CHANGES IN STRUCTURE OF A BOREAL FOREST COMMUNITY FOLLOWING INTENSE HERBIVORY BY MOOSE

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ABSTRACT: Herbivores have influenced the structure, biomass, and species composition of vegetation in heavily browsed or grazed areas. The introduction of moose (*Alces alces*) to Newfoundland in 1878 and 1904, and the subsequent closure of hunting with the establishment of Gros Morne National Park in 1973 have resulted in current moose densities in excess of 4.0 moose/km^2. We hypothesized that browsing by moose has changed the plant species composition, the availability of browse, and influenced forest successional patterns. Browse use, availability, and species diversity indices in 1996 were compared to results of browse surveys conducted during 1977 in Gros Morne National Park, Newfoundland. In the Park, mean pellet group counts from surveys during 1996 were significantly greater than those of surveys in 1977, and were also greater than in sites located outside park boundaries in 1996 ($P = 0.0001$ and $P = 0.017$, respectively). In 1996, the mean browsing intensity was significantly greater than that of 1977. Significant differences ($P < 0.001$) occurred among proportions of available browse species between 1977 and 1996 at all sites. Species preferred by moose in 1977 decreased in availability by 1996 while species not browsed or browsed infrequently in 1977 increased in abundance. Selection of browse species by moose changed with changing availability of forage. Mean indices of species diversity in 1977 were significantly greater ($P < 0.01$) than species diversity indices at the same sites in 1996. No significant difference was found between mean indices for 1977 and 1996 in sites of low moose density located outside the Park boundaries. Data suggest that moose have changed species composition, the proportion of available browse remaining, and hence have influenced forest successional patterns within Gros Morne National Park.

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Key words: *Alces*, browsing intensity, community structure, Gros Morne National Park, hare, herbivore, Newfoundland, preference, species diversity

Moose (*Alces alces*) were introduced to Newfoundland in 1878 and 1904 (Pimlott 1953). Since then, the population has increased and moose are currently distributed over the entire island. Gros Morne National Park (GMNP) was established in 1973. The Park was closed to hunting in 1974 and, subsequently, the moose population increased rapidly. Taylor (1991) reported the moose population was still increasing in 1991. A March 1995 population estimate (7,738 $\pm$ 810 animals) also suggested the population was still increasing (Fig. 1). Moose density averaged 4.0/km^2 for the entire Park and ranged as high as 6.8 moose/km^2 (Sullivan 1995).

Herbivores have influenced structure, biomass, production, and species composi-

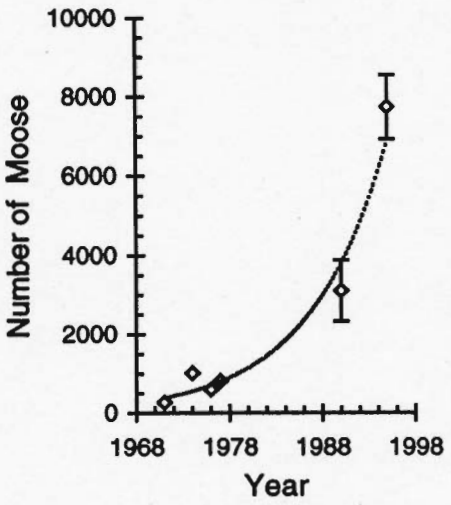

Fig. 1. Moose population estimates (±95% CI) in Gros Morne National Park, 1971-1995. Sources include Gillespie *et al.* (1971), Wentzell (1974), Janes (1976,1977), Taylor (1991), and Sullivan (1995).

tion of vegetation in heavily browsed or grazed areas (Jefferies *et al.* 1979, McNaughton 1979, Naiman 1988). Moose can be detrimental to both coniferous and deciduous forest species (Pimlott 1965, Bergerud and Manuel 1968, Snyder and Janke 1976, Risenhoover and Maass 1987), and influence soil composition and nutrient cycling (Pastor *et al.* 1988, Molvar *et al.* 1993). Previous studies have indicated that browsing by moose affects forest succession patterns (Thompson *et al.* 1992). Molvar *et al.* (1993) and Bryant *et al.* (1991, 1992) indicated that moderate browsing increases growth per growing point until the plant is killed or reverts to juvenility, while Wolff (1978) suggested that shrubs could sustain a maximum browsing intensity of between 50-75%. Krefting *et al.* (1966) determined mountain maple (*Acer spicatum*) could maintain optimum browse production at use levels of ≥80%.

The Federal/Provincial Agreement in 1973 requires that GMNP preserve naturally-occurring ecosystems which are representative of the region and provide timber for domestic harvesting. This agreement was put into place to reduce the impact of Park establishment on individuals and families who were residents of the area at that time. It deals with traditional subsistence use by eligible users. Through the agreement, Parks Canada allows traditional harvesting of timber, regulated by a permit system, in 12 designated cutting blocks (19,735 ha). Specific volumes of wood can be harvested within the limits of a sustainable yield for those areas. Harvesting activity must be conducted in ways to minimize environmental impacts.

In 1988, the National Parks Act was amended to confirm that the maintenance of ecological integrity was the primary mandate of Parks Canada. This implies that the long term viability of ecosystems must be maintained, including biodiversity and structural and functional complexity. Such directives raised questions concerning the effects of moose on vegetation within the Park (Thompson and Curran 1989).

The level of domestic timber harvest doubled during the period, 1983-1993 (Moreland 1993). However, harvest levels have declined since 1993 (C. Wentzell, GMNP Resour. Conserv., *pers. comm.*). Domestic harvesting within Park cutting blocks resulted in small, isolated clearcuts in contrast to commercial harvesting techniques. This practice created favourable habitat for moose: a mixture of successional stages which provide both browse and cover. The increased domestic timber harvest coupled with protection from hunting allowed moose numbers to increase.

Moose populations within the Park are primarily regulated by food supply, as predation exerts minimal influence (Mawhinney and Mahoney 1994). Black bears (*Ursus americanus*) are the only large predators of moose calves in the Park but do not have a major impact on the population (Bateman

1977). Black bears are not significant predators of adult moose (Ballard 1992). Schwartz and Franzmann (1989) stated that predation by black bears was variable (30-70 % of the annual calf crop) but did not regulate moose numbers in situations where habitat was in good condition and the moose population was increasing.

Bergerud and Manuel (1968) reported that in Newfoundland white birch (*Betula papyrifera*) and mountain maple decreased in abundance in areas of excessive moose browsing. Bateman (1977) suggested that Canada yew (*Taxus canadensis*) would be the first species to decline as a result of moose browsing in the Park. Canada yew is an evergreen shrub rarely exceeding 1.5 m in height (Ryan 1989) and consequently, does not escape browsing by growing out of reach of herbivores. Lawlor (1994) indicated that moose browsing was eradicating hardwoods from young, regenerating, insect-killed, and cut over stands on the lowlands of the Park. Current protection of all wildlife species, including moose has the potential to impact indigenous vegetation by altering successional patterns and vegetative species composition.

Gros Morne National Park provides a unique opportunity to study the demography, ecology, and regulation mechanisms of a moose population subjected to minimal natural predation and/or hunting. In addition, its ecoregions are representative of the entire island of Newfoundland (Tress and Hunter 1975). This study investigated the impacts of moose browsing primarily on late seral softwood stands within GMNP. We compared current distribution and abundance of woody browse plants with those reported by Prescott (1977) to examine changes over a 19-year period.

We hypothesized that browsing by a high density moose population had changed the vegetation species composition and abundance of vegetation within softwood stands of Gros Morne National Park. Based on that hypothesis, we predicted: (1) browsing intensity on woody vegetation had increased; (2) availability of preferred forage species had declined; and (3) high browsing intensity had changed browse species composition.

STUDY AREA

Gros Morne National Park is located on the western side of the Great Northern Peninsula of Newfoundland and encompasses 1,805 km^2. The Park is ecologically divided into 3 regions: the Northern Peninsula ecoregion (NPE); the Long Range Barrens ecoregion (LRBE) from Rocky Harbour north; and the Western Newfoundland ecoregion (WNE) to the south (Damman 1983). The NPE includes the coastal plain on the western side of the Great Northern Peninsula including the lower slopes of the Long Range Mountains, extending west to the Gulf of St. Lawrence and north to the Park boundaries. The Coastal Plains subregion is dominated by bogs and scrub forests with a short growing season of 110-150 days compared with 145-170 for other regions in Newfoundland (Meades and Moores 1989). Productive coniferous stands are restricted mainly to the slopes of the mountain range and support balsam fir (*Abies balsamea*), black spruce (*Picea marina*), white spruce (*Picea glauca*), and white birch. The upland areas of the Long Range Mountains are covered with sparsely forested heath and shrub barrens while small stands dominated by balsam fir and black spruce occur in the sheltered valleys. The WNE is characterized by a humid climate with relatively long frost-free periods and supports some of the most productive forest stands in Newfoundland (Meades and Moores 1989). *Dryopteris-Hylocomium*-Balsam Fir is the dominant forest type for this ecoregion (Damman 1983). Upland terrain is uneven

and reaches 807 m in elevation. No extensive coastal plain is found in this ecoregion.

METHODS

Browse surveys were conducted at 10 sites in 3 ecoregions within Gros Morne National Park (Prescott 1977). These sites were initially surveyed during 1977 in an effort to obtain baseline information on the distribution and abundance of browse and to determine browsing intensity by moose and snowshoe hare (*Lepus americanus*). Browse sample sites were selected on the basis of information from biophysical maps of the Park (Tress and Hunter 1975) and results of an aerial survey of moose during 1976 (Janes 1976). Sites were chosen in areas designated as low, (areas 6, 9, and 10) and moderate to high (Areas 1, 2, 3, 4, 5, 7, and 8) winter moose densities by Prescott (1977).

Three additional sites of low moose density were surveyed in 1996 (Fig. 2). These sites, were subjected to hunting as they were located outside and/or near Park boundaries. Biophysical maps of the Park (Tress and Hunter 1975) were used to determine that these sites were of similar age and stand type to those surveyed within the Park in 1977 and 1996. Sites located outside Park boundaries provided an index of vegetation community structure of stands subjected to low browsing intensity during the same time period. Results from moose pellet group surveys were used as indirect estimates of time spent by moose in each sample site (Neff 1968). A pellet group was counted if it consisted of >30 pellets (Neff 1968).

Study sites first surveyed in 1977 were relocated using the transect locations marked on original aerial photos and biophysical resource inventory maps. Browse surveys were completed using the same methodology as initial surveys described by Prescott (1977). Transects were located at regular intervals (50 - 100 m) perpendicular to land contours wherever possible. Quadrats measuring 20 m x 0.5 m were located at 80 m intervals along transects. A cloth tape was used as the left boundary of the quadrat. A 0.5 m rod was held perpendicular to the tape and advanced along the right side of the tape the length of the quadrat to define the right boundary. All woody stems (>30cm) within the quadrat were recorded. Any stems at quadrat borders were included if at least half of their basal area was within the plot. Species, height (cm), basal diameter (mm), and numbers of unbrowsed and browsed twigs for each stem were recorded. Twigs were defined as the current annual growth of stems >5 cm. All twigs (browsed and unbrowsed) between 30 cm and 2 m above ground were recorded.

Analysis of preliminary data from this study indicated that 26 plots per site provided an estimate of total availability of browse within 30% of the mean ($\alpha = 0.05$). Initial browse surveys (Prescott 1977) sampled more than 26 quadrats at some sites. At those sites, a second sampling scheme was used to determine if the proportion of available browse sampled in 1996 was representative of the entire site surveyed in 1977. Within these plots, the number of stems was recorded by species and height. When stand-types were homogenous throughout a site, the 26 plots were chosen randomly. When sites covered more than one stand-type, the 26 plot locations were chosen systematically to represent each stand-type in equal proportions as sampled in 1977.

Browse availability was compared between years (1977 vs. 1996) using χ^2 contingency tables for each species by site. When significant differences were found, Bonferroni *z*-tests were performed to detect what changes in availability or utilization by species had occurred over the 19-year period (Byers and Steinhorst 1984).

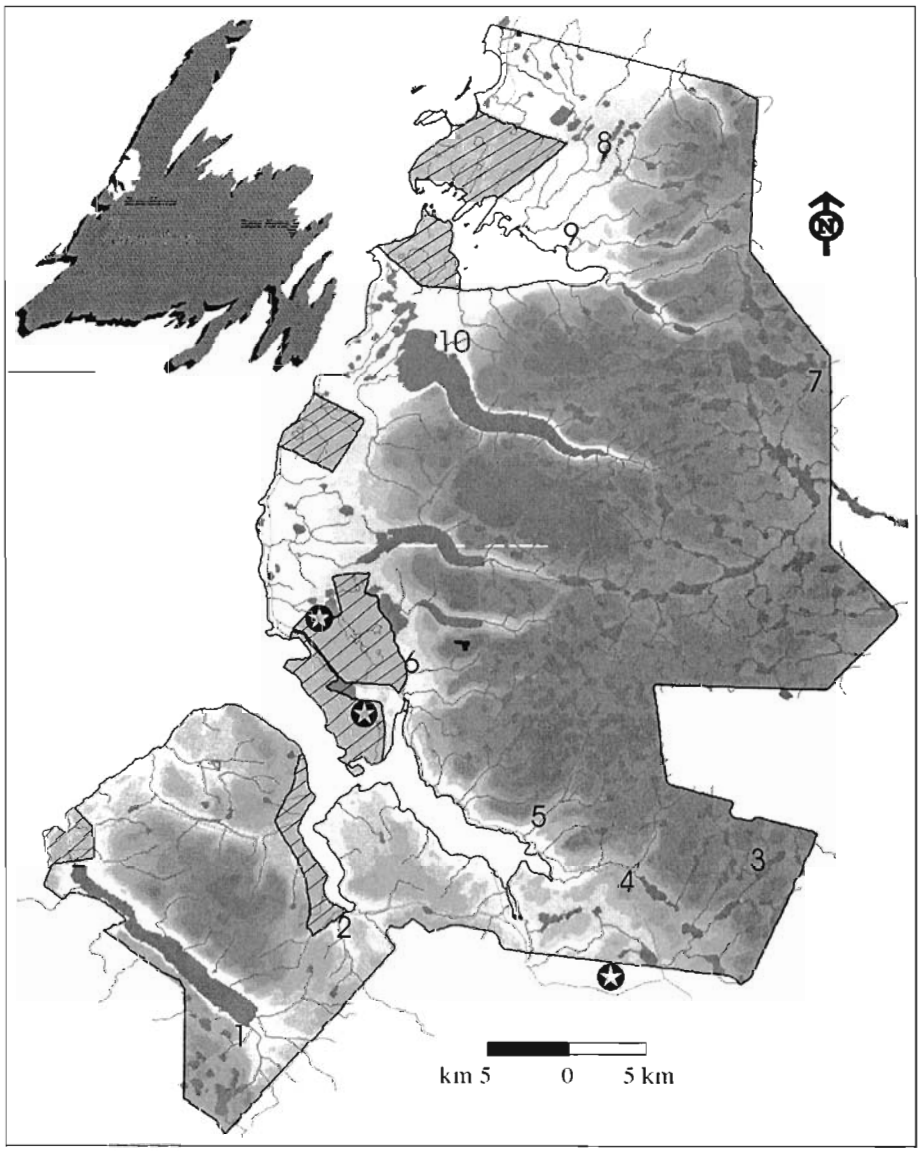

Fig. 2. Location of browse surveys conducted during 1977 and 1996 in Gros Morne National Park, Newfoundland. Stars indicate browse surveys completed outside Park boundaries (hatched areas) during 1996.

The density of twigs and stems of the most abundant species at each site were compared between years and among ecoregions by 1-way ANOVA and Tukey multiple comparisons (Lapin and Barnes 1995).

Vegetative species composition was compared using diversity indices which were calculated based on the total number of stems for all plots at each site. Indices of species richness (number of taxa and Margalef), species heterogeneity (Simpson and Shannon), and species evenness (Sheldon and Pielou) were calculated among ecoregions for the 10 sites surveyed in 1977 and 1996 and for sites surveyed outside Park boundaries in 1996. The simplest index of species richness (number of taxa)

measures only the number of species while a second index of richness (Margalef's index) incorporates both the number of species and the total number of individuals of each species (Brower and Zar 1977). Species evenness measures relative abundance of all species in a community, although not independent from the total number of species (DeBenedictis 1973). The Simpson and Shannon indices incorporate both species richness and the evenness of the individuals' distribution among the species. The Simpson index of diversity (heterogeneity) is less sensitive to changes in numbers of rare species in communities, but requires sample sizes >9 times that of the Shannon index for the same statistical resolution (Magnussen and Boyle 1995). Differences in species diversity among groups were tested by 1-way ANOVA and Tukey multiple comparisons (Lapin and Barnes 1995). All null hypotheses were tested at $\alpha = 0.05$ level of significance.

RESULTS

Browsing Intensity

Densities of moose pellet groups indicated an increase in relative abundance of moose between 1977 and 1996 as did aerial census data collected from 1971 through 1995. Mean pellet group densities did not differ among ecoregions in 1977 ($P = 0.447$) or during 1996 ($P = 0.453$). Mean pellet group densities did not significantly differ between 10 sites in 1977 and sites surveyed outside Park boundaries during 1996 ($P = 0.722$; Fig. 3). Pooled mean pellet group densities from surveys of the 10 sites in 1996 were significantly greater than those of the same 10 sites in 1977 ($P = 0.001$) and sites located outside park boundaries in 1996 ($P = 0.006$).

Overall, browsing intensity (proportion of total available twigs browsed) increased at all sites from 1977 to 1996. The greatest browsing intensity reported in 1977 was

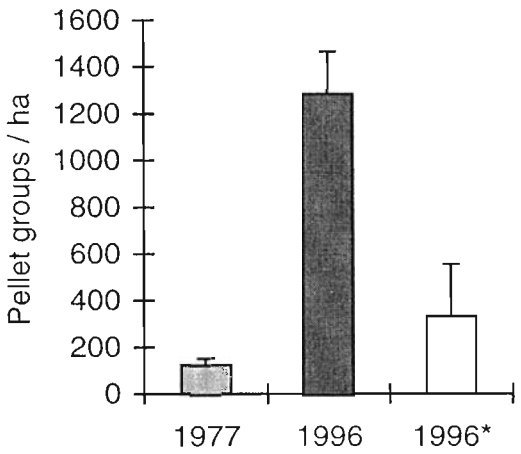

Fig. 3. Pooled mean pellet group counts / ha (± SE) in Gros Morne National Park during 1977, 1996, and at sites located outside Park boundaries (1996*).

10.1% of total available twigs at the Cow Head site. Browsing intensity increased to more than double the levels of the previous browse surveys at all sites by 1996 and exceeded 70% of the total available twigs at Middle Brook. By 1996, use of browse by moose in the Park had increased significantly within all ecoregions of the Park from that of 1977 (Table 1). Mean numbers of browsed twigs / ha did not significantly differ among ecoregions in 1977 ($P = 0.608$) or during 1996 ($P = 0.321$). Pooled mean numbers (all ecoregions) of browsed twigs / ha increased significantly from 1977 to 1996 ($P = 0.001$). Levels of browsing in the Park in 1977 were similar to those outside Park boundaries in 1996 ($P = 0.328$; Fig. 4).

Relative use of browse by snowshoe hares was much lower than that of moose during both surveys. In 1977, snowshoe hares browsed 2.0% of the available twigs. Browsing intensity in 1996 was 0.5% of the available twigs at all sites and reached 4.9% at sites outside the Park. Levels of browsing by hares were significantly greater at sites located outside Park boundaries ($P \leq 0.002$) but did not differ among ecoregions

Table 1. Mean density of browsed twigs (/ha) by ecoregion in Gros Morne National Park, Newfoundland.

Ecoregion	Year	*n*	Mean	SE
WNE	1977	4	7,347	1,606
WNE	1996	4	196,718	35,082
NPE	1977	4	11,279	4,410
NPE	1996	4	183,850	49,720
LRB	1977	2	12,161	3,395
LRB	1996	2	87,324	17,436
Overall	1977	10	9,883	1,918
Overall	1996	10	169,692	26,317

in 1977 or in 1996. Pooled mean numbers of hare browsed twigs did not differ between 1977 and 1996 (P = 0.486). The lowest levels of hare browsing occurred on the Long Range Barrens ecoregion at St. Paul's Big Pond where no hare browsing was observed in 1977 or 1996.

Browse Use and Availability

A total of 36 species (26 browsed) of woody plants were recorded in 1977 in comparison to 29 species (22 browsed) in 1996 (Appendix A). In 1977, the most commonly browsed species were Canada yew, mountain maple, balsam fir, and white birch which made up 31, 16, 13, and 12% of the browsed twigs, respectively. Balsam fir was the most abundant species (72 %) in 1977, but only a small proportion (0.7%) of it was browsed (Tables 2 and 3). The remainder of the above species accounted for 13.0% of the available browse and were used in greater proportions relative to their availability (Fig. 5). During 1996, balsam fir was the most commonly browsed species representing 83.5% of available browse and 92% of browsed twigs. A greater proportion (37.7%) of the available balsam fir was browsed in 1996 (Table 2). Canada yew, white birch, and mountain maple accounted for only 2.0% of the available browse and 4.3% of the total number of browsed twigs (Fig. 6). Preference for browse by moose changed significantly as did the availability of browse (Figs. 5 and 6).

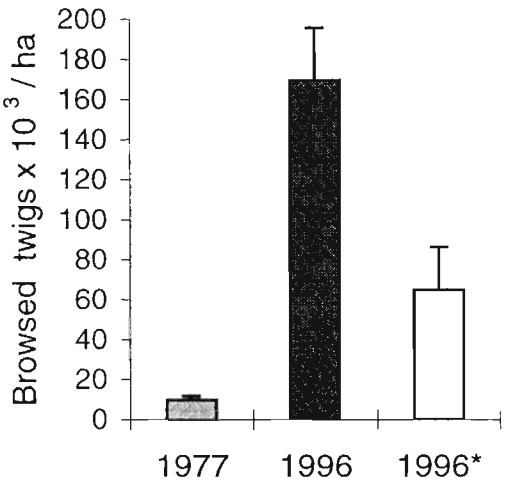

Fig. 4. Pooled mean number of browsed twigs x10^3/ ha (± SE) in Gros Morne National Park during 1977, 1996, and at sites located outside Park boundaries (1996*).

Significant differences ($P < 0.001$) occurred among proportions of available browse species between 1977 and 1996 at all 10 sites. Significant differences ($P < 0.05$) in availability occurred between 1977 and 1996 for most browse species. Species browsed by moose in greater proportions relative to their availability in 1977 decreased in availability by 1996 (Table 3). Species not

Table 2. Browsing intensity (% of available twigs browsed) by species determined during browse surveys in 1977 and 1996, Gros Morne National Park. Species that comprised < 0.1 % of total available twigs in both years are not included. *n* indicates the number of twigs browsed for each species.

Species	1977 (*n*)	1996 (*n*)
Red elderberry	64.3 (180)	66.7 (82)
Chuckley pear	42.1 (390)	65.4 (214)
Ovalleaf bilberry	38.7 (295)	68.3 (28)
White birch	19.1 (519)	71.5 (951)
Canada yew	18.4 (1,317)	90.1 (91)
Mountain maple	18.2 (687)	80.7 (815)
Rhodora	14.0 (76)	0.0
Squashberry	14.0 (16)	4.6 (1)
Red-osier dogwood	11.5 (29)	61.9 (39)
Bristly-black currant	10.2 (17)	0.0
Wild raisin	5.7 (72)	0.0
Mountain alder	4.0 (38)	12.0 (143)
Speckled alder	3.4 (6)	20.8 (208)
Skunk currant	2.2 (9)	20.0 (2)
Raspberry	2.0 (14)	55.5 (141)
Balsam fir	0.7 (545)	37.7 (39,504)
Mountain ash	0.5 (3)	51.0 (188)
White spruce	0.3 (2)	2.6 (46)
Black spruce	0.03 (2)	1.5 (207)
Mountain holly	0.0	72.7 (197)
Total	4.0 (4,239)	33.9 (42,929)

browsed or browsed infrequently in 1977 (spruce spp., alder spp., and mountain holly) increased in abundance by 1996 (Table 3). At lowland sites, alternate browse species (species other than balsam fir) accounted for 19.3% of the available browse in 1977 and only 4.0% in 1996. In 1977, Canada yew was present at all 8 lowland sites. By 1996, availability of Canada yew was significantly lower ($P < 0.05$) at 6 sites and absent at the 2 remaining sites. Mountain maple availability significantly decreased ($P < 0.05$) at all 7 of the lowland sites. In 1996 availability of white birch was significantly lower ($P < 0.05$) at 7 of the 8 sites at which it was located. Black spruce was virtually unbrowsed and significantly increased ($P < 0.05$) in availability at 7 of the 10 sites surveyed.

Long Range Barrens Ecoregion

Balsam fir accounted for 12.5% of the total browsed twigs in 1977. Browsing intensity changed from 0.7% of available balsam fir in 1977 to 37.7% in 1996. Overall availability of balsam fir increased. Sites located within the Long Range Barrens ecoregion did not follow the same trend. At Bowater's Gap and St. Paul's Big Pond during 1977, use of balsam fir was high (29.1 and 34.3%, respectively) relative to that of lowland sites, representing 77.4 and 95.6% of the browsed twigs, respectively, in 1996. Availability (proportion of balsam fir) was significantly lower ($P < 0.05$) at Long Range Barren sites in 1996. Availability of browse was limited primarily to balsam fir at these sites. The low availability of alternate browse species resulted in high use of balsam fir. High browsing intensities of balsam fir resulted in suppressed vertical growth and mortality of regenerating stems within reach of moose. Availability of black spruce significantly increased ($P < 0.05$) at Long Range Barren sites from 1977 to 1996. Densities of black spruce twigs increased but not significantly from 1977 to 1996 (Fig. 7).

Western Newfoundland Ecoregion

In 1977, use of balsam fir in Western Newfoundland ecoregion was moderate relative to sites within the Long Range Barrens ecoregion. Mean stem density of Western Newfoundland ecoregion sites was significantly lower than that of Long Range Barrens ecoregion at $P = 0.08$. Use of balsam fir ranged from 16 to 34% of the total browsed twigs in 1977 and ranged from 73.3 to 96.3% in 1996. While balsam fir

Table 3. Changes in availability of browse species (number of twigs x 10^3/ha) as determined by browse surveys in 1977 and 1996 in Gros Morne National Park. Species that comprised < 0.1 % of total available twigs in both years are not included.

Species	1977 (%)	1996 (%)	% change
Balsam fir	184.6 (71.7)	414.2 (83.5)	124.4
Black spruce	18.5 (7.2)	54.9 (11.1)	197.0
Canada yew[1]	17.6 (6.8)	0.4 (0.1)	-97.7
Mountain maple[1]	9.3 (3.6)	4.0 (0.8)	-57.0
White birch[1]	6.7 (2.6)	5.3 (1.1)	-21.1
Wild raisin	3.1 (1.2)	0.0	-100.0
Chuckley pear[1]	2.3 (0.9)	1.3 (0.3)	-43.3
Mountain alder	2.3 (0.9)	4.7 (1.0)	103.4
Ovalleaf bilberry[1]	1.9 (0.7)	0.2 (0.03)	-91.4
White spruce	1.8 (0.7)	7.0 (1.4)	282.7
Raspberry	1.7 (0.7)	1.0 (0.2)	-41.0
Mountain ash	1.6 (0.6)	1.5 (0.3)	-7.0
Rhodora[1]	1.3 (0.5)	0.0	-100.0
Skunk currant	1.0 (0.4)	0.04 (0.01)	-96.1
Elderberry[1]	0.7 (0.3)	0.5 (0.1)	-29.3
Red-osier dogwood[1]	0.6 (0.2)	0.3 (0.1)	-59.9
Mountain holly	0.6 (0.2)	1.1 (0.2)	77.2
Bristly-black currant[1]	0.4 (0.2)	0.0	-100.0
Speckled alder	0.4 (0.2)	4.0 (0.8)	810.7
Squashberry	0.3 (0.1)	0.1 (0.02)	-69.0
Total (all species)	257.5 (100)	501.0 (100)	94.5

[1]Denotes species that were browsed in significantly greater ($P<0.05$) proportions than their relative availability as determined from 1977 browse surveys.

was the most abundant browse species in 1977, Canada yew, mountain maple, and white birch were most frequently browsed. By 1996 those species were virtually eliminated on all sites and their low abundance precluded high use by moose. Mean stem density of Canada yew and mountain maple in the Western Newfoundland ecoregion in 1977 was similar to that of sites outside the Park but was significantly lower ($P = 0.001$ and $P = 0.011$, respectively) in 1996. Mean stem density of balsam fir was similar while the density of twigs increased significantly from 1977 to 1996 (Fig. 7). Stem density of Canada yew and mountain maple was significantly lower in 1996 while the density of black spruce increased significantly.

Northern Peninsula Ecoregion

Use of balsam fir in the Northern Peninsula ecoregion in 1977 was less than that of other ecoregions. Use of balsam fir ranged from 0 to 24% of the total browsed twigs in 1977 and ranged from 87.5 to 99.8% in 1996. Availability of balsam fir was greater than that of the Western Newfoundland ecoregion and alternate browse species made up a lesser proportion of available browse in 1977. Stem density of balsam fir did not change significantly from 1977 to 1996 while twig density increased. Canada yew, mountain maple, and white birch

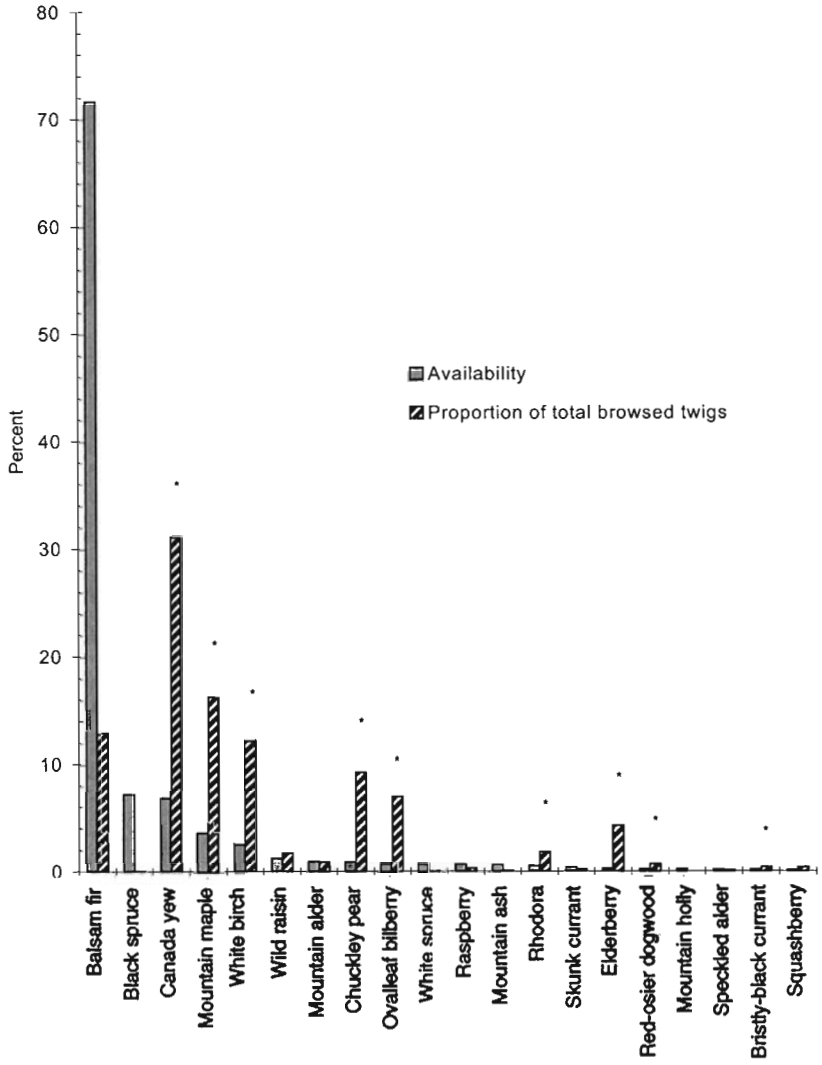

Fig. 5. Availability in relation to use by moose of major browse species within 10 sites in Gros Morne National Park during 1977. Species comprising < 0.1% of available browse were not included. Asterisks indicate species that were browsed in significantly greater ($P < 0.05$) proportions than their relative availability.

were the most freqently browsed species in 1977, and by 1996 those species were virtually eliminated on all sites, their low abundance precluding high use by moose. Densities of black spruce twigs were significantly lower ($P = 0.002$) in the Northern Peninsula ecoregion than that of the Long Range Barrens ecoregion in 1996 (Fig. 7). Mean stem density of black spruce was significantly lower than that of the Long Range Barrens ecoregion in 1977 ($P = 0.047$) and 1996 ($P = 0.01$). Stem density of Canada yew and mountain maple was significantly greater ($P = 0.001$ and $P = 0.006$, respectively) in sites outside the Park than the Northern Peninsula ecoregion sites in 1996 but not 1977. Significant declines occurred in both stem density and density of twigs of Canada yew and mountain maple from 1977 to 1996. Availability of mountain

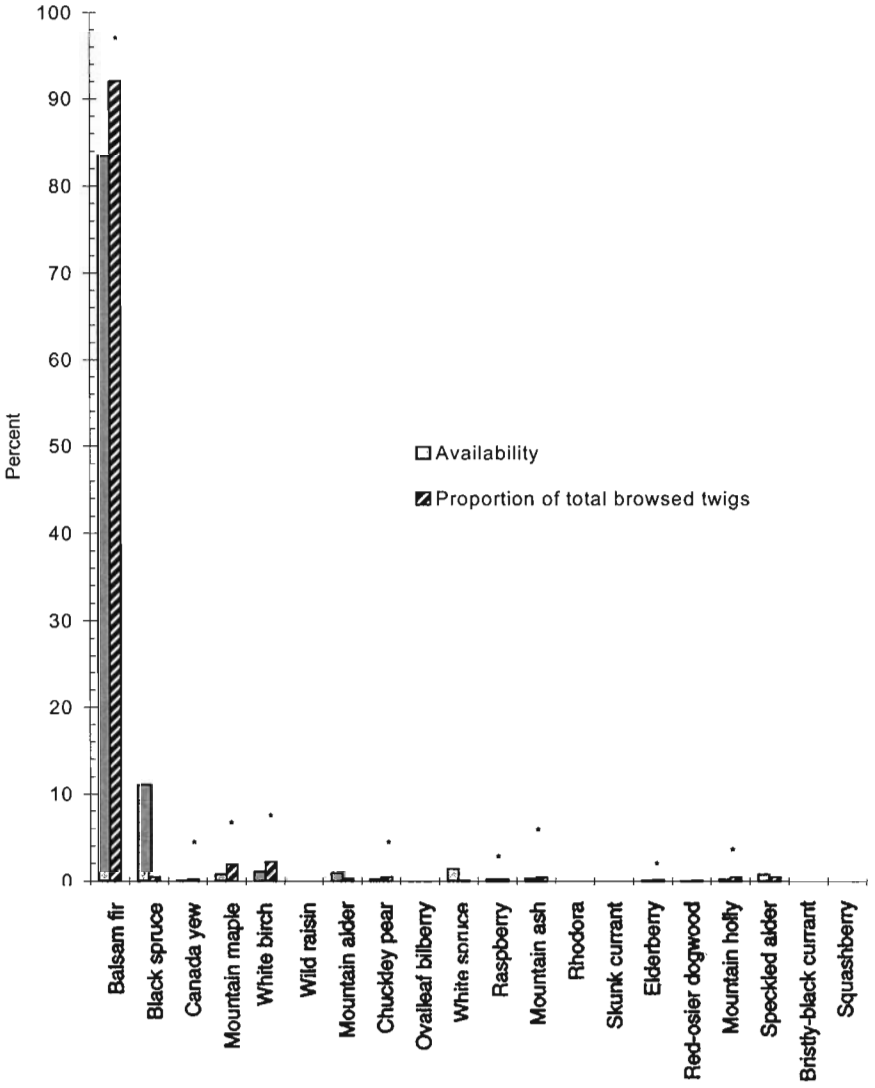

Fig. 6. Availability in relation to use by moose of major browse species within 10 sites in Gros Morne National Park during 1996. Species comprising < 0.1% of available browse were not included. Asterisks indicate species that were browsed in significantly greater ($P < 0.05$) proportions than their relative availability.

maple and Canada yew within low moose density sites outside the Park was 13 and 20%, respectively; greater than any of the 10 sites surveyed within the Park in 1996.

Species Diversity

Measures of community structure including species richness, species heterogeneity, and species evenness were calculated for the 10 sites in 1977 and 1996 as well as for 3 sites outside Park boundaries in 1996. Mean indices of species diversity did not differ among ecoregions in 1977 (Table 4). Similarly, in 1996 mean species diversity indices did not differ significantly among ecoregions with 2 exceptions (Table 5). Due to the lack of significance in 1977 and low significance in 1996 data were pooled. Overall, species diversity decreased significantly from 1977 to 1996 (Table 6).

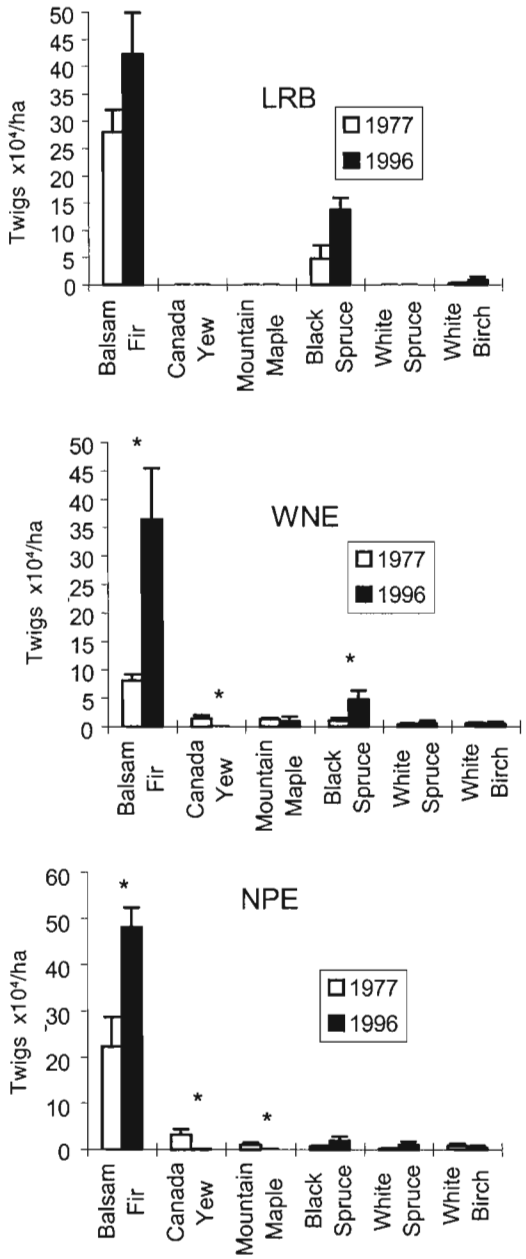

Fig. 7. Mean density of browse (# twigs x 10^4/ha ± SE) by ecoregion in Gros Morne National Park, Newfoundland in 1977 and 1996. Asterisks indicate statistically significant differences ($P < 0.05$) between 1977 and 1996.

Both the Shannon (H') and Simpson indices of species diversity decreased across all sites from 1977 to 1996. Mean indices of species heterogeneity in 1977 were significantly greater than species heterogeneity at the same sites in 1996 (Table 6). In addition, no significant difference was found among mean indices for 1977 and 1996 low moose density sites outside the Park (Table 6).

DISCUSSION

The pooled mean density of browsed twigs (all sites) increased significantly from 1977 to 1996 ($P = 0.001$). Prescott (1978) reported that moose range in Gros Morne National Park was in good condition supporting a relatively abundant and diverse number of preferred woody species. Since that time, however, browsing intensity has increased dramatically, ranging from 9.5 to 70.4% of available browse in 1996; compared to 1977 levels which ranged from 0.3 to 10.1%. These highly significant increases in browsing intensity over the relatively short period of 19 years, cause concerns as to the potential impacts of moose on vegetative species diversity and community structure of the boreal forest of Gros Morne National Park. Wolff (1978) stated that shrubs could withstand browsing intensities between 50-75%. McNicol *et al.* (1980) reported insignificant changes in stem density following 8 years of heavy browsing in a cutover in Ontario where 55% of stems were hedged (> 50% of their twigs browsed). Browsing has occurred in excess of the aforementioned levels within all areas of the Park.

Recent estimates of moose density for the entire Park revealed an increase from < 0.5/km² in 1977 (Janes 1977) to 4.0/km² in 1995 (Sullivan 1995). Crête (1989) suggested moose densities of 2.0/km² in the boreal forest of eastern Quebec were below carrying capacity and reported low winter use of balsam fir and relatively high (29%) use of deciduous twigs. Winter moose densities of 4.7/km² in central Newfoundland resulted in heavy browse dam-

Table 4. Species diversity indices (±SE) by ecoregion in 1977, Gros Morne National Park, Newfoundland.

	Ecoregion			
Index	WNE	NPE	LRB	*P*
Species number	16.25 ± 1.65	13 ± 0.71	14 ± 0.0	0.21
Margalef	2.31 ± 0.29	1.77 ± 0.094	2.02 ± 0.02	0.23
Simpson	0.74 ± 0.024	0.71 ± 0.047	0.72 ± 0.035	0.78
Shannon	1.75 ± 0.12	1.63 ± 0.13	1.57 ± 0.09	0.64
Pielou	0.63 ± 0.038	0.64 ± 0.044	0.6 ± 0.035	0.83
Sheldon	0.37 ± 0.043	0.40 ± 0.043	0.35 ± 0.035	0.75

Table 5. Species diversity indices (±SE) by ecoregion in 1996, Gros Morne National Park, Newfoundland.

	Ecoregion			
Index	WNE	NPE	LRB	*P*
Species number	11.25 ± 2.10	10.25 ± 1.18	9.50 ± 2.50	0.83
Margalef	1.68 ± 0.26	1.60 ± 0.18	1.41 ± 0.39	0.80
Simpson	0.43 ± 0.035	0.30 ± 0.046	0.50 ± 0.06	0.05
Shannon	1.02 ± 0.09	0.76 ± 0.11	1.06 ± 0.16	0.17
Pielou	0.43 ± 0.016	0.32 ± 0.036	0.48 ± 0.015	0.02
Sheldon	0.26 ± 0.027	0.21 ± 0.015	0.32 ± 0.035	0.08

age as evidenced by a halt in growth of white birch and some regeneration mortality (Bergerud and Manuel 1968). Damage to balsam fir was severe, including the suppression of terminal growth and reduced stocking density from uprooted seedlings (Bergerud and Manuel 1968).

Extreme browsing intensities at all sites in Gros Morne National Park indicate that moose density is excessive in relation to the available vegetation resources. Total number of available twigs increased from 257,500/ha in 1977 to 500,900/ha in 1996, primarily due to an increase in balsam fir and spruce species. However, considering the increase in moose density during the same time period, availability of twigs per moose in 1996 was < 25% of 1977 levels. Reductions in available forage within the Park as moose densities stabilize or continue to increase will eventually result in higher winter mortality rates, reduced female productivity, and a decline in moose numbers.

Data suggest that productivity of moose within the Park has declined as has the quality and quantity of forage. Estimates of percent calves in late winter moose surveys of the entire Park decreased from 27.6% in 1976 to 13.3% in 1995 (Appendix B). During periods when browse surveys showed no signs of food shortages, estimates of percent calves for the entire island of Newfoundland ranged from 24 to 29% (Pimlott 1959). Mech *et al.* (1987) reported cumulative winter influences on maternal nutrition can strongly determine fecundity of moose populations. Boer (1992) indicated

Table 6. Mean indices of community structure (± SE) among 1977, 1996, and sites located outside Gros Morne National Park, Newfoundland by ANOVA and Tukey multiple comparisons among groups.

	Group			
Index	1977 ($n=10$)	1996 ($n=10$)	1996* ($n=3$)	P
Species number	14.50 ± 0.82^{a}	10.50 ± 0.98^{b}	11.33 ± 1.20^{ab}	0.014
Margalef	2.04 ± 0.14^{a}	1.60 ± 0.13^{a}	1.67 ± 0.16^{a}	0.075
Simpson	0.72 ± 0.020^{a}	0.39 ± 0.036^{b}	0.70 ± 0.014^{a}	0.0001
Shannon (H')	1.66 ± 0.070^{a}	0.92 ± 0.072^{b}	1.42 ± 0.024^{a}	0.0001
Pielou	0.62 ± 0.022^{a}	0.40 ± 0.025^{b}	0.59 ± 0.019^{a}	0.0001
Sheldon	0.37 ± 0.024^{a}	0.25 ± 0.018^{b}	0.37 ± 0.034^{a}	0.001

[a, b]Groups not sharing common letters denote significant Tukey multiple comparison statistics.

that fecundity of populations approaching carrying capacity declined through delayed sexual maturation of yearlings, reduced incidence of twins, and finally by producing decreasing numbers of calves per adult female. As populations become limited by food resources, fecundity declines (Verme 1969, Clutton-Brock *et al.* 1982), survival of calves declines and finally reduced adult survival occurs (Boer 1992). Fecundity of moose populations within the Park appears to have declined with the availability of vegetation resources.

Browsing intensity by snowshoe hares was not comparable to the relative use of browse by moose. Snowshoe hares browsed 2.0 and 0.5% of the available vegetation in 1977 and 1996, respectively. Although browsing by hares may have an impact on vegetation within the Park, it is minimal when compared to that of moose. Dodds (1960) reported that the hare population peaked on the Northern Peninsula of Newfoundland in 1956-57. Assuming a 9-10 year cycle, the hare population should have peaked again in 1966-68 and again in 1976-1979. Prescott (1978) suggested that the hare population was high and increasing during that period. Information from small game returns during 1966-95 for the Northern Peninsula indicate that the average number of hares killed per return was high during the period of the survey. Similar data for 1995 indicated that numbers of hares killed per return were lower (NF Wildlife Division, *unpubl. data*). Survey data suggested that the hare population was high during the 1977 survey but that additional peaks did not occur between surveys, thereby lessening the possibility that browsing by hares played a large role influencing plant community structure.

Vegetation surveys conducted within the Park revealed that 26 of 36 available browse species were used in 1977, whereas 22 of 29 available species were browsed in 1996. Dodds (1960) reported 35 browse species occurred within areas dominated by balsam fir in Newfoundland. Cumming (1987) found moose browsed 22 of 33 species encountered during 51 browse surveys from 1955-1970 in Ontario, and beaked hazelnut and mountain maple composed 61.3% of the forage. Moose demonstrate different food habits in eastern and western North America as differences in abundance of browse species occur (Krefting 1974). Willows are a major source of winter browse

in the west (Peek 1974), whereas balsam fir, aspen, and white birch are the major species in the east (Krefting 1951). In Newfoundland, white birch and balsam fir are the major browse species (Bergerud and Manuel 1968); balsam fir exceeds white birch in the diet in areas of high moose density and where mature timber predominates (Pimlott 1965). Species of lesser importance included sweetgale, mountain alder, willow, Canada yew, mountain ash, mountain maple, cherry, wild raisin, mountain holly, and chuckley pear. Browse use there was 47% balsam fir, 20% white birch, and 13% raspberry. In areas of relatively low moose density, diet consisted of 44% balsam fir, 22% willow, and 11% alder. Crête and Courtois (1997) also reported use of *Alnus crispa* but not *A. rugosa*. In contrast, Thomas (1990) stated that *Alnus* spp. were used little as forage by moose in many regions. Browse surveys conducted in 1977 within the Park revealed shrubs and deciduous browse made up 87% of the total browsed twigs while in 1996 balsam fir comprised 92% of the total twigs browsed. Changes in the diet composition of moose were reflected in browse surveys as resource use changed with changing availability of forage species. Moose react to the spatial and temporal variability in food resources by selective foraging on the landscape (Senft *et al.* 1987).

Browse surveys revealed significant changes in utilization and availability of woody vegetation in Gros Morne National Park between 1977 and 1996. Canada yew, mountain maple, white birch, chuckley pear, and ovalleaf bilberry were browsed in significantly greater proportions than their relative availability in 1977. However, the availability of these species decreased from 14.6% to 2.2% of available browse in 1977 and 1996, respectively. Balsam fir, a species which is tolerant of browsing, was used in significantly less proportions relative to its availability in 1977, and it increased in abundance from 71.7% to 83.5%. Black spruce and white spruce, species seldom browsed, increased from 7.9% to 12.5% of available browse. Excessive browsing by moose has reduced availability of preferred forage species, allowing other non-browsed species to increase. The capability of Long Range Barren sites to support moose appears lower than that of the lowland regions as both the density of twigs and diversity of browse species was generally lower. Suppression and mortality of browsed species appeared to have released black spruce stems to become the dominant understory species of Long Range Barren sites.

