Moose (*Alces alces* L.) browsing in young Scots pine stands in relation to the characteristics of their winter habitats

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TIIVISTELMÄ: HIRVEN RAVINNONKÄYTTÖ MÄNTYTAIMIKOISSA JA SEN RIIPPUVUUS YMPÄRISTÖ-TEKIJÖISTÄ

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Moose browsing was studied in young Scots pine stands mixed with deciduous trees in high-density winter ranges. The proportional use of twig biomass de-creased as the availability increased. The total as well as proportional biomass consumption were higher on the moist than on the dryish type of forest. The per tree consumption of pine was higher on the moist type, where the availability of pine was lower. Deciduous trees were more consumed on the moist type, where their availability was relatively high. The consumption of pine saplings in-creased as the availability of birch increased. Pine stem breakages were most numerous when birch occurred as overgrowth above pine and at high birch densities. The availability of other deciduous tree species did not correlate with browsing intensity on Scots pine. Moose browsing had seriously inhibited the development of Scots pines in 6 % of the stands, over 60 % of available biomass having been removed. Rowan and aspen were commonly overbrowsed and their height growth was inhibited, which occurred rarely by birch. There was no difference in the proportion of young stands in forest areas with high and low moose density. A high proportion of peatland forests was found to indicate relatively good feeding habitats in the high-density areas.

Hirven ravinnonkäyttöä tutkittiin kymmenvuotiaissa mäntytaimikoissa Uuden-maan metsäalueilla, joilla hirvitiheys oli keskimääräistä suurempi. Hirven oksa-biomassasta kuluttama osuus oli sitä pienempi mitä enemmän biomassaa oli saatavilla. Kulutettu biomassa oli suurempi tuoreen kuin kuivahkon metsätyypin taimikoissa. Mäntyä syötiin etenkin tainta kohti suhteellisen paljon tuoreella metsätyypillä, missä sen taimitiheys oli pieni. Lehtipuita syötiin enemmän tuo-reella metsätyypillä, missä niitä oli myös enemmän saatavilla. Männyntaimia syötiin sitä enemmän, mitä suurempi oli koivun taimitiheys. Latvatuhot olivat keskimääräistä suurempia, kun koivu oli etukasvuista ja suurimmilla koivu-tiheyksillä. Muiden lehtipuiden esiintymisellä ei ollut vastaavaa vaikutusta. Hirvituhot olivat ankarimmat n. 6 %:ssa taimikoista, joissa yli 60 % saatavilla olevasta biomassasta oli syöty. Pihlaja ja haapa olivat yleisesti kuluneet toipumis-kyvyttömiksi, kun taas koivu oli toipunut suhteellisen hyvin. Taimikkovaiheen metsiköiden osuus metsäalueilla ei vaikuttanut hirvitiheyteen. Turvemaiden osuus sensijaan oli suuri korkean hirvitiheyden alueilla todennäköisesti osoittaen nii-den hyvää soveltuvuutta elinympäristöinä.

Keywords: *Alces alces*, *Pinus sylvestris*, browsing, mixed forests, feeding be-haviour, carrying capacity, landscape ecology.
FDC 151 + 451

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1 Introduction

Scots pine (*Pinus sylvestris* L.) is commonly used by moose as winter food (Morow 1976, Cederlund et al. 1980). It is also the main tree species employed in regenerating forests in most parts of Finland. Extensive browsing on Scots pine by moose leads to damage in young stands. The damage depends on the moose density, which is considered to be an important factor in both forestry and moose management (Helle et al. 1987, Lavsund 1987, Löyttyniemi and Lääperi 1988, Nygrén and Pesonen 1993).

The increase in the area of young, planted and naturally regenerated stands resulting from intensive forest management has important effect on the distribution of moose populations (Lykke 1964, Markgren 1974, Ahlén 1975, Strandgaard 1982). Forests with a range of different aged stands include both young successional stages and mature stands that provide good habitats for successful moose management (Kelsall and Telfer 1974, Peek et al. 1976). Moose populations are mainly concentrated in the winter in areas with a good supply of browse (Telfer 1970, Brassard et al. 1974, Pierce and Peek 1984).

The moose can utilize winter ranges of varying plant composition. An abundance of deciduous tree species, partly mixed with a few preferred coniferous trees, characterizes the forage in the most heavily utilized winter habitats in North America (Eastman and Ritcey 1987, Joyal 1987, Thompson and Euler 1987). Habitat choice depends on areal conditions. The variation in climatic conditions affects the choice of tree species composition and the density of mature stands (Peek et al. 1976, Thompson and Vukelich 1981).

High availability of browsable stems (Crête 1977) and suitable range of some palatable tree species (Goulet 1985) are reported to be typical of frequently used young stands. However, moose winter densities do not necessarily correlate with forage factors (Crête and Jordan 1982).

The effect of forage quality has consequences that are important for both habitat selection and consumption rate (Risenhoover 1989). Increasing quality of the feeding habitat leads to increasing selectivity and searching activity for new patches of food (Saether et al. 1989). Winter feeding by moose is related to the quantity and quality of food items (Vivås and Saether 1987, Lundberg et al. 1990, Andersen and Saether 1990).

Dryish sites with a high proportion of young pine stands usually characterize the winter ranges of moose (Morow 1976, Kuznetsov 1987). