberries, balsam fir, white birch, and mountain maple each contributed over 5 percent of the aggregate use.

The 49 feeding sites examined and 13,704 instances of use recorded in February indicated that beaked hazel, balsam fir, willows, aspen, and white birch were most important in the diet. Use of red osier continued to decline.

The March diet was represented by 28 feeding sites and 7,854 instances of use. Balsam fir, beaked hazel, and willows were the most commonly used items in order of importance and utilization. The April diet (14 feeding sites and 3,056 instances of use) contained less balsam fir. Beaked hazel and willows remained important.

Browse Preferences

Willows collectively were the most important plant overall, but received the greatest use from September through December (Fig. 4). The upland willows received more use than *Salix interior* or *S. pedicellaris*, which were characteristic of poorly drained sites (Table 11). Use of *S. bebbiana* probably was underrated in proportion to *S. discolor*. Also, both *S. discolor* and *S. bebbiana* were preferred over *S. humilis*, which was more easily distinguished than the others and hence recorded separately more often.

Utilization of quaking aspen, the most important species in June and second overall, declined through late summer, fall, and early winter, but increased again in midwinter. White birch, third in importance yearlong, remained relatively consistent in the diet throughout the year. Beaked hazel, fourth in importance, was most intensively used in midwinter. Pin cherry, important primarily in summer and early fall, and red osier, important in fall, ranked fifth and

TABLE 11.—UTILIZATION OF DIFFERENT WILLOW SPECIES THROUGH THE ANNUAL CYCLE, NORTHEASTERN MINNESOTA

	Jun–Sep		Oct–Dec		Jan–Apr		Yearlong	
Species	Agg. % Use	Imp. Val.	Agg. % Use	Imp. Val.	Agg. % Use	Imp. Val.	Agg. % Use	Imp. Val.
Salix discolor	12.2	.121	13.0	.062	9.2	.081	11.5	.088
Salix bebbiana	1.9	.019	0.5	.006	0.8	.008	1.1	.011
Salix pedicellaris	0.1	.001	–	–	–	–	0.1	.001
Salix interior	0.9	.012	–	–	–	–	0.3	.004
Salix humilus	2.2	.016	0.6	.011	0.3	.005	1.0	.011
Total willow identified	17.3	.159	14.1	.079	10.3	.094	14.0	.115
Total willow	26.2	.236	32.9	.237	20.6	.145	26.0	.200

TABLE 12.—SUMMARY OF WEIGHT OF FORAGE EATEN PER FEEDING SITE IN FALL AND WINTER, NORTHEASTERN MINNESOTA

				Oct–Dec			Jan–Apr		
Species	Mean Browsing Diam (cm)	Mean Oven-dry Wt. per Twig (g)	Mean Fresh Wt. (g)	% of Diet	Mean No. Twigs Eaten per Site[2]	Fresh Wt. of Twigs[3]	% of Diet	Mean No. Twigs Eaten per Site[2]	Fresh Wt. of Twigs[3]
Balsam fir	0.325	1.60	2.01	1.6	3.4	6.83	10.8	28.7	57.69
Mountain maple	0.337	0.74	0.79	1.2	2.5	1.98	5.2	13.8	10.90
Juneberries	0.316	0.95	0.95	4.3	9.1	8.55	5.0	13.3	12.64
White birch	0.305	0.57	1.26	2.6	5.5	6.93	8.1	21.5	27.09
Beaked hazel	0.295	0.60	0.76	15.5	32.9	25.00	19.7	52.4	39.82
Red osier	0.368	1.28	1.70	18.6	39.4	67.06	8.3	22.1	37.57
Quaking aspen	0.388	0.80	1.57	6.5	13.8	21.65	10.6	28.2	44.25
Pin cherry	0.297	1.05	1.32	6.1	12.9	16.98	3.2	8.5	11.19
Mountain ash	0.513	1.13	1.46	3.6	7.6	11.10	3.9	10.4	15.19
Willows	0.349	1.55	1.75	32.9	69.7	122.04	20.6	54.8	95.95
Other[1]	—	1.03	1.36	7.1	15.1	20.54	4.6	12.2	16.59
Mean use/site					212			266	
Total wt. eaten per site	(g)					308.76			368.88
	(lb)					0.68			0.81

[1] Mean of above species.
[2] Calculated by multiplying percentage in diet for species times mean instances of use per site.
[3] Calculated by multiplying number of twigs eaten per site times mean fresh weight per twig.

sixth, respectively. Juneberries and mountain ash, ranking seventh and eighth, occurred at low but constant levels in the diet yearlong. Balsam fir, ninth in importance, was almost entirely a winter forage. It became especially important in late winter. Mountain maple was used most commonly in late summer and again during the winter.

Browse preferences based on percentage occurrence in the diet by weight were similar to occurrence by number of twigs used during the October–December period (Table 12). Although willows also were the most important forage on the weight basis from January through April, beaked hazel decreased and balsam fir increased in importance as compared to twig use. The mean weight of a beaked hazel twig was 38 percent of the mean weight of a balsam fir twig. Juneberries and mountain maple also decreased in importance when compared on a twig weight rather than twig number basis.

Red osier probably was the only species upon which moose browsed individual twigs more than once on this area. The possibility of browsing individual twigs more than once would cause estimates of weight of forage taken per feeding site to be biased upward. Semenov-Tian-Shanskii (*In* Nasimovich 1955) concluded that moose browsed twigs of a single tree or bush 5 times as intensively during deep snow periods as during earlier periods of shallower snows.

Discussion of Food Habits

Seasonal and year-to-year changes in the food habits of moose on the study area appeared related to seasonal differences in palatability of certain species and availability as influenced by distribution, prior usage, snow depths, and general weather conditions. Use of some plants may also have been influenced by animal behavior. Increased use of red osier in fall occurred concomitantly with the reddening of stems, when starches decrease and sugar concentrations increase in the process of cold acclimation (Li et al. 1965). Many red osier plants were heavily used by late November and the decreased use of this species in winter may be related to prior heavy use

TABLE 13.—UTILIZATION OF 15 BROWSE SPECIES ON THE NORTHEASTERN MINNESOTA STUDY AREA AS MEASURED FROM 30 LINE INTERCEPT TRANSECTS IN MAY 1968, 1969, AND 1970

	Percentage of Leaders Used					
	1968		1969		1970	
Species	Mean	Range	Mean	Range	Mean	Range
Balsam fir	7	0–16	9	0–90	10	0–28
Red maple	–	–	34	–	1	–
Mountain maple	15	0–16	8	0–25	7	1–25
Green alder	3	1–6	1	0–4	1	0–10
Juneberries	38	0–58	9	0–22	21	0–90
White birch	36	0–70	7	0–33	9	0–25
Beaked hazel	12	0–30	13	0–41	17	0–50
Round-leaved dogwood	–	–	90	–	90	–
Red osier	75	0–90	35	0–90	66	0–90
Aspen	23	1–55	11	0–90	18	0–61
Fire cherry	30	0–90	16	0–90	13	0–70
Mountain ash	66	25–90	20	0–90	37	0–90
Willows	48	0–70	29	0–51	30	0–75
Red elder	43	12–98	28	0–98	22	1–38
Mean	33		22		25	

and to a decline in availability as snow cover increased.

Red pine and white pine were eaten primarily in local situations such as wintering areas, plantations containing large quantities of pine and minimal amounts of other forage, or areas exhibiting evidence of rutting activity.

Usage of green alder in early fall also may have been associated with prerutting activities of males. Over 77 percent of all antler rubbing sites were located on alders. This, together with low use during other seasons, suggested that fall usage reflected displacement feeding associated with prerutting behavior rather than preferences.

Food habits in January 1969, when deep, fluffy snows covered the ground, and January 1968, when little snow was present and the movements of moose were much less restricted, illustrated the influence of snow conditions on moose. Balsam fir was about 4 times more prevalent in the diet and species of lower palatability, including mountain maple, beaked hazel, and green alder, were more heavily used in 1969, the severe winter, than in January 1968. Data for January 1970 reflected winter severity and food habits intermediate to the extremes represented by 1968 and 1969. The March diet for all winters reflected the restriction of moose to dense conifer cover during the most severe snow conditions of the year. April diets were indicative of moderating conditions. Decreased usage of balsam fir at this time suggested that this species was primarily a forage of critical periods in late winter. Increased use of aspen in midwinter may be attributed to its height, which makes it more available than shorter shrubs during deep snow periods.

Utilization of aquatic plants by moose apparently varies considerably between areas in North America. Feeding on aquatics may start earlier, reach its highest intensity earlier, but last longer in northeastern Minnesota than farther north in Ontario. Our earliest record of aquatic feeding was 7 May 1969, while the latest was 29 September 1967. DeVos (1956) reported that substantial use of aquatic vegetation occurred in late June, July, and early August in Ontario. The earliest he observed aquatic feeding on St. Ignace Island was 4 June, and feeding in channels of Lake Superior was initiated a month later.

Use of aquatic vegetation may be correlated with its phenology. Yellow pond lily was favored prior to flowering or seed set. The phenology of this species varied considerably between years within individual ponds, especially in June and early July. If feeding on pond lily was influenced by its palatability, high water levels and cool water temperatures which retard development would allow more plants to remain palatable over longer periods of time. This would increase use of aquatic communities by moose and could explain the greater use of aquatics in June 1968, a month of higher than usual precipitation, than June 1969, when precipitation was about normal.

Browse Utilization and Condition

Utilization

Browse utilization levels varied inversely with winter severity. Utilization was highest in 1968, following a very mild winter, and lowest in 1969, after an extremely severe winter (Table 13). Lower use under severe conditions doubtlessly reflected the limited mobility of moose (Van Ballenberghe and Peek 1971) and concentration of use in local areas of dense conifer cover during periods of deep snow. Such areas were not sampled in utilization surveys. Presence of moose in open cover types for longer periods tended to increase utilization of plants generally across the area.

Utilization of individual species varied. Red osier consistently showed the greatest use, while mountain ash ranked second. Both were fed upon primarily during fall and early winter. Among the more commonly or widely distributed species, willows consistently received the highest use. Utilization of balsam fir tended to be restricted to specific trees, as reported by Bergerud and Manuel (1968).

Only 12 percent of all individually tagged plants were browsed each year of the 3-year period (Table 14); and only 3 percent had more than 50 percent of the current annual growth twigs browsed annually. Mountain ash, red osier, and the willows were utilized most intensively. Among tagged plants on which utilization was recorded for only 2 years, 37 percent were browsed in both years and 19 percent received use on more than 50 percent of the current year's twigs each year. Red osier was the most consistently browsed species.

Estimates of leader use may be converted to percentage utilization by weight on the basis of twig diameter–weight relationships (Stickney 1966). Twig diameters at the proximal end of the current year's growth and at the point of browsing were obtained for several browse species on the study area in March 1970 (Table 15). The mean diameter at the point of browsing averaged 111 percent of the basal diameter of current year's growth for all species (Peek et al. 1971), indicating that either more than the current year's growth was browsed or only the larger twigs were eaten. Since the current year's growth usually was completely taken, our estimates of utilization based on percentages of leaders used would appear to underestimate slightly the utilization by weight.

Plant Composition and Condition

The composition, coverage, and degree of hedging of browse plants in 2 areas of different moose density are presented in Table 16. Shrub composition did not change significantly during the 3-year period. Similarly, plant condition as measured by the percentages of plants in each hedging or form class did not change appreciably during the study.

Plant condition varied considerably by species and in relation to moose density. In general, plants of all species were most heavily hedged and in poorest condition in areas of highest moose density (Table 16). Over 50 percent of all red osier dogwood and mountain ash plants were severely hedged on transects in all areas on which they occurred, while over 25 percent of all willow and red osier plants were severely hedged in each case. Severe hedging also predominated among juneberries, white birch, aspen, and pin cherry in the area of highest moose density. Only hazel, mountain maple, and balsam fir were sufficiently represented on transects in the

TABLE 14.—FREQUENCY AND INTENSITY OF UTILIZATION OF INDIVIDUALLY TAGGED BROWSE PLANTS ON THE NORTHEASTERN MINNESOTA STUDY AREA OVER 2- OR 3-YEAR PERIODS

Observation Period		1968, 1969, 1970							1969, 1970					Form Class								
		Total No. Years Plant was Browsed				No. Years over 50% of Twigs Browsed			Total No. Years Plant was Browsed			No. Years over 50% of Twigs Browsed		Lightly hedged			Moderately hedged			Severely hedged		
Species	Total Plants Tagged	3	2	1	0	3	2	1	2	1	0	2	1	1968	1969	1970	1968	1969	1970	1968	1969	1970
Balsam fir	57	0	6	16	4	0	0	10	2	14	15	0	6	5	23	20	4	19	18	0	7	11
Mountain maple	54	4	8	15	16	0	3	6	2	6	3	1	1	25	13	10	20	31	32	5	8	6
Red maple	4	–	–	–	–	–	–	–	1	2	1	0	2	–	–	–	–	–	2	–	4	2
Green alder	70	0	0	11	33	0	0	0	4	2	20	0	0	46	62	63	2	8	6	0	0	0
Juneberries	70	0	6	10	4	0	3	4	14	17	19	6	18	6	9	5	8	34	34	2	27	28
White birch	52	4	16	19	4	0	3	20	1	7	1	0	1	20	4	0	26	32	40	5	16	8
Beaked hazel	107	7	21	22	25	0	6	15	13	10	9	4	10	58	38	24	16	57	43	3	12	9
Round-leaved dogwood	2	0	0	0	0	0	0	0	2	0	0	2	0	–	0	0	–	0	0	–	2	2
Red osier	51	14	9	7	3	9	10	10	14	4	0	14	4	10	2	2	22	12	12	5	37	35
Aspen	91	4	12	23	21	0	3	13	12	4	15	10	6	41	18	10	24	44	41	6	25	31
Fire cherry	34	1	5	10	4	0	2	5	4	6	4	4	2	9	5	1	13	20	27	0	9	4
Chokecherry	36	3	8	2	4	0	3	8	8	7	4	3	6	4	1	2	11	15	19	1	20	13
Mountain ash	31	5	12	10	1	2	9	13	–	3	–	–	2	2	0	0	15	2	8	9	29	28
Red elder	17	3	6	4	1	0	3	6	3	0	0	1	1	2	0	5	8	10	5	3	7	5
Willows	124	13	27	21	1	4	15	25	35	17	10	16	24	24	5	2	40	57	67	7	62	50
Sums	800	58	136	170	121	15	60	135	115	99	101	61	83	252	180	144	209	341	354	46	265	232

TABLE 15.—COMPARISON OF DIAMETER AT POINT OF BROWSING WITH DIAMETER OF CURRENT YEAR'S GROWTH, ISABELLA AREA, WINTER 1970

Species	Diameter of Proximal End Current Year's Growth (DCG) in mm		Diameter at Point of Browsing (DPB) by Moose		% DPB/DCG
	Mean	SD	Mean	SD	
Balsam fir	3.67	1.02	3.25	0.13	89
Mountain maple	3.05	0.65	3.37	0.16	110
Juneberries	2.37	0.525	3.16	0.38	133
White birch	2.44	0.616	3.05	0.03	125
Beaked hazel	2.55	0.571	2.95	0.09	116
Red osier	2.90	0.861	3.68	0.25	127
Fire cherry	2.84	0.939	2.97	0.09	105
Chokecherry	2.99	0.761	3.04	0.57	102
Aspen	3.13	1.13	3.88	0.15	124
Mountain ash	4.76	0.821	5.13	0.19	108
Willows	3.09	0.651	3.49	0.32	113

high-density area south of Isabella to be indicative of plant conditions in that area.

