EFFECTS OF BEAVER AND MOOSE ON THE VEGETATION OF ISLE ROYALE NATIONAL PARK

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ABSTRACT: We studied the cumulative effect of browsing by moose (*Alces alces*) and tree-cutting by beaver (*Castor canadensis*) on tree density, basal area, and species composition on the northeastern end of Isle Royale National Park. Beaver-affected land (abandoned ponds, occupied ponds, and foraging areas) in one representative area increased from 26% of the land area in 1957 to 34% in 1978. Beaver significantly decreased aspen (*Populus tremuloides*) tree density from 140 ± 23 (SE) to 27 ± 10 stems/ha and basal area from 10.2 ± 1.6 to 3.6 ± 1.4 m^2/ha adjacent to ponds and streams. Balsam fir (*Abies balsamea*) tree density was significantly greater in beaver-cut areas than in uncut forest (417 ± 77 compared to 227 ± 55 stems/ha). Moose browsed preferentially on aspen in the summer and winter in both beaver-cut areas and uncut forest. Moose neither preferred nor avoided balsam fir in the beaver-cut area, but avoided it in the uncut forest. White spruce (*Picea glauca*) was not browsed. The density of coniferous species with diameter at breast height <15 cm was greater than 400 stems/ha, while stem densities of the heavily browsed deciduous species were less than 20 stems/ha in both beaver-cut areas and uncut forest. Changes in plant species composition affected by moose and beaver populations may decrease soil fertility and alter successional patterns in stream side areas and adjacent forests.

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Moose and beaver have browsed on the vegetation of Isle Royale for almost a century. Moose feed on the leaves and twigs of woody species throughout the year. Beaver cut down trees and shrubs in the spring and fall for dam-building and feeding. Aspen (*Populus tremuloides*) is a preferred item in the diet of both beaver and moose when it is available (Shelton 1966, Krefting 1974, Joyal 1976). Balsam fir (*Abies balsamea*) is an important winter browse for moose in some areas (Bergerud and Manuel 1968, Cumming 1987). Selective browsing by beaver and moose has caused measurable changes in tree species density and basal area on Isle Royale forests adjacent to streams and lakes.

Moose browse mainly on the dormant twigs of woody species in winter. Balsam fir and beaked hazel (*Corylus cornuta*) increased in importance in the diet, while paper birch (*Betula papyrifera*) and aspen decreased in importance, between 1945 and 1972 on Isle Royale (Krefting 1974). The changes were related to availability-excessive cropping had reduced the density of the preferred species. Balsam fir was the most important browse species on the west end of Isle Royale in the mid-1980's, although diet composition varied with habitat type (Risenhoover 1987). Other important species were mountain ash (*Sorbus americana*), paper birch, red-osier dogwood (*Cornus stolonifera*), and cedar (*Thuja occidentalis*). Juneberry (*Amelanchier* sp.), beaked hazel, willows (*Salix* sp.), paper birch, and balsam fir were important browse species in the winter in northeastern Minnesota (Peek *et al.* 1976). The most important winter browse species in Ontario were beaked hazel and mountain maple, while preferred but less available species included mountain ash, alternate-leaved dogwood (*Cornus alternifolia*), and juneberry (Cumming 1987).

In summer, moose strip the growing leaves from twigs of deciduous species. Leaves are completely removed from a growing twig, and some regrowth may occur if the leaf-stripping occurs early in the summer (Miquelle 1983). Sugar maple (*Acer saccharum*), mountain maple (*A. spicatum*), mountain ash, paper birch, and trembling aspen were the major species in the summer diet of moose in 1946 on the western end of Isle Royale (Krefting 1974). Mountain ash, mountain maple, and paper birch comprised 89% of the diet 25 years later (Krefting 1974). Mountain ash, mountain maple, yellow birch (*Betula lutea*), and paper birch made up 88% of the summer diet in 1977 and 1978, although a total of 24 woody species were eaten (Miquelle 1979). The same four species plus sugar maple were the major components of the summer diet in 1986 (Ackerman 1987). Aspen, pin cherry (*Prunus pennsylvanicus*), willows, and paper birch were the main summer browse species in northeastern Minnesota (Peek *et al.* 1976). These species are also eaten on Isle Royale, but some of them are only locally abundant, e.g., pin cherry.