The decline in abundance of forage species through selective browsing by moose has been previously reported (Krefting 1974, Snyder and Janke 1976, Risenhoover and Maass 1987, Thompson *et al.* 1992). Prescott (1977) indicated that the most important browse species for moose in Gros Morne National Park were Canada yew, mountain maple, balsam fir, white birch, and chuckley pear which composed 79% of twigs browsed by moose in 1977. Bateman (1977) suggested that Canada yew would be eradicated from the Park as a result of excessive moose browsing. Overall, availability of Canada yew decreased from 6.8% of available forage in 1977 to 0.1% in 1996 and was eradicated on 2 sites. Bergerud and Manuel (1968) found that white birch and mountain maple declined in areas of excessive moose browsing. Moose can affect structure and species composition in heavily browsed areas (Naiman 1988), and can influence forest successional patterns (Brandner *et al.* 1990, McInnes *et al.* 1992, Thompson *et al.* 1992). Browse species susceptible to high levels of browsing and/or preferred by moose have been lost in heavily utilized habitats in both Newfoundland (Pimlott 1953) and Isle Royale (Krefting 1951).

If moose browsing continues at the same

levels documented during this study, deciduous species such as white birch will be eliminated from the canopy of future forest stands. Suppression of vertical growth and subsequent mortality of balsam fir regeneration will allow spruce to replace balsam fir as the dominant species in stands within the Park. Snyder and Janke (1976) reported lower density of balsam fir and higher density of white spruce on moose-browsed versus unbrowsed sites on Isle Royale. Albright and Keith (1987) found that heavy moose browsing of understory regeneration tended to convert fir woods to fir scrub and sparse stands of black spruce.

Low moose density sites located outside the Park surveyed in 1996 reflected similar availability of vegetation and species composition to those of the surveys in 1977, when moose densities were relatively low. Preferred browse species that were not found at sites in the Park were present at sites located outside Park boundaries. Our findings suggest that within a relatively short period of 19 years moose have significantly altered forest successional patterns within Gros Morne National Park due to intensive browsing on many browse species resulting in significant changes in structure and composition of vegetation within the Park.

CONCLUSIONS

Moose browsing intensity in 1996 has more than doubled since the initial surveys in 1977. Increased browsing pressure has led to mortality of preferred browse species through selective browsing. Species that made up the greatest proportion of browse in 1977 were eradicated from some sites and were greatly reduced in others. Canada yew, mountain maple, white birch, chuckley pear, and wild raisin are all species that have decreased in abundance. Surveys during 1996 in low density moose areas adjacent to Park boundaries reveal availability and composition of woody vegetation similar to that in the Park in 1977 when moose densities were lower. Species diversity in the Park during 1996 was significantly lower than that of 1977 as well as low moose density areas outside the Park surveyed in 1996.

Data suggest that moose have changed species composition, the proportion of available browse remaining, and hence forest succession patterns within Gros Morne National Park. It is apparent that moose are currently diminishing the ecological integrity of Gros Morne National Park. Under a regime of protection from hunting and in the absence of active management, data suggest that the moose population is altering successional patterns and vegetative species composition. This will continue as the population increases, and subsequently, becomes regulated by a declining food supply. The diversity of shrubs and trees has been significantly reduced over the past 19 years. If current processes continue without intervention, the structure of future forests may be significantly altered.

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Appendix A. List of common and scientific names of all woody vegetation species encountered during browse surveys in Gros Morne National Park, Newfoundland in 1977 and 1996. An asterisk denotes that a species was encountered, while blanks indicate species that were not encountered

Common Name	Scientific Name	1977	1996
Balsam fir	*Abies balsamea*	*	*
Red maple	*Acer rubrum*	*	
Mountain maple	*Acer spicatum*	*	*
Mountain alder	*Alnus crispa*	*	*
Speckled alder	*Alnus rugosa*	*	*
Chuckley pear	*Amelanchier spp.*	*	*
White birch	*Betula papyrifera*	*	*
Leatherleaf	*Chamaedaphne calyculata*	*	
Alternate-leaved dogwood	*Cornus alternifolia*	*	
Red-osier dogwood	*Cornus stolonifera*	*	*
Beaked hazelnut	*Corylus cornuta*		*
Northern bush honeysuckle	*Diervilla lonicera*	*	
Dwarf huckleberry	*Galussacia dumosa*	*	
Sheep laurel	*Kalmia angustifolia*	*	*
Bog laurel	*Kalmia polifolia*	*	
Larch	*Larix laricina*	*	
Labrador tea	*Ledum groenlandicum*	*	*
Northern honeysuckle	*Lonicera villosa*		*
Sweet gale	*Myrica gale*	*	
Mountain holly	*Nemopanthus mucronata*	*	*
White spruce	*Picea glauca*	*	*
Black spruce	*Picea mariana*	*	*
Cherry	*Prunus spp.*		*
Skunk currant	*Ribes glandulosum*	*	*
Smooth gooseberry	*Ribes hirtellum*	*	*
Bristly-black currant	*Ribes lacustre*	*	*
Red currant	*Ribes triste*	*	
Rhodora	*Rhododendron canadense*	*	*
Wild rose	*Rosa spp.*		*
Raspberry	*Rubus idaeus*	*	*
Blackberry	*Rubus spp.*	*	
Willow	*Salix spp.*	*	*
Red elderberry	*Sambucus pubens*	*	*
Soapberry	*Shepherdia canadensis*	*	
Mountain ash	*Sorbus spp.*	*	*
Canada yew	*Taxus canadensis*	*	*
Ovalleaf bilberry	*Vaccinium ovalifolium*	*	*
Wild raisin	*Viburnum cassinoides*	*	*
Squashberry	*Viburnum edulum*	*	*
Highbush cranberry	*Viburnum trilobum*	*	*

Appendix B. Occurrence of calves in moose populations within Gros Morne National Park and Eastern Canada. Percent calves = calves/(calves+yearlings+adults) * 100.

Location	Total number of adults in survey	% calves	Reference	Estimates based on
GMNP, 1976	416	27.6	Janes 1976	aerial census
GMNP, 1977	419	22.9	Janes 1977	aerial census
GMNP, 1990	227	15.0	Taylor 1991	aerial census
GMNP, 1995	579	13.3	Sullivan 1995	aerial census
NF, 1953	763	29	Pimlott 1959	hunter kill data
NF, 1954	243	24	Pimlott 1959	hunter kill data
NF, 1955	220	26	Pimlott 1959	hunter kill data
NF, 1956	791	26	Pimlott 1959	hunter kill data
NF, 1959	7,590	16.4	Pimlott 1959	observations
NB	2,331	19.9	Wright 1956	observations
Quebec	1,819	19.3	Moisan 1952	observations
Quebec	—	25.4 - 35	Courtois *et al.* 1994	aerial census
Ontario	2,944	17.9	Peterson 1955	observations