Forage Trends and Relationships

Moderately high moose densities and satisfactory calf production have been maintained for many years in Newfoundland on winter forage consisting primarily of white birch and balsam fir (Bergerud and Manuel 1968). If, as generally recognized by ungulate ecologists, the presence of a diversity of palatable forage plants is an indication of high-quality moose range, then most of the moose range in northeastern Minnesota may be considered prime habitat.

The lack of significant change in availability and condition of browse plants on the area during the study might be interpreted as indicative of relatively stable forage conditions for moose. Krefting (1951) found significant changes in availability of preferred moose browse on Isle Royale between 1945, 1948, and 1950 following an irruption when 7 species were utilized in excess of their regenerative ability. Peek (1963) recorded changes in the form class of willows from moderate to severely

TABLE 16.—COMPOSITION AND DEGREE OF HEDGING OF BROWSE PLANTS IN HIGH AND LOW MOOSE DENSITY AREAS AS DETERMINED FOR 30 33-M LINE INTERCEPT TRANSECTS. TOTAL LENGTH OF INTERCEPT ON HIGH-DENSITY AREAS WAS 178.1 M; ON LOW-DENSITY AREAS 206.5 M

Species	High Moose Density				Low Moose Density			
	% Composition[1]	Degree of Hedging (%)			% Composition[1]	Degree of Hedging (%)		
		Light	Moderate	Severe		Light	Moderate	Severe
Balsam fir	3.3	69	22	8	2.3	76	24	0
Mountain maple	21.1	15	70	15	13.9	30	58	12
Juneberries	0.6	0	42	58	5.2	23	38	38
White birch	2.6	7	34	59	1.5	33	43	24
Beaked hazel	46.0	33	49	18	30.5	69	30	1
Red osier	5.7	5	19	76	4.3	18	22	59
Aspen	2.4	6	23	71	3.7	31	34	35
Pin cherry	0.4	6	25	69	2.3	34	50	16
Mountain ash	0.8	6	33	61	1.0	4	27	69
Willows	3.2	5	31	64	7.8	11	52	37
Other species	13.7				27.4			

[1] Mean intercepts.

hedged condition between successive years of generally heavy utilization by moose on a southwestern Montana range. Subsequently, light use permitted improvements in plant form and condition in that area (Stevens 1966).

Levels of utilization in this study area would not appear excessive with respect to plant vigor and production for most species. Although the effects of browsing on shrubs varies with season of utilization, frequency and intensity, age of the plant, and extrinsic factors such as site moisture, soil fertility, weather conditions, and overstory crown closure, most have been shown to withstand removal of 50 percent or more of the current year's growth without detrimental effect. Aldous (1952), in a study of responses of key deer forage species to clipping on the Superior National Forest, found that mountain maple, white birch, beaked hazel, pin cherry, and willows were able to withstand clipping of 50 percent of current year's growth over a 6-year period with no detrimental effects on production. Only mountain ash and red osier could not withstand repeated heavy use. Aspen root suckers could recover or maintain themselves under browsing intensities of 65–70 percent in summer in northern Arizona (Julander 1937). Krefting (1951) determined that white birch could withstand heavier use than aspen root suckers on Isle Royale. In this case, aspen was intensively utilized in summer while birch was used more during the dormant period. Use of aspen in June would occur during the period of most rapid growth and lowest reserves, when plants are least capable of withstanding utilization. However, heavy browsing of aspen may stimulate sprouting of root suckers, which would offset to some extent the direct detrimental effect of browsing upon the plant.

Bergerud and Manuel (1968) reported that balsam fir trees 3 m tall were able to survive up to 12 years of browsing without dying under intensive utilization on the more fertile soil types in Newfoundland. If the above responses can be applied to plants on the study area, only red osier and mountain ash may have been utilized heavily and consistently enough to effect downward trends in availability. These species, although important in the food habits of moose, comprised only 10 percent of the major forage species on the area. Mountain ash was generally of limited distribution. Red osier was more common but still of limited distribution.

The feeding site examinations show that over 50 percent of the recorded yearlong use was on willow, aspen, and beaked hazel. In view of the variation in food habits found between areas, and in the case of Isle Royale (Krefting 1951) and southwestern Montana (Knowlton 1960, Peek 1963) between years on the same area, it would appear that even if mountain ash and red osier were entirely absent from the study area, moose populations may not be appreciably affected.

Cowan et al. (1950) considered mountain maple, red osier, and juneberries low quality foods on a British Columbia moose range based on protein content during the dormant period. In Minnesota, red osier was considered by Fashingbauer and Moyle (1963) to have no apparent serious nutrient deficiencies for white-tailed deer, while Magruder et al. (1957) indicated that protein concentration was near the minimum required by deer. The percentage of protein in red osier during September and October, when most heavily browsed by moose, was the lowest of the dormant period forage species. In view of this, it is doubtful if termination of heavy use of this species would lead to nutritional deficiencies in moose forage. Decreased utilization of red osier would likely be balanced by greater use of willows, aspen, and white birch, species which ranked higher than red osier in nutritional analysis.

All of this leads us to conclude that overbrowsing was not a problem on the area, at least during the period of study. We do not believe that in this area at least, heavy utilization of 1 or 2 browse species of limited distribution can or should be con-

TABLE 17.—PERCENTAGE OF MOOSE TRACKS RECORDED IN UPLAND, PLANTATION, AND LOWLAND HABITATS DOMINATED BY VARIOUS TREE SPECIES/PERCENTAGE OCCURRENCE OF TREE SPECIES AS DOMINANTS ALONG OBSERVATION ROUTES DURING SEASONAL PERIODS FROM EARLY SUMMER THROUGH EARLY WINTER. TOTAL NUMBERS OF TRACKS RECORDED FOR EACH SEASON ARE SHOWN IN PARENTHESES

Dominant Species	Early Summer	Mid-Summer	Late Summer	Prerut	Rut	Postrut	Early Winter
	(302)	(806)	(278)	(319)	(456)	(180)	(184)
Uplands	63	60	71	62	59	65	61
Balsam fir	41/43	38/42	18/40	35/42	43/40	38/48	44/40
White birch	19/20	20/19	26/19	25/19	22/22	21/15	30/19
Black spruce	3/3	7/3	18/4	11/4	7/3	16/3	4/3
Jackpine	3/3	4/3	4/5	4/5	3/5	6/2	0/5
Red pine/white pine	0/3	1/3	0/3	0/2	1/3	1/2	0/3
Quaking aspen	24/21	25/20	34/22	18/21	22/21	15/15	23/22
Other species	10/8	6/9	1/7	8/8	3/6	3/16	0/8
Plantations	12	10	6	10	8	12	11
Balsam fir	14/4	15/3	13/2	19/3	5/3	23/3	11/2
White birch	14/12	5/12	0/13	3/14	5/14	10/18	0/13
Black spruce	14/13	9/11	13/7	13/10	14/12	14/9	0/9
Jackpine	43/34	34/33	25/30	42/30	46/33	24/28	47/32
Red pine/white pine	5/24	16/26	0/29	3/24	5/26	24/24	0/27
Quaking aspen	11/13	17/13	25/29	13/18	19/12	5/16	42/16
Other species	0/1	5/1	25/1	6/1	5/1	0/1	0/1
Lowlands	25	29	23	28	32	23	28
Balsam fir	25/31	19/29	11/30	23/32	24/27	31/40	14/29
White birch	18/8	29/9	5/8	19/8	18/9	15/6	24/7
Black spruce	47/48	35/47	63/50	48/46	45/51	39/39	41/49
Jackpine	0/0	5/1	5/3	3/3	3/0	0/0	4/0
Red pine/white pine	0/3	0/4	0/0	0/0	1/3	0/2	0/4
Quaking aspen	1/2	9/2	13/2	4/2	5/2	10/1	16/2
Other species	8/8	3/0	3/7	2/10	3/8	5/12	2/8

sidered as indicative of overbrowsing. Moose apparently have alternative forage sources for all times of the year, many of which are capable of withstanding heavy utilization. The intensity of utilization which did occur on most of the 10 major browse species during the study was not severe enough to adversely affect more than a small percentage of the moose forage supply.

HABITAT USE

Seasonal Use of Terrestrial Habitats

Early Summer (June).—Upland, lowland, and plantation types were used approximately in proportion to their occurrence on the area during early summer (Table 17). Upland communities, collectively, received 63 percent of the recorded use for June while comprising 60 percent of the vegetation along track routes. Stands dominated by balsam fir, aspen, and/or white birch were used most frequently, and in approximate proportion to their occurrence. Usage of upland cover types was similar for 1968 and 1969. Stands 9–15 m tall, indicative of mature balsam fir and medium age aspen–birch (U.S. Forest Service 1965), were utilized more frequently than stands of other height classes (Table 18). Although stands with 124–988 trees/ha received the greatest usage among density classifications (Fig. 5), those with less than 124 trees/ha received greater than expected usage based on relative occurrence along routes. This, together with an apparent negative preference for densely stocked stands (over 988 trees/ha) suggested selection for more open, cutover areas which commonly contained

TABLE 18.—PERCENTAGES OF MOOSE TRACKS RECORDED IN HEIGHT CLASSES OF THE FOLLOWING: (1) DECIDUOUS AND CONIFEROUS TREES OF SIMILAR HEIGHT BUT LESS THAN 9 M TALL; (2) DECIDUOUS AND CONIFEROUS TREES DISSIMILAR IN HEIGHT BETWEEN 9 AND 15 M TALL; (3) DECIDUOUS AND CONIFEROUS TREES OF SIMILAR HEIGHT, 9 TO 15 M TALL; (4) DECIDUOUS AND CONIFEROUS TREES OF DISSIMILAR HEIGHT, 1 COMPONENT OVER 15 M TALL/AVAILABILITY OF EACH CATEGORY ALONG OBSERVATION ROUTES DURING SEASONAL PERIODS FROM EARLY SUMMER THROUGH EARLY WINTER

Seasonal Period	Height Class	Lowlands	Plantations	Uplands	All Types
Early summer	1	36/28	100/77	13/9	27/19
	2	14/6	0/8	8/6	9/6
	3	45/57	0/8	42/38	38/37
	4	5/9	0/4	35/47	25/38
Midsummer	1	39/25	87/53	9/8	23/15
	2	17/4	3/6	4/6	8/6
	3	30/58	3/14	33/40	30/41
	4	15/13	6/27	53/45	39/39
Late summer	1	18/27	57/45	5/6	14/11
	2	24/3	14/0	7/46	12/4
	3	41/51	0/0	23/39	26/39
	4	18/19	29/55	64/9	48/46
Prerut	1	21/20	80/51	1/9	13/13
	2	3/4	0/9	8/7	6/6
	3	58/61	20/13	42/42	44/43
	4	19/14	0/26	48/42	37/37
Rut	1	17/26	83/54	5/11	14/17
	2	19/7	6/5	12/7	13/7
	3	38/54	11/13	30/37	31/37
	4	25/14	0/28	53/46	42/39
Postrut	1	18/21	55/53	10/5	19/11
	2	18/5	18/7	15/6	17/6
	3	32/38	9/15	23/62	24/55
	4	32/36	18/25	51/27	40/28
Early winter	1	38/25	100/51	22/8	34/15
	2	13/3	0/6	6/6	6/6
	3	38/58	0/15	32/43	29/42

white birch, aspen, and balsam fir as remnants after logging.

Lowland habitats ranked second in usage during June, receiving one-fourth of the recorded usage (Table 17). Stands dominated by black spruce and balsam fir were utilized most intensively, but only in proportion to their occurrence along routes (Table 17). Stands dominated by white birch received greater than expected usage. The only difference in usage of lowland communities between years was slightly greater utilization of balsam fir stands in 1969 and black spruce stands in 1968. Again, more open stands (Fig. 6) with shorter and perhaps younger trees (Table 18) appeared to be preferred.