Browsing at moderate to high levels keeps twigs within reach of moose (Aldous 1952, Danell *et al.* 1985). If browsing pressure is removed, for example with exclosures, even severely hedged stems grow out of reach of moose (e.g., Bergerud and Manuel 1968). Most browse species can survive removal of half or more of the current annual growth (CAG) twigs. Julander (1937) found that aspen could withstand browsing on up to 70% of twigs each summer and still grow taller and produce more shoots. However, Olmsted (1979) suggested that aspen could tolerate browsing on only 30% of its current annual growth twigs throughout the year. Removal of all CAG twigs of mountain maple for 10 years reduced twig production by only 17% (Krefting *et al.* 1966). Only 1 of 90 balsam fir trees died after up to 50% removal of twigs for two years (Bergerud and Manuel 1968).

In contrast to moose, beaver cut trees and small shrubs at ground level, primarily in the spring and fall. Branches are cut off of felled trees and carried to water for feeding or winter storage. Aspen is generally reported to be the species most preferred by beaver (e.g., Shadle *et al.* 1943, Shelton 1966, Dalton 1984). However, beaver survive when aspen is not available, and it has been suggested that the observed preference for aspen is due to availability (Jenkins 1981). On Isle Royale, other tree species close to a pond are bypassed in favor of aspen trees farther away by beaver (Shelton 1966, Shelton and Peterson 1983). In the summer, the beaver diet consists mainly of herbaceous and aquatic plants (Shelton 1966, Svendsen 1980).

Although the number of trees cut each year is small, beaver can have a significant long-term effect on the landscape. Beaver impounded 12% of the land area of the Kabetogama Peninsula in northern Minnesota in 46 years, and an additional 12-15% of the upland forest was affected by beaver foraging (Naiman *et al.* 1988). Beaver meadows are created when a beaver pond is drained. Beaver ponds were drained and then reflooded every 10 to 30 years in the Adirondack Mountains (Remillard *et al.* 1987). None of the beaver ponds or meadows in the study by Remillard *et al.* returned to upland forest after being impounded by beaver.

Others have demonstrated the effect that moose alone have on forests of Isle Royale. Moose browsing significantly decreased height and diameter growth of browsed species after 20 years, but did not affect stem density, relative to stems inside of exclosures (Krefting 1974). Stem density inside the exclosures had begun to decrease because of shading by 1982 (Risenhoover and Maass 1987). A more thorough study of the unbrowsed exclosures and browsed control plots showed that tree biomass was significantly greater, shrub biomass was not different, and herb biomass was significantly less inside the exclosures in 1987 (McInnes 1990). Balsam fir biomass was significantly greater inside than outside moose exclosures. Long-term moose browsing caused mountain ash and balsam fir densities to decrease, while the density of white spruce trees increased, in areas within 100 m of Lake Superior (Snyder and Janke 1976).

Where beaver and moose occur together, it is possible to investigate the cumulative effect of the two herbivores on forest and streamside vegetation. In this study we: (1) interpreted aerial photography to determine how much land area beaver have affected by building dams and cutting trees; (2) determined how selective cutting by beaver and browsing by moose has affected tree species composition; (3) determined browsing intensity of moose on vegetation in both the winter and the summer; and (4) determined seasonal browse preferences of moose. From these results, we inferred how moose and beaver affect current and future landscape patterns on the northeastern end of Isle Royale.

STUDY AREA

Isle Royale is a 500 km^2 island in Lake Superior. It is approximately 80 km long and 10 km wide, oriented in a southwest - northeast direction. Most of the studies cited above were done on the southwest end of the island. The Lane Cove study site was located on the northeastern end of Isle Royale (48°08'N, 88°34'W).

Moose were first observed on Isle Royale National Park in the early 1900's. At that time, balsam fir was the most common conifer, and aspen and paper birch occurred in uniform age stands originating from burns in the 1800's (Hansen *et al.* 1973). Growth of the moose population resulted in overbrowsing in the 1930's (Murie 1934). Since the 1950's the moose population has fluctuated between 500 and 1700 individuals (R.O. Peterson, Michigan Technological Univ., pers. commun.). Birch and aspen are the dominant species in the upland forests of the northeastern end of Isle Royale (Hansen *et al.* 1973). White spruce and balsam fir are the most common coniferous species.

Beaver were present on Isle Royale in the 1800's. It is thought that they were extirpated by trapping, but then recolonized the island sometime prior to the 1920's (Krefting 1963). The population increased to 1600 animals in the 1970's, then declined below 500 animals in the 1980's (Shelton and Peterson 1983). The best beaver habitat on Isle Royale is the series of parallel valleys and ridges on the northeastern end (Shelton 1966).