Plantations comprised 11 percent of the vegetation along routes and accounted for 12 percent of the tracks recorded in June (Table 17). Those dominated by jackpine less than 10 m tall (Table 18) and having fewer than 124 trees/ha (Fig. 7) were most frequently used.

Midsummer (1 July–15 August).—Upland habitats continued to receive the greatest total use during midsummer, though lowlands were used to a greater extent than expected.

Among upland communities, only moderately stocked aspen or white birch stands received greater usage than expected on the basis of relative occurrence (Table 17, Fig.

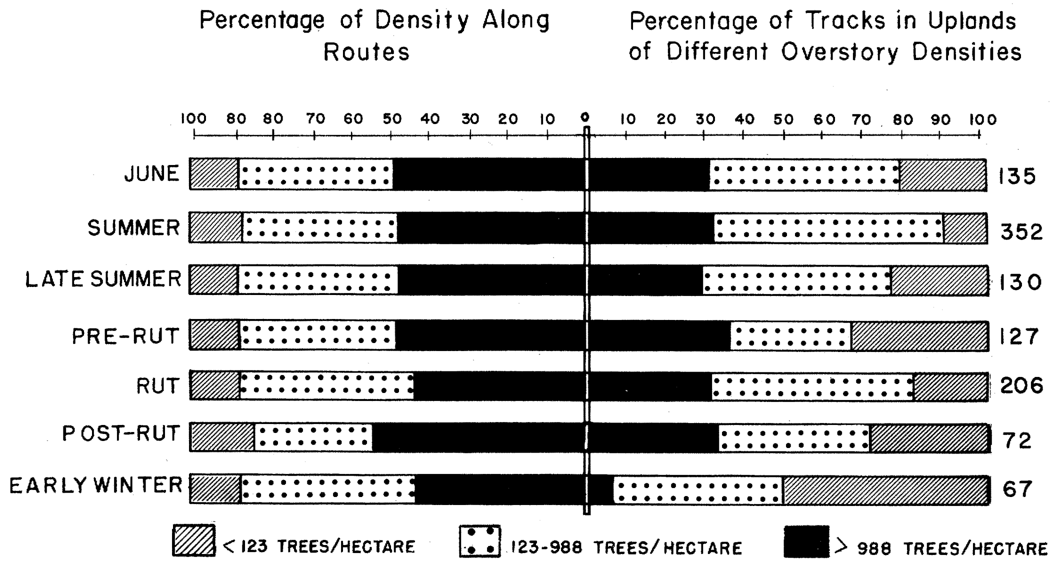

FIG. 5. Percentages of tracks in uplands of different overstory vegetational density, and percentage occurrence of each density along observation routes for 7 time periods. Figures at ends of bars indicate numbers of tracks recorded.

5). Stands dominated by balsam fir appeared to be avoided, while percentages of total tracks occurring in spruce–fir and aspen–birch were similar.

Stands dominated by black spruce or balsam fir constituted 71 percent of the vegetation and accounted for slightly over half the total tracks in lowlands (Table 17),

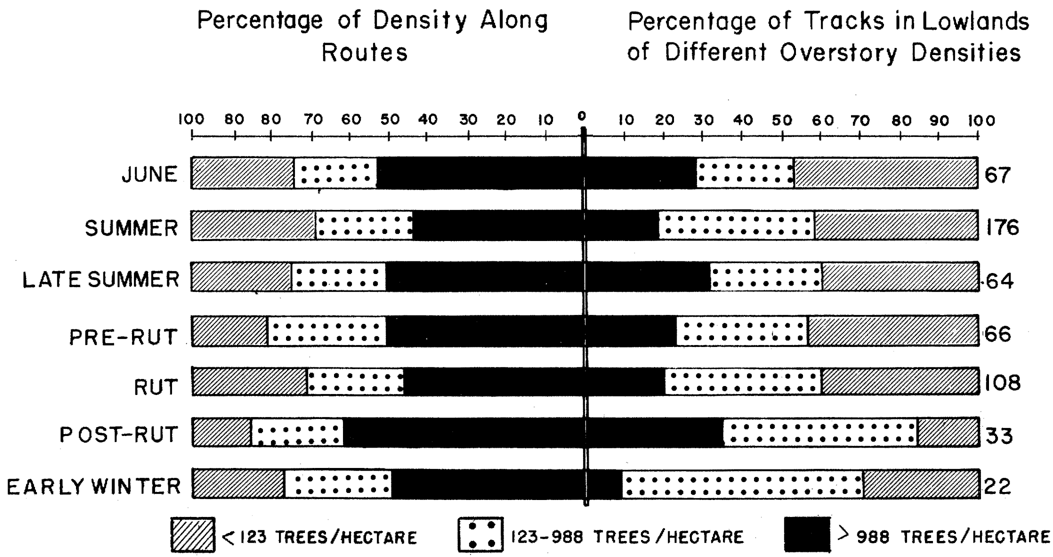

FIG. 6. Percentages of tracks in lowlands of different overstory vegetational density, and percentage occurrence of each density along observation routes for 7 time periods. Figures at ends of bars indicate numbers of tracks recorded.

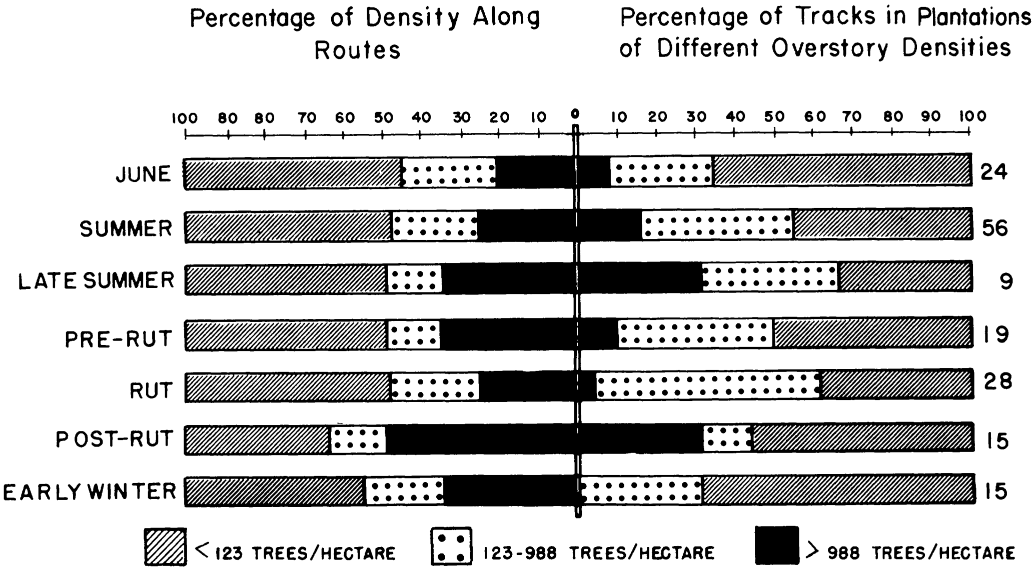

FIG. 7. Percentages of tracks in plantations of different overstory vegetational density, and percentage occurrence of each density along observation routes for 7 time periods. Figures at ends of bars indicate numbers of tracks recorded.

with the relative proportion of this use in stands dominated by each species varying only slightly between years. Stands dominated by deciduous trees, especially white birch, received greater usage than expected.

Use of poorly stocked plantations (Fig. 7) and which were dominated by nonplanted species, especially aspen, was greater than expected (Table 17).

Usage of moderately stocked stands in all types generally increased from June, indicating a shift from the most open areas. Extremely dense stands were avoided. A definite preference for taller stands was apparent on uplands (Table 18).

Late Summer (15 August–7 September).— The relatively fewer animal and track observations during this time suggested that movement decreased as compared with early and midsummer (Table 19). As in midsummer, use of lowland habitats was greater than expected, while the upland communities, combined, still received the greatest total use. Tracks were observed less frequently than expected in plantations. Use of moderately to sparsely stocked stands was also more than expected, suggesting a return of moose to more open cover (Figs. 5–7). This may have been associated with the initiation of prerutting activity in early September. In lowlands, communities dominated by black spruce and aspen received both the greatest and proportionately greater than expected use (Table 17). Neither stand density nor tree height appeared influential in use of lowland cover types (Fig. 6, Table 18).

Plantations dominated by aspen, balsam fir, and black spruce, indicative of more mesic sites, were used in preference to other plantations. No selection for stands of one density over another occurred (Fig. 7). Most plantations were less than 10 m tall, having been planted less than 20 years previously, so prevalent use of stands of lower height classes was of no comparative significance (Table 18).

Stands dominated by aspen or white birch accounted for 60 percent of the total track observations in the upland types (Table 17). This was proportionately greater usage than occurrence along the routes. Spruce and/or fir stands received 36 percent of the observed use, or less than expected on the basis of occurrence. Less

TABLE 19.—MOOSE ACTIVITY AS DETERMINED FROM OBSERVATIONS OF MOOSE IN THE STUDY AREA, AND OBSERVATIONS OF MOOSE TRACKS ALONG 3 ROUTES WITHIN THE HIGHEST DENSITY RANGE INSIDE THE BOUNDARY WATERS CANOE AREA, JUNE THROUGH OCTOBER, ALL YEARS' DATA COMBINED

Time Period	Total Mileage	Total Tracks Seen	Tracks per Mile	Total Moose Observed
Jun	69.0	87	1.26	32
Jul–15 Aug	156.7	196	1.25	35
15 Aug–7 Sep	66.5	49	0.73	6
8 Sep–31 Oct	208.4	215	1.03	49

TABLE 20.—PERCENTAGE OF OCCURRENCE OF ANTLER RUBBING BY MOOSE ON 6 WOODY SPECIES IN SEPTEMBER 1968 AND 1969. TOTAL OBSERVED IN PARENTHESES

Woody Species	1968	1969
	(36)	(39)
Alders	78	77
Willows	11	15
Jackpine	3	3
Quaking aspen	5	0
Balsam poplar	3	3
White birch	0	3

densely stocked stands were preferred over the most densely stocked stands (Fig. 5). A significant preference for the taller stands was also evident (Table 18). A radio-marked cow moose was most frequently observed in an upland aspen–white birch stand on the study area from 24 July to 22 August 1969 (Van Ballenberghe and Peek 1971).

Prerutting Period (7–21 September).—Observations of rutting pits, antler rubbing sites, and general moose activity along the roads increased significantly during the second and third weeks of September (Table 19). In the Jackson Hole, Wyoming, area both yearling and adult males began to remove velvet as early as 8 September (Houston 1968), while Dodds (1958) reported that breeding apparently began 9 September in Newfoundland and coincided with a shift in locations of groups from feeding areas to open burn areas of poor browse. In British Columbia, Edwards and Ritcey (1958) reported that most bulls were actively seeking cows by mid-September. Although prerutting activity on the study area may have started somewhat earlier than 8 September, activity along the routes and indications of prerutting behavior were not generally apparent until then. The earliest observation of a bull with velvet free antlers on the study area was on 15 September 1969. Little rutting activity was observed by Markgren (1969) in Sweden until the antlers were rubbed free of velvet.

Lowland communities received greater than expected usage during this period, averaging 28 percent of the track observations over 3 years (Table 17). Black spruce and balsam fir stands combined received the greatest use but only proportional to their occurrence within lowlands (Table 17). No preference was indicated for any tree height category (Table 18), but the least dense stands were most often used (Fig. 6).

Plantations accounted for 10 percent of the observed tracks during the prerutting period (Table 17). Jackpine plantings, sparsely stocked and under 10 m tall, received the major share of the use (Fig. 7, Table 18). Such stands were typical of the most xeric sites planted in the area.

Upland communities received the greatest use during the prerut, but in proportion to their occurrence (Table 17). No preference for coniferous or deciduous cover was evident. A preference for the most open stands was evident (Fig. 5).

Observations of woody species used for antler rubbing sites showed a preference for speckled alder which commonly occurs in lowland communities (Table 20). This indicated that much of the prerutting activity among males may be centered in lowland communities, as observed in southwestern Montana (Peek 1962), and that the preference for lowlands during this period may be attributable to this behavioral characteristic.

Rutting Period (22 September–14 October).—We consider the principal rutting period to be the last week of September and the first week of October. The main moose rut occurred during this period in Alaska (Rausch 1959, unpublished master's thesis, University of Alaska, College, Alaska), Ontario (Simkin 1965), British Columbia (Edwards and Ritcey 1958), Montana (Peek 1962), and Sweden (Markgren 1969).

Lowland communities were used proportionately more than expected, but no preference for one cover type over another was evident (Table 17). Balsam fir and black spruce stands received a majority of the recorded use. Preference for the moderately stocked (Fig. 6) taller stands was evident. Minor differences between years were not significant.

Plantations were used less frequently than expected during the rut (Table 17). Since vegetation in most plantations was low, these areas may lack suitable cover for rutting activities, as contrasted to prerutting activity.

Upland communities received the greatest total use during the rut, but this usage was only in proportion to occurrence (Fig. 5). Taller, moderately stocked stands, more dense than those used during prerut, were used most commonly (Table 18, Fig. 5). No selection for or against one stand type over another was evident.

An important behavioral pattern of moose during breeding season consists of pawing a rutting pit (Peterson 1955). Rutting pits were often observed in softer, deeper soils in and adjacent to lowlands, suggesting that breeding behavior may be centered on the more mesic sites in the study area.

Postrut Period (5 October–14 November).—During the postrut period, bulls were found in large groups (Peek et al. 1974). Males were still aggressive, as indicated by track aggregations and shredded vegetation along the routes.

Lowlands, plantations, and uplands were used in proportion to their occurrence along the routes with no apparent selection for one stand type or height being apparent (Tables 17, 18). As during the prerutting period, a preference for the most open stands was apparent (Fig. 6).

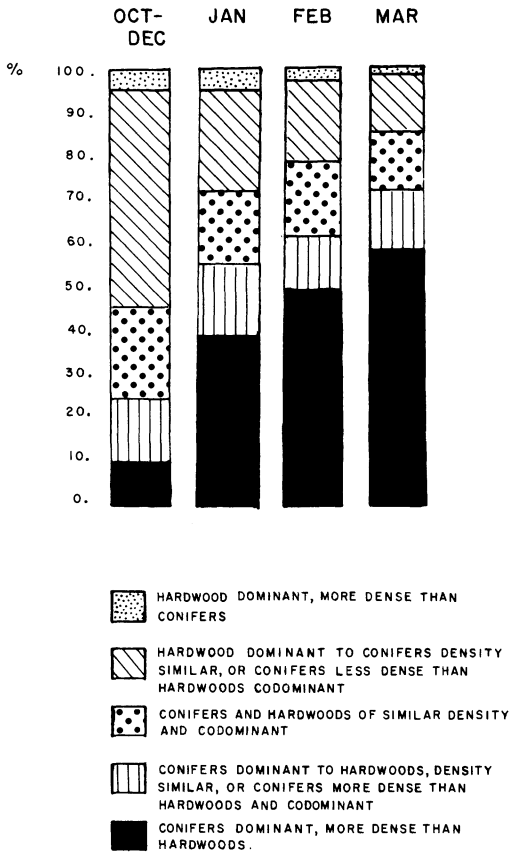

FIG. 8. Aerial observations of moose and moose track locations according to overstory density and relative abundance of coniferous and deciduous cover, October–March, all years' data combined.

Aerial observations provided supporting evidence of the preference for more open cover types during late October and early November. These data also suggested a preference for aspen–birch stands, at least during mornings. Most aerial observations were of feeding or moving animals, suggesting that deciduous stands may have been preferred for feeding and postrutting activities while coniferous cover types were used for resting.

Early Winter (15 November–31 December).—Although early winter was consid-

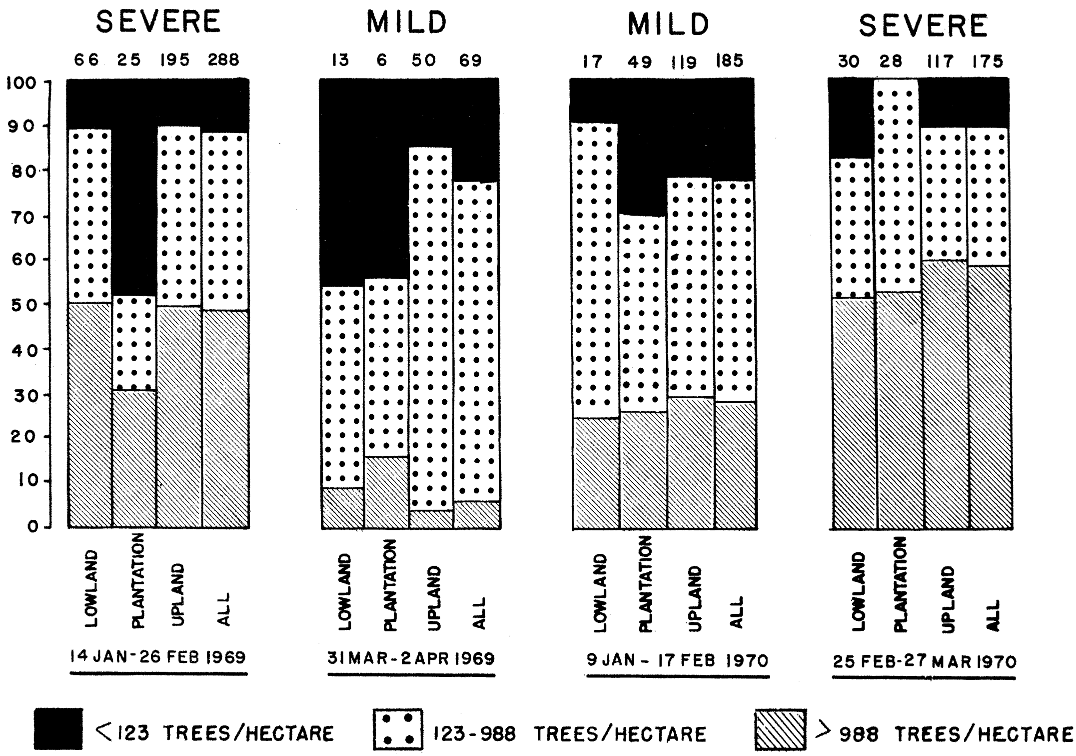

FIG. 9. Locations of moose tracks in midwinter 1969 and 1970 according to overstory density, as obtained by following trails on snowshoes. Figures at tops of bars indicate numbers of tracks recorded.

ered to extend from mid-November through December, data for the first 2 weeks of January 1968, a period of exceptionally mild weather, were also included. Utilization of upland, lowland, and plantation types was proportional to their occurrence (Table 17). Uplands accounted for 60 percent of the total track observations. A preference for the more open stands, and avoidance of the most dense stands, was evident (Fig. 5).

Aspen and white birch stands in uplands and lowlands were preferred (Table 17). Plantations dominated by aspen, jackpine, and balsam fir were commonly used. The most clear preference for open deciduous stands of any seasonal period existed at this time (Figs. 5, 7). Also, the lower stands were selected in greater proportion than according to occurrence (Table 18).

Midwinter (January–April).—All data for this period were obtained by aerial observation and tracking moose on snowshoes. Aerial surveys showed that moose shifted into denser cover dominated by conifer (Fig. 8) as snow depths and hardness increased. Track data afforded comparisons in habitat use between the exceptionally deep snow period in January–March 1969 and the milder periods of early April 1969 and January–February 1970 with a more typical period in March 1970.

Tracking data indicated selection for upland over lowland types in midwinter (Fig. 9). Upland spruce–fir stands were used most often during severe winter periods (Table 21) while stands dominated by aspen were used most when conditions were moderate. Also, shifts from the denser cover to more open cover occurred when weather

TABLE 21.—PERCENTAGES OF MOOSE TRACKS WITHIN UPLANDS, PLANTATIONS, AND LOWLANDS ACCORDING TO DOMINANT OVERSTORY SPECIES DURING THE DEEP SNOW AND MILDER PERIODS OF THE 1969 AND 1970 WINTERS. NUMBERS OF TRACKS OBSERVED ARE IN PARENTHESES

Major Overstory Species	14 Jan–26 Feb 1969			25 Feb–27 Mar 1970			Both Winters		
	Lowland	Plantation	Upland	Lowland	Plantation	Upland	Lowland	Plantation	Upland
Severe Winter Periods									
	(81)	(38)	(258)	(36)	(44)	(136)	(117)	(82)	(394)
Balsam fir	23	0	39	33	0	56	26	0	45
White birch	12	18	9	14	2	0	13	10	6
Black spruce	46	18	26	39	7	13	44	12	21
Jackpine	6	24	7	0	59	0	4	43	5
Red pine/white pine	2	29	4	0	25	0	2	27	3
Quaking aspen	2	5	14	11	7	21	5	6	16
Other species	7	5	2	3	0	10	6	2	4

Major Overstory Species	31 Mar–4 Apr 1969			9 Jan–17 Feb 1970			Both Winters		
	Lowland	Plantation	Upland	Lowland	Plantation	Upland	Lowland	Plantation	Upland
Mild Winter Periods									
	(15)	(8)	(69)	(19)	(65)	(156)	(34)	(73)	(22)
Balsam fir	27	0	10	47	8	38	38	7	30
White birch	13	0	26	0	6	10	6	5	15
Black spruce	53	0	16	37	6	12	44	5	13
Jackpine	0	13	4	5	22	7	3	21	6
Red pine/white pine	0	63	0	0	15	4	0	21	3
Quaking aspen	7	25	43	11	42	27	9	40	32
Other species	0	0	0	0	2	3	0	1	2

was less severe. The tallest stands were preferred for midwinter use (Table 22).

Plantation use was greater during milder periods than severe periods (Table 21). Plantations dominated by pines received most use during severe winters, while those dominated by aspen received equal use under moderate conditions.

Lowlands received more use during severe winter periods than during milder periods (Table 21). Stands dominated by black spruce and balsam fir were used most often during both periods.

During midwinter, moose beds were most common in the densest cover (Table 23). No difference in selection of cover density between bed locations and track locations occurred during the severe parts of either winter, but when conditions moderated, beds occurred in more dense cover than did tracks. Since no difference in track or bed locations was apparent in late 1970 when snow depths were less than 76 cm but crusts were quite hard in open areas, indications were that crusting rather than depth determined habitat selection under those conditions.

During the critical portion of the 1969 winter, a yearling female spent 28 days in about 8 ha of dense balsam fir, and an adult female spent 25 days in a 2.43-ha area. Both animals moved to more open deciduous dominated stands under ameliorating conditions (Van Ballenberghe and Peek 1971). Thus, aerial observations, radio-marked moose relocations, and tracking data support each other in patterns of habitat selection described for midwinter.

Use of Aquatic Habitats

Use of aquatic areas and communities by moose may be important where suitable aquatic habitats occur (Peterson 1955), but may not be important in some areas which contain relatively high populations (Telfer 1967). Observations in northeastern Minne-

TABLE 22.—PERCENTAGES OF MOOSE TRACKS IN MIDWINTER 1969 AND 1970 ACCORDING TO OVERSTORY HEIGHT CATEGORIES DESCRIBED IN TABLE 20. NUMBERS OF TRACKS OBSERVED ARE IN PARENTHESES

Time Period	Habitat Type	Height Category 1	2	3	4
14 Jan–	Lowland	12	10	29	49
26 Feb 1969	Plantation	83	0	4	13
(219)	Upland	3	6	26	63
	All	13	6	25	55
31 Mar–	Lowland	50	0	17	33
2 Apr 1969	Plantation	40	0	60	0
(67)	Upland	24	2	30	44
	All	30	1	30	39
9 Jan–	Lowland	30	8	54	8
17 Feb 1970	Plantation	37	6	37	20
(181)	Upland	12	7	25	56
	All	20	7	30	43
25 Feb–	Lowland	29	0	29	41
27 Mar 1970	Plantation	13	9	78	0
(155)	Upland	0	0	13	87
	All	5	1	25	69
All periods	Lowland	24	6	31	39
	Plantation	42	5	40	13
(622)	Upland	7	4	23	65
	All	15	5	27	53

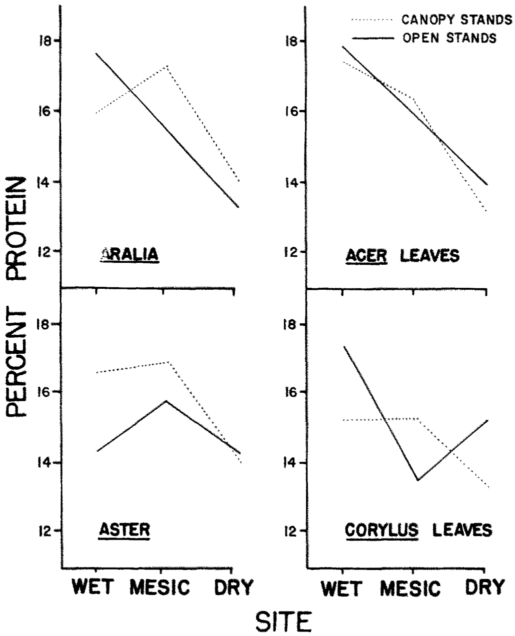

FIG. 10. Mean protein levels based on 9 collections from 19 July to 29 September 1971 and 29 May to 25 June 1972 in Lake County, Minnesota, as related to overstory canopy coverage and available soil moisture.

sota during the summer of 1967 indicated that moose used aquatic habitats rather extensively, feeding on both emergent and submergent vegetation. Because of this, specific efforts were made to evaluate the pattern and extent of use of waters during the summers of 1968 and 1969.

Heaviest use of aquatic areas occurred in early summer (Table 24), decreased in mid- and late summer, and increased again in early fall. Observations from the ground or canoe corroborated the trend in use as observed from the air. Moose were observed at a lake from 21 May through 7 July 1968. In 1969, moose were seen on 11 of 13 visits to the lake in June, 3 of 10 occasions in July, and 2 of 6 in August. General observations in lakes and streams across the study area corroborated the more systematic efforts. Use of aquatic areas by moose decreased as a majority of the yellow pond lilies were flowering and wild rice was beginning to emerge from the water surface.

NUTRIENT CONTENT OF COMMON UNDERSTORY SPECIES

Characteristics of stands in which shrub nutrient determinations were made are presented in Table 25. All stands over 10 years old were virtually closed canopies, ranging from 74 to 98 percent. Shrub understories were generally better developed in aspen than in jackpine stands. The balsam fir stand exhibited the densest canopy and lowest understory stem density and height of all forested stands sampled. The sodded opening was least productive of stands without overstory canopies.

Nutrient components were positively correlated with available soil moisture. Protein percentages were significantly greater for all species on wet or mesic sites than on dry sites (Table 26). Ash content was significantly greater on wet or mesic sites than on dry sites for all species except beaked hazel and mountain maple twigs. Ether extract and ADF levels showed no

TABLE 23.—NUMBERS OF MOOSE BEDS ACCORDING TO VEGETATION DENSITY, HEIGHT, AND SPECIES, MIDWINTER 1969 AND 1970. BEDS ADJACENT TO MORE THAN 1 SPECIES OMITTED IN THE LISTINGS UNDER SPECIES

	Upland	Plantation	Lowland	All
DENSITY				
Trees less than 3 m apart	82	15	16	113
Trees 3–9 m apart	29	6	3	38
Trees over 9 m apart	5	1	1	7
Totals	116	22	20	158
SPECIES				
Adjacent to balsam fir	70	1	12	83
Adjacent to black spruce	11	1	6	18
Adjacent to other conifer	5	7	1	13
Adjacent to deciduous species	7	0	0	7
Totals	93	9	19	121
HEIGHT				
Canopy even, less than 9 m	1	8	1	10
Canopy uneven, less than 15 m	8	5	1	14
Canopy even, 9–15 m	27	6	11	44
Canopy even or uneven, one component over 15 m	79	2	9	90
Totals	115	21	22	158

clear trends. Phosphorus content in plants from wet or mesic sites was significantly greater than from plants on dry sites.