METHODS

Aerial Photo Interpretation

We interpreted aerial photographs of the Lane Cove study site and surrounding areas (about 200 ha) from 1957 (1:30,000 Black/White on 4 May) and 1978 (1:24,000 Color Infrared on 9 August) onto mylar film. We classified cover types as: (1) upland - upland forest that had not been impounded by beaver; (2) water - standing water impounded by beaver dams; and (3) beaver meadows - areas that had been impounded by beaver but were drained when the photograph was taken. The interpreted data was transferred to 1:24,000 United States Geological Survey Topographic maps using a Bausch and Lomb® Zoom Transferscope. The geographically referenced transparencies were digitized into the Arc/Info® Geographic Information System (GIS). The area of each cover type was calculated with the Arc/Info GIS.

We estimated the distance beaver forage from ponds from aerial photography taken in 1986 (1:16,840, Black/white infrared on 28 June). We measured the distance from pond edges (currently-used and drained ponds) to the distinct line of aspen trees visible on the photographs. The average beaver foraging distance from current and abandoned ponds was 27.7 m (SD = 7.9, n = 21). The GIS was then used to calculate the amount of land area within 27.7 and 35 m around the water and beaver-meadow cover types in 1957 and 1978.

Tree Species and Size Classes

We established 33 transect lines across approximately 12 ha of one valley in May

1988. We located 100 plots randomly on the transect lines. Transects were oriented perpendicular to the northeast-southwest direction of the valley floor. Transect lines were 25 to 120 m long and separated by 15 to 50 m. The same plot centers were used for the 100-m^2 plots for tree density and basal area and for the 2-m^2 plots used to measure browse use and availability.

The transect lines were located in areas where beaver had cut trees in the past and extended into the adjacent uncut areas. We classified plots into one of three types: uncut forest, beaver-cut area, or rock opening. Plots that were in rock openings were not used in the analysis because they did not represent the surrounding area. The beaver-cut area and uncut forest plot types corresponded to areas identified as upland during photo interpretation.

We measured the diameter at breast height (dbh) of each tree (dbh $\geq$ 2.5 cm) in a circular 100-m^2 plot in July 1988. Tree density and basal area were compared between the uncut forest and beaver-cut plot types with the Mann-Whitney U test ($a = 0.05$).

Browse Availability and Use

We sampled a circular 2-m^2 plot at each randomly-located plot center in 1988 and 1989. Plots were sampled after the end of growth but before leaf fall in late September, and before leaf-out in early May to determine availability and use in summer and winter, respectively. The number of twigs that were available and the number of bites taken was counted for all stems of species browsed by moose rooted inside the plots. We defined available twigs in winter as CAG twigs >10 cm long that were less than 3 m above ground level. We defined available twigs in summer as CAG twigs with 6 or more leaves, which is an average moose bite in summer (Miquelle 1979).

We calculated the percentage of twigs browsed on each species and associated confidence intervals according to Neu *et al.* (1974) for uncut forest and beaver-cut areas. A species was considered preferred if the lower 95% confidence interval for percent use of that species was greater than the percent of that species available among twigs of all species. A species was considered avoided if the upper 95% confidence interval for percent use of that species was less than the percent of that species available among twigs of all species. The amount of available browse in uncut forest and beaver-cut areas was compared with the Mann-Whitney U test.

Condition of Tree Regeneration

We estimated past browsing and condition for the aspen, spruce, and balsam fir stems < 2.5 cm dbh and > 1 m high nearest each plot center. Stem condition was classified as either unbrowsed, browsed, hedged from repeated browsing, or dead; a modification of a method used by McNicol *et al.* (1980). When a species was not present within a 5.64-m radius, the species was not counted in that plot. Browsed twig ends and branching history were used to determine evidence of past browsing. We used a contingency table analysis of species and condition to compare stem conditions among species.

RESULTS

Aerial Photo Interpretation

Total pond area did not change over 20 years, but locations of ponds did, as beaver impounded areas that were forested in 1957 (Figure 1). Beaver meadow area increased from 10% to 15% of the land area. Beaver meadow area includes foraging areas from previous years that have been flooded and then drained. The area within the 27.7 m foraging strip around active and drained ponds increased from 26 to 34 ha from 1957 to 1978. The total area of beaver-affected land (current ponds, drained ponds, and foraging area assuming a 27.7 m foraging distance around all ponds) increased from 48 to 68 ha during the 20 years. In this 200 ha part of Isle Royale, the amount of beaver-affected land increased from 25 to 34% of the total land area over 20 years. Nearly all aspen within the 27.7 m distance have been cut by beaver. If the beaver foraging distance increases to 35 m, and no new ponds are built, then the total area of beaver-affected land would be 76 ha, about 38% of the 200 ha we digitized.