Crafts (1968) and Kozlowski (1964) reported changes in plant metabolism attributed to water stress and may reflect observed changes in nutrient levels. In herbs, water deficit may decrease photosynthesis by closing stomata which in turn reduces carbon dioxide assimilation. This results in reduced enzyme activity, dehydration of cuticle and cell membrane, causing leaves to become thick and leathery with reduction in area and cell size (Kramer 1969), plus reduction in absorption and translocation of minerals (Crafts 1968). Water-stressed trees may show decreased growth and respiration (Kramer 1969). Lower protein levels due to water deficit may also be due in part to protein breakdown during wilting (Thompson and Morris 1966) and to decreased protein and amino acid synthesis as a result of lower photosynthetic and respiration levels (Gates 1968, Naylor 1972).

Average protein content during the growing season of plants sampled on dry sites generally was less for stands with tree overstory canopies than for open stands (Fig. 10). Similarly, protein content of wild sarsaparilla, mountain maple leaves, and beaked hazel leaves was greater for wet open stands than wet canopied stands. Average growing season ADF percentages behaved similarly on wet, mesic, and dry sites in open and canopied stands (Fig. 11). The variability in nutrient levels of shrubs and herbs associated with canopy coverage may be due in part to the individual response by each species to the interaction of overstory canopy coverage and available soil moisture. Beaked hazel was the only species with higher protein and lower ADF percentages in wet open sites than wet canopied sites. Hsuing (1951, unpublished doctoral dissertation, University of Minnesota, St. Paul, Minnesota) observed that beaked hazel was found in a wide range of habitats and responded best to high light intensities of open areas.

Nutrient composition was less influenced by overstory species composition and age than available soil moisture and canopy coverage. Protein percentages were greater

TABLE 24.—AERIAL OBSERVATIONS OF MOOSE ALONG A WATER ROUTE CONSISTING OF 27 LAKES AND 166 KM OF STREAM FROM JUNE TO SEPTEMBER 1968 AND 1969

Time Period	Number Routes Run 1968	Number Routes Run 1969	Number of Moose Seen 1968	Number of Moose Seen 1969	Moose Seen per Route 1968	Moose Seen per Route 1969
1 Jun–15 Jul	2	4	36	31	18.0	7.8
16 Jul–31 Aug	5	8	10	28	2.0	3.5
1–30 Sep	2	3	9	31	4.5	10.3

for all species in quaking aspen stands than in jackpine stands, with large-leaf aster, bush honeysuckle, and beaked hazel leaves significantly greater (Table 27). Ether extract content showed no trend. There was no significant difference in ether extract or NFE content between quaking aspen and jackpine stands less than 25 years old or greater than 25 years old (Table 28). Only wild sarsaparilla and mountain maple leaves had significantly higher protein levels in stands less than 25 years old. Cook and Harris (1950) concluded that soil moisture was important in determining nutrient content of native grasses in Utah. Cowan et al. (1950), in British Columbia, reported that with forest maturity, quality and quantity of palatable moose browse declined. Total

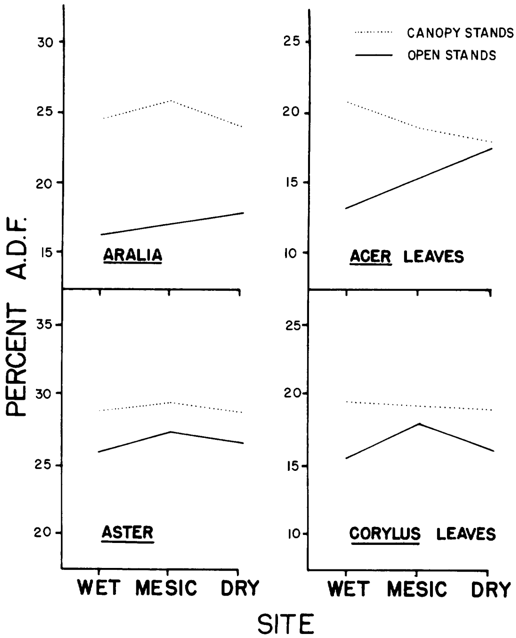

FIG. 11. Mean acid detergent fiber levels based on 6 collections from 19 July to 29 September 1971 and 29 May to 25 June 1972 in Lake County, Minnesota, as related to overstory canopy coverage and available soil moisture.

height of shrubs increased and density of shrubs decreased with forest maturity in Lake County (Table 25), but plants in mature stands on wet or mesic sites were of

TABLE 25.—OVERSTORY AGE, AVAILABLE SOIL MOISTURE, AND QUANTITATIVE VEGETATION CHARACTERISTICS OF 13 STANDS SAMPLED FOR NUTRIENT CONTENT FROM JULY 1971 TO JUNE 1972 IN LAKE COUNTY, MINNESOTA. THE WILDFIRE AND SLASH BURNS OCCURRED IN SPRING OF 1971

	OVERSTORY				UNDERSTORY			
Stand	Age (years)	Density (stems/ha)	Basal Area (m^2/ha)	Canopy Closure (%)	Density (stems/ha)	Average Height (m)	Available Soil Moisture	Soil Category
Quaking aspen	15	3,342	13	88	69,435	1.3	8.7	Mesic
Quaking aspen	22	2,443	18	94	34,594	1.3	11.4	Mesic
Quaking aspen	54	981	35	93	38,548	1.6	9.0	Mesic
Quaking aspen	80	1,827	62	98	52,385	1.7	6.1	Dry
Jackpine	23	1,451	22	86	32,247	1.0	12.7	Wet
Jackpine	53	1,093	36	95	39,289	1.5	8.7	Mesic
Jackpine	93	1,189	45	74	21,621	1.4	4.8	Dry
Red pine	80	496	28	81	53,620	1.2	7.4	Dry
Balsam fir	40	2,690	40	98	13,467	0.7	15.6	Wet
Opening	—	—	—	—	31,134	0.5	12.2	Wet
Pine plantation	9	—	—	—	117,001	1.4	8.7	Mesic
Wildfire burn	—	—	—	—	136,028	0.6	14.0	Wet
Slash burn	—	—	—	—	73,265	0.7	6.2	Dry

TABLE 26.—AVERAGE PERCENTAGE NUTRIENT CONTENT OF 5 SPECIES COLLECTED ON WET, MESIC, AND DRY SITES IN LAKE COUNTY, MINNESOTA, FROM JULY 1971 TO JUNE 1972. MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 25 COLLECTIONS, 19 JULY 1971–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER AND NITROGEN FREE EXTRACT MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 15 COLLECTIONS. OTHER MEANS ARE AVERAGES OF 9 COLLECTIONS, 19 JULY–29 SEPTEMBER 1971 AND 29 MAY–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER AND NITROGEN FREE EXTRACT MEANS ARE AVERAGES OF 6 COLLECTIONS

Nutrient	Site	Large-Leaf Aster	Wild Sarsaparilla	Bush Honeysuckle	Beaked Hazel leaves	Mountain Maple leaves	Beaked Hazel twigs	Mountain Maple twigs
Ether extract	Wet	4.3 *ab*[1]	2.9 *b*	4.4	2.8	4.2	2.8	2.5
	Mesic	3.6 *b*	3.8 *a*	3.9	2.9	4.9	2.6	3.4
	Dry	4.6 *a*	3.3 *ab*	4.0	2.8	4.2	2.5	3.0
Protein	Wet	15.4 *a*	17.1 *a*	11.7 *b*	15.9 *a*	17.5 *a*	8.8 *a*	7.7 *a*
	Mesic	16.5 *a*	17.4 *a*	14.3 *a*	14.9 *ab*	16.2 *a*	8.0 *ab*	6.4 *ab*
	Dry	14.2 *b*	14.0 *b*	11.8 *b*	13.8 *b*	13.4 *b*	7.2 *b*	6.0 *b*
Ash	Wet	13.3 *a*	7.2 *ab*	7.3 *ab*	5.8	6.5 *ab*	5.6 *a*	4.0
	Mesic	14.6 *b*	7.9 *a*	7.7 *a*	6.2	6.7 *a*	3.8 *b*	4.1
	Dry	13.9 *a*	6.6 *b*	6.3 *b*	5.7	5.9 *b*	3.6 *b*	3.9
Acid detergent fiber	Wet	29.5	21.2	15.1	21.1	16.4	38.4	46.0
	Mesic	31.6	25.8	16.2	21.9	18.3	40.0	47.5
	Dry	29.6	25.3	14.1	20.6	16.8	40.4	45.2
Nitrogen free extract	Wet	36.2 *a*	49.3	60.2 *a*	53.5 *a*	54.1 *a*	43.4	38.3
	Mesic	32.4 *b*	42.8	57.1 *b*	53.5 *a*	52.8 *a*	43.7	38.7
	Dry	36.3 *a*	50.5	62.9 *a*	56.4 *b*	58.7 *b*	44.3	40.6
Phosphorus	Wet	0.25	0.33 *a*	0.27 *a*	0.28 *a*	0.29	0.17	0.18 *a*
	Mesic	0.29	0.38 *b*	0.27 *a*	0.26 *b*	0.30	0.16	0.16 *b*
	Dry	0.28	0.32 *a*	0.25 *b*	0.26 *ab*	0.30	0.16	0.16 *b*
Calcium	Wet	1.33 *a*	1.21	0.92	1.13 *a*	1.01	0.89	0.88
	Mesic	1.39 *b*	1.25	0.90	1.25 *b*	1.01	0.95	0.97
	Dry	1.39 *b*	1.21	0.81	1.15 *a*	0.98	0.94	0.95

[1] Means followed by the same letter are not significantly different ($P < .05$) on each row.

TABLE 27.—AVERAGE PERCENTAGE NUTRIENT CONTENT OF 5 SPECIES COLLECTED IN QUAKING ASPEN AND JACKPINE STANDS IN LAKE COUNTY, MINNESOTA, FROM JULY 1971 TO JUNE 1972. MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 25 COLLECTIONS, 19 JULY 1971–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER AND NITROGEN FREE EXTRACT MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 15 COLLECTIONS. OTHER MEANS ARE AVERAGES OF 9 COLLECTIONS, 19 JULY–29 SEPTEMBER 1971 AND 29 MAY–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER AND NITROGEN FREE EXTRACT MEANS ARE AVERAGES OF 6 COLLECTIONS. MEANS FOLLOWED BY AN ASTERISK (*) ARE SIGNIFICANTLY DIFFERENT ($P < .05$)

Nutrient	Site	Large-Leaf Aster	Wild Sarsaparilla	Bush Honeysuckle	Beaked Hazel leaves	Mountain Maple leaves	Beaked Hazel twigs	Mountain Maple twigs
Ether extract	Aspen	3.4	3.8	3.8	2.8	4.6	2.6	3.5
	Jackpine	4.2*	3.2*	4.2	2.8	4.9	2.9	3.2
Protein	Aspen	16.3	16.5	14.3	15.1	15.2	7.7	6.4
	Jackpine	15.0*	16.1	12.5*	13.9*	14.6	7.3	6.2
Ash	Aspen	15.3	7.7	7.8	6.7	6.8	3.8	4.2
	Jackpine	13.6*	7.2	7.0*	5.8*	6.0*	3.8	4.0
Acid detergent fiber	Aspen	32.0	26.6	15.8	22.8	18.4	40.3	46.9
	Jackpine	30.3	24.2*	15.9	21.2*	17.2	39.2	47.6
Nitrogen free extract	Aspen	31.8	42.6	57.5	52.1	54.3	43.6	39.0
	Jackpine	35.4*	46.8*	59.2	55.5*	55.9	44.8	39.1
Phosphorus	Aspen	0.31	0.36	0.27	0.28	0.32	0.17	0.16
	Jackpine	0.29*	0.36	0.26	0.28	0.29	0.17	0.17
Calcium	Aspen	1.34	1.25	0.93	1.30	1.00	0.97	1.01
	Jackpine	1.37	1.17	0.84*	1.15*	0.95	0.95	0.94

higher nutritive quality than those on dry sites.

The nutrient quality of plants following fire appeared to depend on available soil moisture as well as intensity of burn. All species collected on the hotter wildfire burn during the growing season were higher in protein and lower in acid detergent fiber than the cooler slash burn (Table 29). Phosphorus levels were also higher on the wildfire burn for all species except large-leaf aster. Protein, calcium, and phosphorus percentages of plants in burned stands were generally not greater than in plants sampled in wet canopied stands (Tables 26, 29). Lutz (1956) in Alaska and Ahlgren (1963) in Minnesota reported that following fire in forests, soil moisture decreased and soil temperature increased due to loss of surface litter and dead standing vegetation. Kucera et al. (1967) and Anderson (1965) observed that burning reduced soil moisture on a midwestern prairie.

Ahlgren (1963) found increased nitrogen, calcium, phosphorus, magnesium, and potash in soil following a fire in northeastern Minnesota but nitrogen, magnesium, and potash returned to preburn levels after 1 year. Minerals in the soil also increased following a wildfire in Alaska (Lutz 1956). Lay (1957) observed a 42.8 percent increase in protein and a 77.8 percent increase in phosphoric acid content of plants collected after a spring fire in Texas. Similar increases in protein and phosphorus levels occurred after a fire in Maryland (DeWitt and Derby 1955). Plants from the 2 burns in this study did not accumulate more phosphorus or have higher protein levels than plants in moist canopied stands.

CHARACTERISTICS OF CONIFER PLANTATIONS RELATED TO USE BY MOOSE

Various investigators (Gysel 1966, Bailey and Alexander 1960) have reported that

TABLE 28.—AVERAGE PERCENTAGE NUTRIENT CONTENT OF 5 SPECIES COLLECTED IN QUAKING ASPEN AND JACKPINE STANDS LESS THAN 25 YEARS OLD AND GREATER THAN 25 YEARS OLD IN LAKE COUNTY, MINNESOTA, FROM JULY 1971 TO JUNE 1972. MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 25 COLLECTIONS, 19 JULY 1971–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER AND NITROGEN FREE EXTRACT MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 15 COLLECTIONS. OTHER MEANS ARE AVERAGES OF 9 COLLECTIONS, 19 JULY–29 SEPTEMBER 1971 AND 29 MAY–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER AND NITROGEN FREE EXTRACT MEANS ARE AVERAGES OF 6 COLLECTIONS. MEANS FOLLOWED BY AN ASTERISK (*) ARE SIGNIFICANTLY DIFFERENT ($P < .05$)

Nutrient	Site	Large-Leaf Aster	Wild Sarsaparilla	Bush Honeysuckle	Beaked Hazel leaves	Mountain Maple leaves	Beaked Hazel twigs	Mountain Maple twigs
Ether extract	< 25 years	3.8	3.6	4.1	2.9	4.8	2.6	3.4
	> 25 years	3.7	3.6	3.9	2.7	4.7	2.7	3.4
Protein	< 25 years	15.9	17.2	13.5	14.5	16.5	7.5	6.8
	> 25 years	15.6	15.7*	13.3	14.6	14.6*	7.5	6.2
Ash	< 25 years	14.7	7.8	7.6	6.0	6.7	3.7	4.1
	> 25 years	14.6	7.3	7.2	6.5*	6.4	3.9	4.1
Acid detergent fiber	< 25 years	30.9	23.8	15.2	21.9	17.3	39.5	46.7
	> 25 years	31.5	26.9*	16.6	22.2	18.1	40.3	37.3
Nitrogen free extract	< 25 years	33.5	44.9	58.6	54.0	53.4	44.8	39.0
	> 25 years	33.1	44.1	58.0	53.2	55.3	43.7	39.0
Phosphorus	< 25 years	0.29	0.37	0.26	0.26	0.26	0.16	0.16
	> 25 years	0.31	0.36	0.27	0.29*	0.32*	0.17	0.17
Calcium	< 25 years	1.35	1.28	0.90	1.15	1.01	0.93	0.98
	> 25 years	1.36	1.17*	0.86	1.30*	0.97	0.99*	0.98

reforestation of logged areas to conifers generally decreases their suitability as wildlife habitat. Conifer plantations comprise an increasingly greater share of the moose range in northeastern Minnesota, and thus warranted investigation.

Density of planted trees and stocking rates (Rudolph 1950) for the 25 plantations sampled (Table 30) showed that considering only conifers, 8 plantations were rated excellent, 3 good, 2 average, 4 fair, and 8 poor in stocking rate. Five of the poorly stocked stands had been treated with herbicide. Importance values indicated that planted species and/or volunteer jackpine dominated the stands 9 years old or older. Domination of conifers was similar in magnitude in stands that were or were not treated with herbicides.

Jackpine occurred as a volunteer in 12 of 25 stands, probably reflecting the abundant seed source, the ability of this species to establish readily on disturbed sites, and the suitability of the planting sites for establishment of this species. Most stands occupied locations where jackpine had been logged. Volunteer jackpine densities exceeded planted red pine densities in 4 plantations and occurred as 25 percent or more of the conifer composition in 11 other stands.

When all tree species were considered in the stocking rate, 13 were rated excellent, 4 good, 4 fair, and 4 poor. Aspen was the major contributor to stand stocking rate increases in this comparison.

Aspen and white birch assumed less conspicuous roles in stands treated with herbi-

TABLE 29.—AVERAGE PERCENTAGE PROTEIN, ACID DETERGENT FIBER, PHOSPHORUS, AND CALCIUM CONTENT OF 5 SPECIES COLLECTED ON 2 BURN SITES IN LAKE COUNTY, MINNESOTA, FROM JULY 1971 TO JUNE 1972. MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 25 COLLECTIONS, 19 JULY 1971–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER MEANS OF BEAKED HAZEL AND MOUNTAIN MAPLE TWIGS ARE AVERAGES OF 15 COLLECTIONS. OTHER MEANS ARE AVERAGES OF 9 COLLECTIONS, 19 JULY–29 SEPTEMBER 1971 AND 29 MAY–25 JUNE 1972, EXCEPT ACID DETERGENT FIBER MEANS ARE AVERAGES OF 6 COLLECTIONS. MEANS FOLLOWED BY AN ASTERISK (*) ARE SIGNIFICANTLY DIFFERENT ($P < .05$)

Nutrient	Site	Large-Leaf Aster	Wild Sarsaparilla	Beaked Hazel leaves	Mountain Maple leaves	Beaked Hazel twigs	Mountain Maple twigs
Protein	Wildfire	16.7	17.7	17.2	17.7	7.2	5.7
	Slash	14.4*	13.7*	15.1*	14.0*	6.9	5.1
Acid detergent fiber	Wildfire	28.0	15.9	16.2	13.0	48.0	51.5
	Slash	28.8	17.2*	17.5	15.6*	47.0	50.7
Phosphorus	Wildfire	0.25	0.31	0.26	0.26	0.14	0.14
	Slash	0.26	0.28	0.21*	0.24	0.13	0.13
Calcium	Wildfire	1.29	1.18	0.95	0.92	0.75	0.73
	Slash	1.40	1.21	1.07	1.06	1.00	0.85

cide than in untreated stands. Balsam fir, red maple, pin cherry, and pussy willow were other canopy height species of minor importance.

Shrub Composition and Density

Tree species (pines, spruces, aspen, white birch, and balsam fir) occurring in 7-year-old and younger stands as part of the shrub union assumed dominance in stands treated with herbicides (Table 31). Shrub densities in untreated stands ranged from approximately 1.8 to 21.5 stems/m^2 (Table 32). No correlation between shrub density and stand age was apparent. Shrub densities in treated stands ranged from 1.51 to 11.00 stems/m^2, with no correlation between age and density. Shrub densities in untreated stands were greater than in treated stands up through 7 years of age. Densities of nonplanted species in the shrub layer (actually the canopy layer) of treated stands 7 years old or less comprised 50 to 60 percent of the total density, while in untreated stands in this age category, nonplanted species comprised about 80 percent of the total density.

Another major change in shrub unions apparently due to treatment with herbicide was the change in species which dominated the union. Importance values for deciduous species were less than for coniferous species in 7 of 11 treated stands, while deciduous species dominated all shrub unions of all untreated stands. In one plantation, sprayed by fixed-wing aircraft and therefore probably only partially effective, beaked hazel dominated the shrub union. No coniferous species showed importance values of 20 or more in untreated stands, while importance values of 20 or more occurred in 9 of 11 treated stands (Table 31).

Aspen, beaked hazel, juneberries, and bebb willow were the most important species in shrub unions of untreated stands. A single species with an importance value at least 50 percent greater than the next most important species dominated 8 of 11 stands. Five of the 11 treated stands were dominated by a single species with an importance value 50 percent greater than the next most important species. The highest importance value of any shrub species occurred for beaked hazel in a 12-year-old treated stand. Red pine, aspen, or combina-

TABLE 30.—HEIGHT (M) AND DENSITY PER HECTARE OF PLANTED AND VOLUNTEER CONIFEROUS SPECIES, AND PLANTATION STOCKING RATES

Age (years)		Red Pine		Jackpine		White Spruce		White Pine		Black Spruce		Stand Stocking: Conifer		Stand Stocking: All species	
		Density	Height	Density	Height	Density	Height	Density	Height	Density	Height	Density	Rate	Density	Rate[2]
35		642	10.5	17	9.1	321	7.3	–	–	54	6.1	1035	F	1436	G
32		538	11.3	909	11.6	417	11.6	741	8.8	–	–	2595	E	2698	E
21		1527	4.9	573	6.7	32	3.0	–	–	–	–	2133	G	2545	E
19		255	6.4	618	8.2	72	8.5	–	–	326	7.9	1270	F	1451	F
22		853	8.2	427	9.1	–	–	25	9.1	–	–	1305	F	1895	G
11		524	3.7	12	3.0	–	–	–	–	12	3.0	549	P	1075	P
11		62	3.1	796	4.3	20	7.6	–	–	20	4.6	922	P	1006	P
9		230	3.7	2901	6.1	138	3.9	–	–	–	–	3269	E	3682	E
5		2239	1.0	1426	2.2	–	–	–	–	408	1.5	4072	E	4885	E
7		1789	1.5	1132	1.0	–	–	–	–	–	–	908	G	10749	E
6		509	0.9	4072	1.5	–	–	–	–	–	–	4581	E	10689	E
3		0	0	1302	0.5	3647	0.7	–	–	–	–	4950	E	10423	E
4		346	1.1	–	–	578	0.7	–	–	–	–	924	P	2483	A
4		0	–	–	–	2100	0.5	–	–	–	–	2100	F	4201	E
11	(herb)	3689	2.4	–	–	–	–	–	–	–	–	3689	E	4480	E
12	"	3068	3.0	42	9.1	42	2.4	–	–	–	–	3153	E	4346	E
11	"	203	2.4	1754	2.4	–	–	–	–	–	–	1957	A	2669	G
7[2]	"	949	1.3	99	2.6	–	–	–	–	–	–	1047	P	1932	F
7[2]	"	([3])	–	319	2.6	57	1.6	–	–	203	1.6	578	P	717	P
7[2]	"	544	0.9	156	2.0	–	–	–	–	–	–	699	P	1127	F
7	"	2496	1.5	1448	1.5	–	–	–	–	–	–	3944	E	5473	E
7	"	712	1.3	193	1.3	–	–	–	–	–	–	904	P	2649	G
4	"	74	0.3	445	0.4	1853	0.6	–	–	–	–	2372	A	3484	E
5	"	2839	1.2	292	1.4	–	–	–	–	–	–	3130	G	5535	E
5	"	1043	0.6	425	1.0	–	–	–	–	–	–	1468	P	2086	F

[1] Stands treated with herbicide 3 years after planting unless footnoted; footnote (1) indicates 5 years after.
[2] Rating after Rudolph (1950). P = poor, F = fair, G = good, E = excellent, A = average.
[3] Indicates species planted but not recorded in stand.

TABLE 31.—IMPORTANCE VALUES (IV) OF SPECIES WHICH HAVE VALUES GREATER THAN 50 PERCENT OF THE NEXT MOST IMPORTANT SPECIES IN THE SHRUB UNION

Not Treated with Herbicide					Treated with Herbicide				
Age (years)	Species	IV	Next Species	IV	Age (years)	Species	IV	Next Species	IV
32	Bebb willow	39	Bush honeysuckle	12	11	Red pine	37	Beaked hazel	22
22	Beaked hazel	46	Mountain maple	21	12	Beaked hazel	65	Red pine	13
11	Aspen	29	Green alder	12	11	Green alder	29	Aspen	17
7	Beaked hazel	47	Aspen	19	7	Red pine	37	Jackpine	22
6	Beaked hazel	32	Aspen	17	5	Red pine, Aspen	47 41	Jackpine	8
4	Beaked hazel	48	Mountain maple	12	7	Aspen	28	Red pine	18
3	Aspen	37	Beaked hazel	22	5	Red pine, Aspen	24 20	Pussy willow	14
11	Green alder	28	Beaked hazel	17	7	Red pine, Aspen	34 25	Jackpine	15

tions of these 2 species dominated 5 stands with importance values 50 percent greater than the next most important species.

Shrub Production

Shrub canopy area may be used as a measure of shrub production (Peek 1970). Except for the oldest age class, total shrub canopy area was much lower in treated stands than in untreated stands (Table 32). The reduction appeared to be most pronounced in 7-year-old stands sprayed 5 years after planting.

Shrub Nutrient Levels

A summary of nitrogen, phosphorus, potassium, and calcium levels in the terminal 5.1 cm of woody growth of beaked hazel, quaking aspen, and pussy willow twigs (Table 33) indicate that beaked hazel was lowest in nitrogen and phosphorus but highest in potassium and calcium. Aspen contained the highest mean nitrogen level. There were no significant differences in nutrient levels between sprayed and unsprayed stands.

Correlations between overstory canopy closure and twig nutrient levels were generally weak (Table 34). Phosphorus and potassium decreased in beaked hazel and willow and increased in aspen as overstory canopy closure and age of stand increased. There was no significant change in nitrogen levels associated with age of stand or closure of canopy.

Multiple regression analyses, using calcium, nitrogen, potassium, and phosphorus levels in beaked hazel and quaking aspen as independent variables showed significant changes associated with age of stand and closure of canopy. Calcium levels increased and levels of potassium and phosphorus decreased in beaked hazel as age and closure increased. Nutrient levels in quaking aspen showed positive significant increases with age and closure probably reflecting the changes associated with decreased competition with understory species as the tree species reached greater heights. No cor-

TABLE 32.—DENSITIES PER HECTARE OF PLANTED AND NONPLANTED SPECIES IN SHRUB UNIONS OF 25 PLANTATIONS GROUPED ACCORDING TO AGE CLASS AND WHETHER TREATED WITH HERBICIDE OR NOT FOLLOWING PLANTING. NUMBERS IN PARENTHESES INDICATE YEARS AFTER PLANTING WHEN STAND WAS TREATED WITH HERBICIDE

Age Group (years)	Mean Density of All Shrubs	Mean Density of Nonplanted Species	Total Shrub Canopy Area (m^2)	Age Group (years)	Mean Density of All Shrubs	Mean Density of Nonplanted Species	Total Shrub Canopy Area (m^2)
32–35	4336	4336	3874	11–12	9237	7247	13741
19–22	13482	13482	19385	7(5)	2164	1307	2496
9–11	6709	6299	12349	7(3)	5804	3380	6826
5–7	18503	14732	27996	4–5	4944	2646	3333
3–4	15414	12832	8915				

relations between pussy willow nutrient levels and age or closure were significant.

Beaked hazel apparently was capable of concentrating calcium at higher levels than quaking aspen or pussy willow. The resulting calcium–phosphorus ratios in beaked hazel range from 5.44 to 10.14 and increased as canopy closure increased.

Quaking aspen plants sampled undoubtedly share a common root system with plants in the overstory which would not be influenced by canopy closure. Also, plants which occur in the older stands appear to occupy spaces which allow sunlight to penetrate the canopy. It is possible that these factors help to account for the positive association of nutrients and stand age and closure in this clonal tree species.

Soil Nutrient Levels

Phosphorus, potassium, calcium, magnesium, and iron levels in each soil horizon of 15 plantations were measured quantitatively. Soils were classified as loams, acidic, and low in organic matter except for the mul or mor horizons. Phosphorus and calcium were considered high, and potassium levels were moderately high. Calcium, phosphorus, potassium, and magnesium levels generally decreased with soil depth (Table 35).

A total of 45 regressions of twig nutrient levels on soil nutrient levels in the mul/mor, A_1, and B_{21} horizons were run, of which 2 were significant (Table 36). Calcium levels in beaked hazel twigs were correlated with calcium levels in the mul/mor horizon, and phosphorus levels in aspen twigs were correlated with phosphorus levels in the mul/mor horizon. Nitrogen content of beaked hazel, aspen, and pussy willow were not significantly correlated with presence or absence of the mul/mor horizons in the soil, these horizons being highest in organic matter. Regression analyses of soil nutrient levels on area of total shrub canopy were also not significant. It was concluded that, despite the variation in soil nutrient levels between stands, twig nutrient levels were not correlated with soil nutrients within the range of levels encountered in this area. The lack of correlation is not unexpected in view of findings by Grigal and Arneman (1970) that overstory vegetation was poorly related to soil characteristics in this area. The 3 species sampled occur over a wide range of conditions in Minnesota (Bakuzis and Hansen 1960, 1962), and all stands were young enough so that plant associations would be expected to be changing rapidly in comparison to the soil component. Plants appear to accumulate nutrients at levels which were influenced by intrinsic factors as much as by the soil, as indicated by Gerloff et al. (1966) and Ovington (1968).

Discussion

Variation between individual plantations in soil nutrients, overstory canopy closure, shrub production, and nutrient levels precludes correlation between either age of

TABLE 33.—SUMMARY OF NITGOGEN, PHOSPHORUS, POTASSIUM, AND CALCIUM LEVELS IN BEAKED HAZEL, QUAKING ASPEN, AND PUSSY WILLOW TWIGS COLLECTED IN DECEMBER 1969 IN PINE PLANTATIONS, NORTHEASTERN MINNESOTA

Species	# Sites Collected	Nutrient Level (%) in Terminal 3″ of Current Year's Growth				
		Nitrogen x̄ range	Phosphorus x̄ range	Potassium x̄ range	Calcium x̄ range	Protein % Crude x̄
Beaked hazel	8	1.024 (0.944–1.632)	0.236 (0.229–0.319)	1.365 (1.111–1.791)	2.083 (1.294–2.730)	7.08 (5.9–10.2)
Aspen	13	1.367 (1.120–2.144)	0.338 (0.254–0.396)	1.142 (0.718–1.523)	1.425 (0.920–1.541)	8.7 (7.0–13.0)
Pussy willow	13	1.076 (1.072–1.584)	0.280 (0.188–0.459)	0.729 (0.298–0.941)	1.345 (0.726–2.373)	8.19 (6.7–10.0)

stand and canopy closure or soil nutrients with nutrient levels in twigs of the 3 species sampled. Some plantations, particularly if not treated with herbicide, provided large amounts of forage suitable as moose browse.

Levels of nitrogen and phosphorus in twig ends found in this study would be inadequate to sustain weight gains in deer according to Magruder et al. (1957), while calcium levels would be considered high. However, nitrogen levels compared favorably with those found on high quality moose range by Cowan et al. (1950) for the same time of year. Potassium levels were within the range considered adequate by Church (1971) for ruminants. It is probable that forage production rather than forage quality is the important factor in determining the value of a plantation as a foraging area for moose, although nutrients such as sodium have been suggested by Botkin et al. (1973) as possibly limiting moose populations, or at least influencing habitat use patterns, on nearby Isle Royale and were not investigated here.

On areas where early winter and early summer moose range are limited, intensive reforestation practices probably will adversely affect moose populations. Shrub production apparently decreased proportionately with increased efficiency of the reforestation effort, as has been reported by Gysel (1957), Roe and Buchman (1953), and Goodrum and Reid (1956). Also, since most plantations consisted of the pine species which were not preferred winter cover for moose, these areas, if stocked at levels suggested by Rudolph (1950) as satisfactory, may become progressively less favorable moose habitat as they mature, much as Gysel (1966) reported for deer in a Michigan plantation. However, as stands become older and are thinned, reinvasion of shrubs may again occur (Brown 1958, unpublished doctoral dissertation, University of Minnesota, St. Paul, Minnesota), and they may again serve as foraging areas for a population existing at much lower levels than reported in this study

It is concluded that reforestation may

TABLE 34.—SUMMARY OF CORRELATION COEFFICIENTS OF TWIG NUTRIENT LEVELS AND STAND AGE AND CANOPY CLOSURE

	Beaked Hazel		Quaking Aspen		Pussy Willow	
Nutrient	Stand Age	Stand Canopy Closure	Stand Age	Stand Canopy Closure	Stand Age	Stand Canopy Closure
Nitrogen	−.09	.00	+.10	+.21	+.28	+.31
Phosphorus	−.16	−.32	+.44	+.35	−.33	−.42
Potassium	−.23	−.30	+.49[1]	+.62[1]	−.48	−.50[1]
Calcium	+.68[1]	+.57	+.71[2]	+.62	−.13	−.01
Nitrogen, Phosphorus, Potassium, and Calcium	.91[2]	.86[2]	.72[2]	.68[1]	.43	.42

[1] Significant, $P < 0.10$.
[2] Significant, $P < 0.05$.

have neutral or negative benefits to moose in this area. The effect appears neutral if plantation stocking is low and no treatment with herbicide is done, or if treatment is not as efficient as would be desired from the silvicultural standpoint. The effect becomes progressively more negative as conifer stocking rates increase and herbiciding becomes more efficient. As plantation management becomes more effective, the resulting stands may become less valuable to moose.

DISCUSSION

Aquatic communities and sparsely stocked stands were most frequently used by moose in early summer. They are undoubtedly more important to moose in this area than our observations indicate. Palatability of important aquatics probably was responsible for this high use, although insect attacks may be implicated. Mosquitoes (Culicidae), blackflies (Simuliidae), and biting midges (Ceratopogonidae), were the most prevalent biting and sucking Diptera in early summer (Barr 1958, Nicholson and Mickel 1950). Blackflies have been known to cause mortality and severe irritation to livestock (Nicholson and Mickel 1950) and it was possible that moose could be affected similarly. However, all moose observed in water were either feeding or standing with most of the body exposed to insect attack rather than submerged as if they were trying to escape insect irritation.

Not infrequently, moose were seen in late summer with bloody abrasions on the hind leg above the heel, probably the result of attacks by the larger Tabanidae which were most common in mid- and late summer (Phillip 1931). The mature hardwood stands with their cool, shaded, and dense shrub understories may provide more effective escape cover from these larger flies than aquatic areas, since moose appear to be more irritated by insects in late than early summer.

As discussed earlier, upland habitats dominated by aspen and white birch, moderately to sparsely stocked, and relatively mature, received the major share of the use during summer. Such stands included the cutover portions of the study area. Use of uplands was generally proportional to their occurrence along routes. Sparsely stocked and young plantations were most frequently used. Avoidance of plantations during summer and late summer was apparent. Lowland communities dominated by the deciduous species, primarily white birch, received proportionately greater use than according to occurrence along the routes. Moderately to sparsely stocked stands, generally shorter than those on uplands, were used most frequently.

Shifts in habitat use as summer progressed may be correlated with decreased palatability of open grown species and aquatics, which probably mature more quickly than plants growing underneath shade, and become less succulent. Also, the larger Diptera may influence habitat

TABLE 35.—SUMMARY OF pH AND NUTRIENT LEVELS (PPM) IN 7 SOIL HORIZONS OF 15 CONIFER PLANTATIONS

Horizon	# Sites with Horizon	pH $\bar{x}$ (range)	P $\bar{x}$ (range)	K $\bar{x}$ (range)	Fe $\bar{x}$ (range)	Ca $\bar{x}$ (range)	Mg $\bar{x}$ (range)
mul, mor, LHF	11	5.3 (4.3–6.9)	17 (10–33)	173 (105–270)	321 (190–880)	26638 (6120–60000)	5489 (1336–11840)
A_1	6	5.5 (5.2–6.1)	11 (7–17)	93 (45–145)	382 (290–560)	13050 (2240–21200)	1500 (1270–2190)
AB	2	5.8 (5.5–6.0)	3 (3–4)	48 (40–55)	425 (260–590)	7500 (5580–9420)	1106 (1028–1184)
B_{21}	12	5.7 (5.0–7.1)	7 (3–14)	44 (20–75)	283 (130–500)	4447 (1440–6860)	410 (186–1000)
B_{22}	13	5.8 (5.5–6.9)	6 (2–15)	32 (15–55)	328 (90–1000)	4655 (1180–11000)	471 (156–992)
B_{23}	10	5.7 (5.4–6.6)	8 (4–22)	29 (10–45)	261 (110–430)	3250 (840–7120)	346 (142–744)
B^3	10	5.7 (5.2–6.1)	10 (4–17)	24 (10–55)	242 (130–380)	2840 (800–9280)	352 (100–944)

selection in late summer as has been reported for red deer *Cervus elaphus* (Darling 1937), for elk (Brazda 1953), and for caribou (Kelsall 1968). Tall aspen–white birch stands may be preferred resting cover when these insects were prevalent, since beds were common in such stands at that time, while lowlands and less densely stocked stands still may be the primary feeding areas. As the summer continued, a general decline in movement on roads took place.

Habitat selection during the prerut, rut, and postrut probably was as much contingent upon breeding activity and social interaction as upon environmental factors such as location of preferred forages, insects, snow, wind, and inclement weather. If interaction between individual moose was intensive, it may be assumed that the more open areas that facilitate observation between individuals would be used. Except for antler rubbing sites, there was no evidence that vegetation was integrated into rutting behavior except possibly for use as escape cover during chases and for actual breeding,

A shift in preference from the most open areas during the prerut to moderately stocked stands during the rut may result from differential habitat selection by the 2 sexes, although this was not evident during postrut when it could be checked. If cows preferred more dense cover than bulls, bulls may spend more time in denser covers when actively searching for sexually receptive females. Although a sexually receptive female may also search for a male and thereby use the more open cover types, Houston (1968) and Phillips et al. (1973) suggested more movement by males than females during the rut, indicating that the bull was searching more actively than the cow.

The winter period encompassed the most pronounced changes in habitat use. The large aggregations of moose seen in early winter were concentrated on the most open areas. Habitats used during January–March, when moose aggregations were smallest, depended upon snow characteristics and

TABLE 36.—SUMMARY OF CORRELATIONS BETWEEN CALCIUM, IRON, MAGNESIUM, PHOSPHORUS, AND POTASSIUM LEVELS IN SOIL HORIZONS AND BEAKED HAZEL, QUAKING ASPEN, AND PUSSY WILLOW TWIGS

Species	Soil Horizon	Correlation Coefficients				
		P	K	Ca	Fe	Mg
Beaked hazel	mul/mor	.67	.47	.84[1]	−.13	.73
Pussy willow		.15	.29	.45	.44	.08
Quaking aspen		.95[1]	−.13	−.34	.16	−.36
Beaked hazel	A_1	−.44	.62	−.34	.16	.22
Pussy willow		−.18	−.76	−.09	.78	−.73
Quaking aspen		−.77	.21	.81	−.33	−.72
Beaked hazel	B_{21}	.18	.42	−.34	.17	.60
Pussy willow		.11	−.08	−.01	.45	.08
Quaking aspen		.53	−.40	.52	.19	−.52

[1] $P < 0.05$.

weather conditions (Peek 1971). During the more severe winter periods, use of upland spruce–fir was common. Shifts to dense cover in January 1968 occurred when snow depths in open areas were 45 cm or less, suggesting that snow hardness and density may also influence habitat selection at that time (Peek 1971). When conditions moderated, use of more open areas occurred, mostly for feeding because bedding cover remained in the dense spruce–fir stands throughout the winter.

On a yearlong basis, 60 percent of the track locations were in uplands, 30 percent in lowlands, and 10 percent in plantations. Use of uplands was proportional to occurrence except in midwinter, while lowlands were used more frequently than expected from July through mid-October. Plantations were used less frequently than expected during July through early September and the rut. Upland communities dominated by aspen, white birch, black spruce, and balsam fir received about 90 percent of the observed use. These species, except for the ubiquitous aspen, were common to the more mesic sites of boreal forest. Stands dominated by jackpine, red pine, and white pine received only limited use, although no selection for or against pines was especially evident. Upland stands dominated by deciduous species were selected over spruce–fir stands in late summer and early winter, while the opposite was apparent in midwinter; at other times, no preference for one type over another was apparent.