Tree Species and Size Classes

Tree density was not different between the uncut forest and beaver-cut areas, but basal area was greater in the uncut forest (Z =

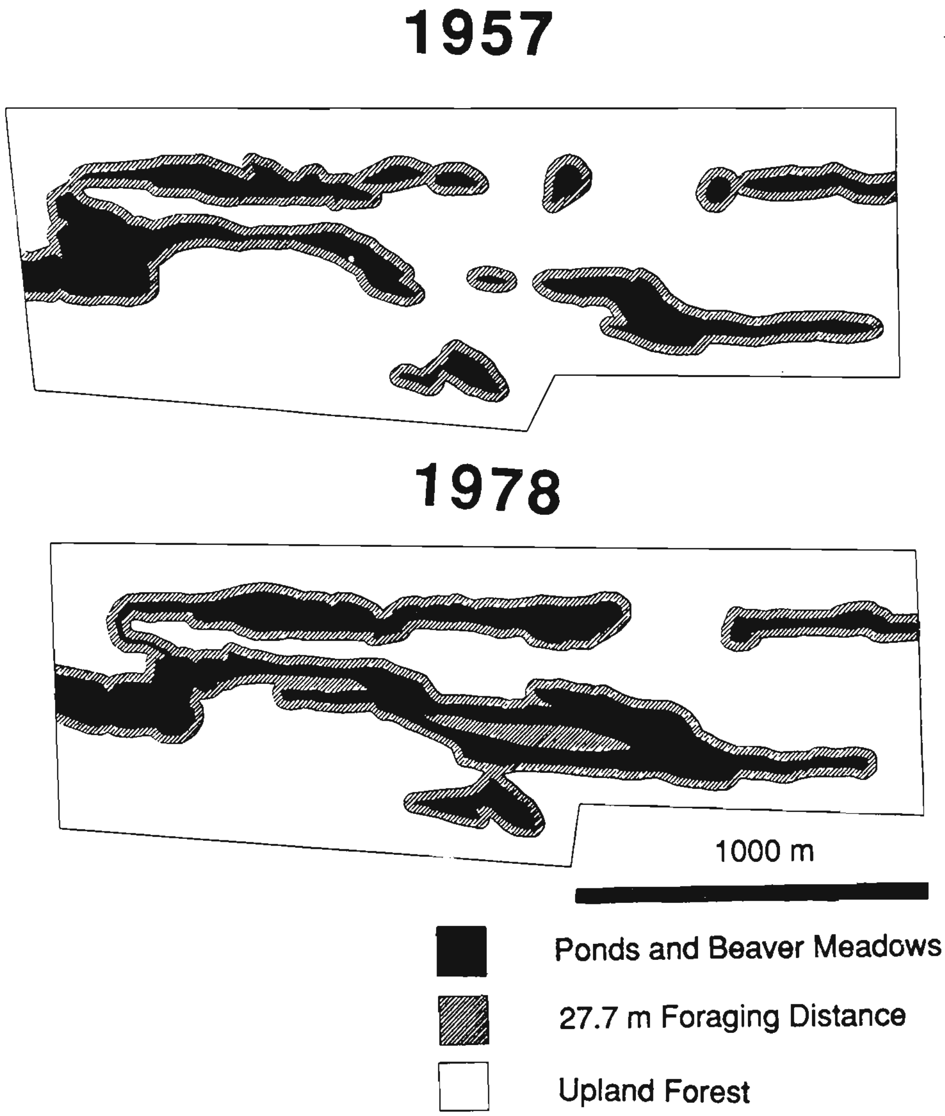

Fig. 1. Locations of ponds and beaver meadows, beaver-foraging areas, and upland forest in 1957 and 1978 as determined from aerial photograph interpretation of the Lane Cove study site, Isle Royale National Park. A mean foraging distance of 27.7 m from water and drained ponds by beaver is assumed for both of these time periods.

1.579 for tree density, $0.10 > P > 0.05$, $Z = 2.491$ for basal area, $P < 0.01$). While we could not measure the number of aspen trees cut by beaver over the past 20 years, it is apparent from Table 1 that aspen is the tree species decreased most in the beaver-cut area relative to the uncut forest. Aspen tree density and basal area were lower in the beaver-cut area ($Z = 4.047$ for tree density, $P < 0.005$, $Z = 3.337$ for basal area, $P < 0.005$). Balsam fir tree density and basal area were greater in the beaver-cut area than in the uncut forest ($Z = 2.668$ for tree density, $P < 0.005$, $Z = 1.849$ for basal area, $P < 0.03$). White spruce and paper birch tree densities and basal area were similar in both plot types (Fig. 2).

The density distribution of balsam fir trees was skewed to smaller size classes, the distribution of white spruce was flat, and the distribution of aspen and birch was skewed to larger size classes (Fig. 2a). Aspen and birch trees less than 15 cm dbh were rare in both the uncut forest and beaver-cut areas. Balsam fir was particularly abundant in beaver-cut areas, and greater than 95% of the trees were < 15 cm dbh. White spruce density was similar between the two plot types, but large white spruce trees were more common than large balsam fir trees.

Alder (*Alnus rugosa*) was the most common species in the "Other Species" category (Fig. 2). More than 80% of the trees in the "Other species" category in the beaver-cut area were alders. About 40% of the stems in the "Other species" category in the uncut forest were black ash. The "Other species" category also included white pine, mountain ash, and cedar. These species either were not browsed, or they were so scarce the amount of browse they produced was insignificant relative to other species.

Moose Browsing in Summer and Winter

There were significant differences among species in percent of bites in the diet (Table 2). Moose preferred aspen in both summer and winter in the uncut and beaver-cut forest. The only other preferred species was juneberry during the winter of 1989 in the uncut forest. Moose avoided balsam fir in both winters in the uncut forest, but it was neither preferred nor avoided in the beaver-cut area. Beaked hazel was avoided by moose in the beaver-cut and the uncut forest. There was insufficient moose browsing in the study area in Summer 1989 to calculate meaningful diet percentages or preference.

About 40% of the CAG twigs of aspen were browsed in both the winter and summer

Table 1. Mean tree density (stems ha^{-1}) and basal area (m^2 ha^{-1}) for major tree species within uncut forest and beaver-cut plot types (S.E. in parentheses) in the Lane Cove study area, Isle Royale National Park, 1988.

Species	Tree Density		Basal Area	
	Uncut forest $n = 60$	Beaver cut $n = 30$	Uncut forest	Beaver cut
Balsam fir	227 (55)	417 (77)	1.4 (0.4)	1.4 (0.4)
White spruce	288 (48)	237 (51)	4.5 (0.8)	3.8 (1.1)
Aspen	140 (23)	27 (10)	10.2 (1.6)	3.6 (1.4)
Paper birch	82 (19)	113 (48)	4.8 (1.1)	7.4 (3.0)
Other species	92 (38)	253 (113)	1.7 (0.6)	1.6 (1.1)
Total	829 (70)	1047 (118)	22.6 (1.7)	17.6 (3.4)

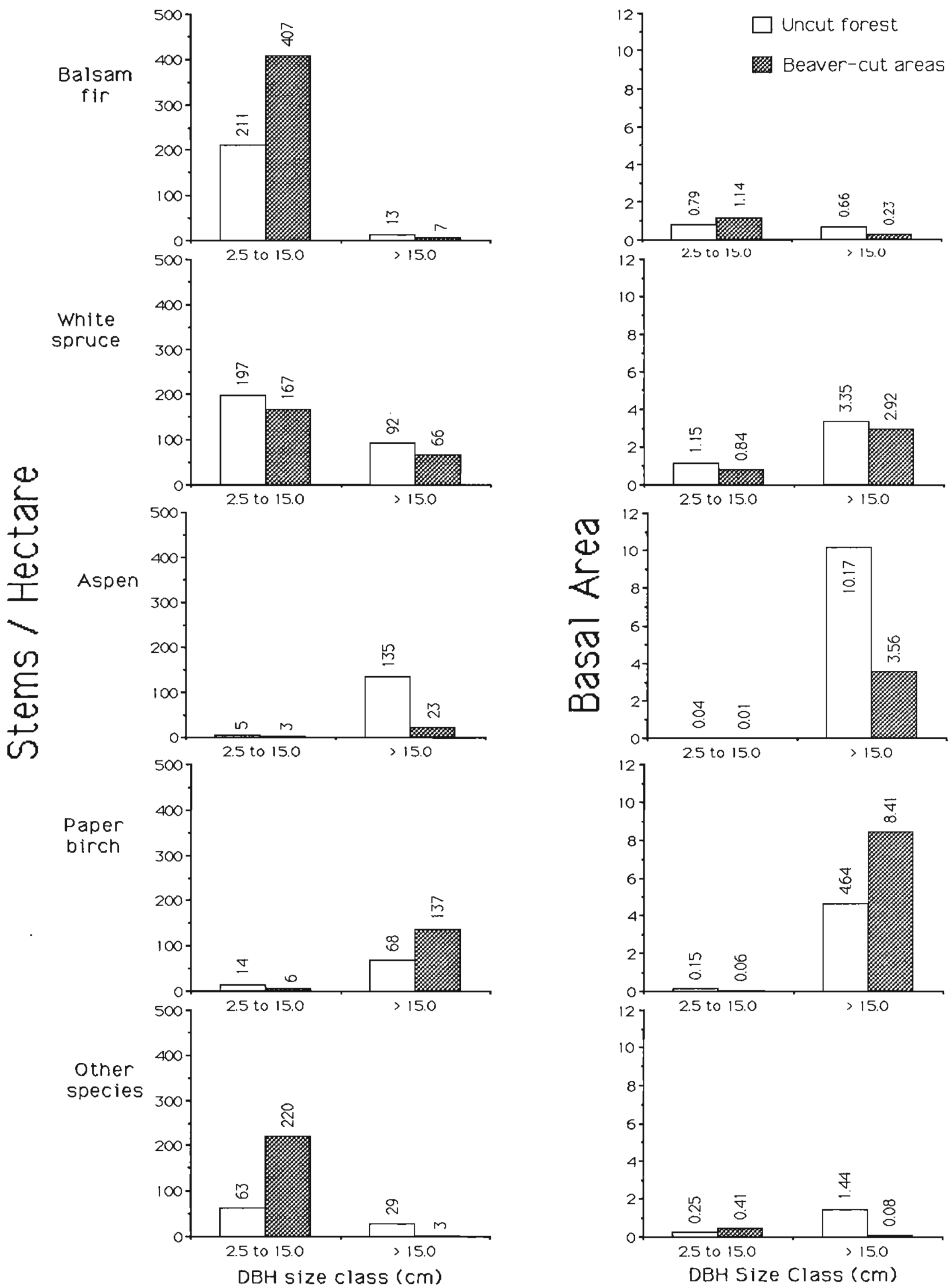

Fig. 2. Stem densities and basal area of the most common tree species in the uncut forest and beaver-cut plot types. In the uncut forest plot type n = 60, and in the beaver-cut plot type, n = 30. The actual value for each measurement is given above the bar.

Table 2. Browse availability and use data for each season in the uncut forest and beaver-cut plot types in 1988 and 1989. Confidence intervals (95%) for percent of twigs removed were calculated according to Neu *et al.* (1974).

	Uncut forest			Beaver-cut areas		
	Available (%)	Bites (%)	Preference[a] Class	Available (%)	Bites (%)	Preference[a] Class
Winter 1988						
Balsam Fir	32	15 ± 7	-	24	24 ± 12	[a]
Juneberry	30	43 ± 10	+	6	—	
Beaked Hazel	12	14 ± 7	[a]	40	20 ± 11	-
Aspen	14	18 ± 7	[a]	26	48 ± 14	+
Red-osier	12	11 ± 6	[a]	4	7 ± 7	[a]
Total Number	513	178		393	83	
Summer 1988						
Juneberry	29	15 ± 9	-	9	17 ± 14	[a]
Beaked Hazel	28	0		77	17 ± 14	-
Aspen	26	74 ± 11	+	12	58 ± 18	+
Red-osier	16	11 ± 8	[a]	2	8 ± 10	[a]
Total Number	529	99		590	48	
Winter 1989						
Balsam Fir	22	14 ± 5	-	13	21 ± 8	[a]
Juneberry	27	32 ± 6	[a]	7	6 ± 5	[a]
Beaked Hazel	18	9 ± 4	-	59	24 ± 8	-
Aspen	19	35 ± 6	+	17	42 ± 10	+
Red-osier	14	9 ± 4	[a]	4	8 ± 5	[a]
Total Number	1418	367	1241	173		
Summer 1989						
Juneberry	30	0	[b]	12	0	[b]
Beaked Hazel	28	0		77	0	
Aspen	24	100		6	0	
Red-osier	18	0		5	0	
Total Number	182	5		235	0	

[a]+ preferred, - non-preferred, [a] neutral preference ranking

[b] insufficient browsing to calculate preference in this column

each year (Table 3). Some aspen twigs which had leaves stripped in the summer were also browsed the following winter. Balsam fir, on the other hand, was not browsed in the summer and only about 20% of the twigs were browsed in the winter. Juneberry, red-osier, and hazel were all browsed more in the winter than in the summer (Table 3).

Twig availability did not differ between beaver-cut areas and uncut forest except for beaked hazel. There were more beaked hazel twigs available in both summer and winter in beaver-cut areas than in uncut forests ($Z \geq 3.188$ and $P < 0.005$ for all seasons and both years). Balsam fir and aspen twig densities were not different between beaver-cut areas and uncut forest. Juneberry twig density was greater in the uncut forest than in the beaver-cut forest only in the winter of 1989 ($Z > 2.260, P < 0.01$).

Condition of Tree Regeneration

There were significant differences in condition among aspen, balsam fir, and spruce ($x^2 = 274.9$, $p < 0.001$, 6 df). Aspen regeneration was either dead or hedged (Fig. 3). At the other extreme, most white spruce stems were unbrowsed. More than half of the balsam fir stems were hedged, but, in contrast to aspen, only 7% of the stems were dead. Regeneration of other tree species was minimal. Aspen, balsam fir, and white spruce stems made up more than 90% of the tree species stems which were less than 2.5 cm dbh in the 2-m^2 plots. Small trees were predominantly bal-

Table 3. Percent of twigs browsed on major browse species during 1988 and 1989.

Species	Winter	Summer
1988		
Balsam Fir	18	0
Juneberry	43	11
Beaked Hazel	19	1
Aspen	41	48
Red-osier	32	15
1989		
Balsam Fir	19	0
Juneberry	27	a
Beaked Hazel	8	a
Aspen	42	a
Red-osier	18	a

a= insufficient browsing to calculate a meaningful percentage

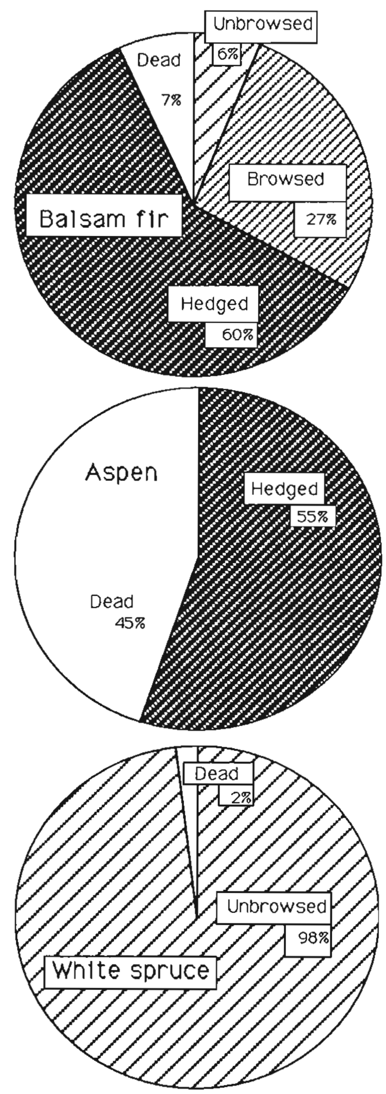

Fig. 3. Condition of balsam fir (n = 88), white spruce (n = 63), and aspen (n = 87) regeneration, if present, at each of the 100 plots on the study site. Condition classes are unbrowsed, browsed, hedged, and dead.

sam fir and spruce (Fig. 2). Most stems of deciduous browse species have been hedged by repeated browsing.

DISCUSSION

One reviewer argued that the twigs which we counted were not independent samples, thus invalidating our conclusions about moose browsing preferences. This is partly correct. However, we are measuring the seasonal browsing response of a population of moose which has wandered over all the landscape. For a single moose on a single feeding bout counting twigs as we did would not result in independent samples. For a population of moose, with numerous feeding bouts each day over a 5 to 7 month period, foraging over a different path each time, we believe that there is a sufficiently close approximation to each twig being an independent sample.