Lowland communities dominated by black spruce and balsam fir received more use than white birch and aspen stands. Preference for deciduous stands was evident in June and early winter, while preference for lowland conifers occurred in midwinter.

The most open communities were used especially in June, the prerut, and early winter periods. During summer and the rut, selection of moderately stocked stands was evident. In midwinter, especially during the most severe parts, a high preference for the densest stands occurred.

Habitat preferences by moose probably were more pronounced than the data suggest; the extreme diversity of vegetation, topography, logging, and fire history of each site may obscure preferences. However, the extreme diversity undoubtedly contributes toward a high quality moose habitat.

Habitat selection by moose in this area could be correlated primarily with forage and cover requirements and breeding behavior. Wood et al. (1962) reported that a phase of rapid growth occurs in black-tailed deer *Odocoileus hemionus columbianus* in early summer which slows in late summer. High food consumption occurred among white-tailed deer in early summer, followed by a decline during breeding and an increase after breeding (Magruder et al. 1957, French et al. 1956), which coincides with the period of rapid growth in early summer, weight loss during breeding, and a decrease in rate of weight loss following the rut. Among penned deer, Ozoga and Verme (1970) and Silver and Colovos (1957) showed that a high intake of forage occurred in early winter, a reduction in midwinter, and an increase towards spring.

A general decline in kidney fat index from early fall through spring occurred in elk, but some recovery in fat reserves occurred following the rut (Flook 1970). A decline in kidney fat indices of males to lower levels than in other sex–age groups was apparent during the rut, as Riney (1955) also showed for red deer. The elk breeding cycle corresponds more closely to that of the moose than to deer (Morrison et al. 1959, Edwards and Ritcey 1958, Cheatum and Morton 1946). If there is a leveling off in loss of weight of male deer after the rut, and an increase in forage intake, it is likely that such occurs for the 2 larger cervids also. Thus, it appears that early summer and postrutting habitats may provide forage sources which account for most of the energy for growth and replenishment of fat reserves, both of which would affect subsequent survival through the severe winter periods.

Although a general relationship between forage quality and quantity and population responses is well known (Einarsen 1946, Leopold et al. 1951), wild ruminants apparently are able to adjust to some extent to poor forage supplies. Schmidt-Neilsen et al. (1958) demonstrated that urea may be retained in the bloodstream of domestic sheep *Ovis aries* and reused when food nitrogen is low. Nutrient levels in the rumen may be higher than in forage because of the composition in microorganisms, addition of saliva, and recycling of nutrients back to the rumen (Church 1969). Nevertheless, Hungate (1966) reported that blood urea concentration decreases as protein level decreases in the diet, and that loss of appetite may occur in ruminants on nitrogen poor rations. The reduced metabolic rates observed in white-tailed deer by Seal et al. (1972), and in moose by LeResche et al. (1974) in winter are considered a response to naturally deteriorating forage supplies.

However, animals probably have the capability of selecting higher quality forages than those which may be sampled randomly within a stand. Such a variety of species as domestic cattle *Bos taurus* (Cable and Shumway 1966), white-tailed deer (Swift 1948), red grouse *Lagopus lagopus* (Moss 1967), and hares *Lepus timidus* and rabbits *Oryctolagus cuniculus* (Miller 1968) have been shown to select plants of higher nutrient levels than randomly occurs in a stand, so it is reasonable to assume that the moose does also. Therefore, examination of forage quality to indicate why moose use various cover types, if indeed forage quality is a criterion influencing selection, may not reveal the presence of highly nutrient rich plants within cover types where nutrients are generally of lower quality than in other areas. Nevertheless, seasonal trends in weight and forage consumption observed for deer and elk, and thereby postulated for moose, may be compared directly with seasonal levels in forage nutrients.

Dry matter, caloric values, and fat content of deciduous shrubs in Colorado (Short et al. 1966), Louisiana (Blair and Epps 1969), and alpine plants in Wyoming (Mooney and Billings 1960) were high in winter, decreased in spring and summer, and increased in fall. Crude protein decreased in 5 commonly used moose forage species through the winter (Cowan et al. 1950), fat decreased in all but red osier which showed no change, and carbohydrates increased in aspen, birch, and red osier, but decreased in willow, beaked hazel, and juneberry. Decreases in all species occurred in all nutrients in plants growing in dense cover, when compared with open grown plants. However, McEwen and Dietz (1965) reported that Kentucky bluegrass *Poa pratensis* growing in shade contained less nitrogen free extract but higher protein than bluegrass growing in open meadows. Open grown browse contained more crude protein than browse growing beneath pine (Halls and Epps 1969), but these authors stated that the relationship, as indicated in this review, varies regionally.

Use of the high forage producing areas by moose where overstory density is least in early summer, is then correlated with high protein levels in forages. In early winter, use of these areas is correlated with a decreased protein level, but high levels of ether extract and nitrogen free extract. Growth in the individual moose probably is most rapid in June, as protein levels are highest, and use of open areas in early winter probably is correlated with a recovery in fat reserves following the rut, or at least a decrease in weight decline. Since protein levels in forage are lower in early winter than in summer, it is probable that protein is used for maintenance and the higher nitrogen free extracts and ether extracts are used for body fat accumulation, as Blaxter (1962) indicated.

If early winter habitat selection is influenced primarily by a need for forage supplies of high quality and quantity, which then serves to sustain moose through subsequent severe winter periods, forage selection may be more critical at this time than in midwinter, when cover requirements may also become important. The fasting metabolic rate of deer tends to drop (Silver et al. 1969) as winter progresses, probably an adjustment to poorer quality forage and lower nutrient intake (Blaxter 1962). Forage preferences are still evident in midwinter since some plants of the preferred forage species seem to be browsed more frequently than others, as also occurs earlier in the more open areas. Nevertheless, the most prevalent species, beaked hazel and balsam fir, receive high use while species preferred in early winter are used less.

Winter range and condition of winter forage supplies were considered the ultimate limiting factors for deer populations in the Jawbone Area of California (Leopold ea al. 1951) where winter conditions force deer to concentrate onto rather well-defined winter ranges, and this concept has been widely accepted as ultimately limiting many cervid populations in North America. More recently, ranges used at other seasons have been given consideration in this regard (Edwards and Ritcey 1958, Julander et al. 1961, Klein 1965, Markgren 1969). When population densities, production, and survival data for this moose population were considered in conjunction with forage utilization and condition, it was apparent that late winter forage supplies were not the most important limiting factor to this population. It appears that the open covers used in late fall and early winter, and again in spring, must be considered the major habitats sustaining this population at present levels.

MANAGEMENT IMPLICATIONS

It seems redundant to state that increases in this moose population appear to correlate well with logging activities, since this has so frequently been observed across North America and Eurasia. Nevertheless, the moose of northeastern Minnesota have, since hunting was closed in 1923, increased, decreased, and increased once again. The increase in 1925 through 1934 coincided with sawtimber harvests in the Cloquet Lake area (Fig. 2), where moose populations have persisted since. The increase of moose in the 1950's coincided with pulpwood harvests, primarily within the Boundary Waters Canoe Area. Apparently, this logging inadvertently created ideal moose habitat by removing large acreages of jackpine pulp timber and creating extensive shrub communities, interspersed with balsam fir and aspen and white birch stands. Management of vegetation both inside and outside of the Boundary Waters Canoe Area undoubtedly will be the major factor influencing these moose populations in the future.

Current trends in timber management are towards smaller cutting units and more intensified regeneration of pines. Even as earlier logging benefited moose, current trends may adversely affect them by not creating sufficiently extensive areas of cutover, and by shortening the longevity of the early seral stages involved. The following suggestions are intended to minimize the problem.

Moose movements, food habits, habitat selection, and census data all indicate that the primary or key moose habitat appears to be the open cutover used in early summer and late fall. Also, spruce–fir and more mature aspen–white birch communities, plus the aquatic areas, were preferred habitats at other times of the year. Based on this field study, it appears that areas of highest potential for moose habitat management are township-sized blocks within the current high-density range, with the following composition:

(1) Cutover less than 20 years old .... 40–50 percent
(2) Spruce–fir .... 5–15 percent
(3) Aspen–white birch over 20 years old, and water .... 55–35 percent

Cutting should be done where white birch and aspen may be expected to regenerate naturally. Current economic conditions indicate that aspen may become valuable enough to facilitate such management. If cutting units are restricted in size, they should be placed as close to each other as possible to create blocks of approximately 80 ha, a size which appears characteristic of the present prime moose range.

Should jackpine and red pine remain the most economically valuable species on the area, some accommodation between pine management and moose management, which are not generally complementary, should be made. One obvious means is to restrict management of pine to the most suitable sites and to manage aspen and other species elsewhere and not attempt conversion of stands to pine.

Browsing intensity was not severe enough to cause appreciable deterioration in forage supplies during this study. Also, calf production during the period was rated only moderate, suggesting that the population had reached a peak and may have begun to decline. The proximate mortality factors, including cerebrospinal nematodiasis, wolf predation, and malnutrition, did not appear to stimulate moose production to high levels and may serve to roughly balance survival with mortality over periods of several years. The relationship of mortality factors appeared complex, with each factor operating most effectively upon the population at different times of the year, and with variations of consequence between years as well. It probably was significant that the population increases in the 1950's occurred even though cerebrospinal nematodiasis and timber wolf populations were prevalent in the area.

The Portal Zone of the Boundary Waters Canoe Area has generated bitter controversy between timber and wilderness interests. If the moose is to be identified as part of the wilderness, it is ironic that logging has created high-quality moose habitat (as well as habitat for other desirable species). The Portal Zone has a network of logging trails and other substantial evidence of human intervention through it. While in time, direct evidence will decrease, total protection will not recreate true wilderness or preserve important wilderness species such as moose. Wildfire has, in the past, created seral communities typical of high-quality moose habitat, and retention of this dynamic wilderness community with which moose are inextricably associated reduces to solving the means to integrate fire back into the area. This is a biopolitical problem as well as a technical one.

The controversy and misunderstanding about wilderness, wildlife, fire, and logging is keenly argued in northeastern Minnesota. Man has been the creator of moose habitat and moose populations of large size through logging, albeit inadvertently. Man can readily diminish this population as well as those of other species by ignoring the significance of logging and fire in the ecosystem. It is hoped that this study will help to provide an impetus to manage the moose population and its habitat.

SUMMARY

This study deals with moose population characteristics and relationships to forest management and habitat in northeastern Minnesota. Records of moose and vegetational history, including logging, fire, and pollen deposits in lake sediments, suggested that moose habitat, and therefore probably moose, had been present in the area since the postglacial hypsithermal period about 2000 years BP and perhaps earlier. Moose densities, based on intensive aerial search of 2.6-km^2 plots in early winter of representative portions of the study area, averaged about 0.77 moose/km^2, with 1.93/km^2 existing on a large, recently logged area within the Boundary Waters Canoe Area. Calves comprised 17–19 percent of the fall population. A decrease in survival of calves following a particularly severe winter, indicated by a drop in the percentage of yearlings observed from the air in fall of the following year, was observed. Moose aggregations were highest in late fall and early winter. The increase in aggregation size was attributable to a tendency for bulls rather than cows to congregate. This increase was attributed to pre- and postrutting behavior, wherein the aggregating tendency may facilitate interaction among bulls. Age distributions of 34 moose based on jaws from animals dead of natural causes suggested that highest mortality occurred prior to 5 years of age. Wolf predation, cerebrospinal nematodiasis, and losses related to malnutrition were major mortality factors in this unhunted population. The presence of *Parelaphostrongylus tenuis* appeared to predispose yearling and young adult moose to wolf predation. Mortality due to this disease was concentrated in January through April, while predation appeared more prevalent in summer. Food habits varied considerably through the year. Aspen and aquatics, primarily yellow pondweed and wild rice, were important in June, while willows, mountain maple, white birch, and fire cherry were important in July through August. Red osier became important in fall. Balsam fir and beaked hazel were primarily winter forages, with fir especially important in March. Forbs were unimportant in the diet. Aquatic communities were used more frequently in June than later in summer. Use appeared to correlate with palatability of key forage species rather than insect attacks, since uplands were used commonly during peak populations of Tabanidae in August. Browse utilization and condition did not suggest that intensity of browsing by moose was severe enough to adversely affect more than a small percentage of forage sources. During the 1967–1968 winter, moose moved to dense conifer cover when snow depths were 46 cm or less. Subsequently, snow hardness and density, as well as depth, affected moose winter distributions in conifer and deciduous cover. Moose used the open cutover areas of least cover and most abundant forage supplies in June and early winter. This correlated with periods of high protein (June) or high ether extract and nitrogen free extract (early winter) in key forage species, as determined from literature review. Dense conifer cover was preferred midwinter bedding cover and was used commonly during severe winter periods for feeding. Lowland communities apparently were preferred habitats except during midwinter when uplands were preferred. Moose rutting activity, palatability and availability of forage species, insects, snow, and weather appeared to influence habitat selection by moose. Many plantations apparently contained abundant forage supplies, but forage abundance appeared to be inversely related to the effectiveness of postplanting herbicide treatment of plantations. Logging activities on over 21 percent of the study area during 1948–1967, which created large fields of palatable browse species used by moose in June, November, and December, appeared to be the prime reason that a high moose population existed on the study area. Township-sized areas, containing considerable amounts of lakes and streams and aspen timber, appeared most suitable for attempting to manage moose habitat. Clearcutting

of large areas up to 81 or more hectares in size appeared desirable to create large quantities of palatable shrub communities. The future of the moose population depended upon logging and the successful reintroduction of fire into the Boundary Waters Canoe Area.

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