Aspen is a major component of the moose diet on the northeastern end of Isle Royale. Moose often browse beyond the CAG and into the previous year's growth in the winter. The percent of bites of aspen in the winter diet of moose declined from 22% in 1945 to 11% in 1970. About 25% of the summer diet was aspen in 1970 (Krefting 1974). About 40% of the bites in both winter and summer were aspen in our study area. In beaver-cut areas and in uncut forest, aspen was the only browse species that was preferred in both summer and winter. Hansen *et al.* (1973) concluded that moose browsing prevented the growth of aspen reproduction into trees. The same can be said 20 years later for our study site. The generally moribund and hedged appearance of small aspen stems which are still alive indicated that these stems have been heavily browsed for years. The long-term nature of this preference is demonstrated by the lack of 2.5- to 15-cm dbh aspen in both the beaver-cut areas (where moose and beaver browse) and the uncut forest (where only moose browse).

Browsing on balsam fir reproduction was not sufficient to prevent regeneration. There is a large size-cohort of balsam fir, especially in the beaver-cut areas, which is < 10 cm dbh. Balsam fir was avoided in the upland forest, but it was neither avoided nor preferred in the beaver-cut areas. If moose browse more in beaver-cut areas than in upland forest, the greater use of balsam fir in these areas may be incidental to browsing in patches of beaked hazel in the beaver-cut areas. Alternatively, balsam fir in the open beaver-cut areas may be more visible, or nutrient content may vary between plot types. The amount of balsam fir in the winter diet of moose on the northeastern end of Isle Royale declined from 1945 to the 1960's, and then increased to almost 40% of recorded bites in 1970 (Krefting 1974). In areas of Isle Royale with high wintering moose densities, moose browsing has stunted and killed balsam fir regeneration (Brandner *et al.* 1990). While moose browsing can prevent the regeneration of balsam fir, it is not doing so in this area of Isle Royale.

Juneberry, red-osier, and hazel are shrubs or small trees which will not become a dominant part of the tree canopy. Juneberrry and red-osier are found mostly on the uplands. Beaked hazel grows in dense patches in beaver-cut areas and also in the understory of the uncut forest. It is lightly browsed by moose in both the dormant and growing seasons now, but the hedged appearance of hazel patches in the beaver-cut area suggests they have undergone intense, long-term browsing by moose in the past.

Nearly all the aspen within the 27.7-m foraging distance have been cut around every active or abandoned pond in the study site. Beaver prefer to cut small trees first (Basey *et al.* 1988), and most of the aspen trees remaining were greater than 35-cm dbh. If beaver forage further from shore, energy and time costs are greater (Jenkins 1980, Dalton 1984). The probability of predation by wolves also increases with distance from shore. The alternative to long distance foraging is to move to a new site where food trees are located closer to shore. Moving is not a viable alternative for many colonies in this area, because browsing by moose is preventing regeneration of aspen in old beaver-cut areas, and most suitable impoundment sites have already been dammed.

Beaver had already affected 25% of the land area with impoundments, drained ponds, and foraging areas by 1957. Over the next 21 years, an additional 9% of the land area was either flooded, drained, or foraged on. If the colonies do not move, but instead increase their average foraging distance from 27.7 to 35 m, then beaver-affected land would increase to 38%. These calculations are based on a 200 ha part of one drainage on the northeastern end of Isle Royale. We are currently interpreting photos from other parts of Isle Royale to determine how consistent the significant impact of beaver on landscape features is across different drainages over time.

Miquelle and Van Ballenberghe (1989) concluded that moose-induced stem mortality was accelerating succession to a forest dominated by white spruce in Denali National Park and Preserve, Alaska. Risenhoover and Maass (1987) suggested that moose browsing was slowing the rate of succession in Isle Royale forests. Results from this study suggest that moose and beaver can change the rate and the path of succession in this part of Isle Royale. Where moose alone are the major browsers, the canopy of deciduous trees provides an annual input of high quality deciduous litter, which increases soil fertility (Pastor *et al.* 1988). Because browsing prevents establishment of aspen regeneration, succession to conifers occurs at a faster pace. When beaver cut down aspen trees near ponds, and subsequent intensive browsing by moose prevents aspen regeneration, balsam fir and spruce become an important component of the forest in the openings. Litter quality of conifers is less than that of aspen, and a negative feedback loop of declining soil fertility can be entered (Pastor *et al.* 1988). Thus, it is necessary to evaluate the effects of both herbivores when considering future patterns of species composition in streamside areas and adjacent upland forest.

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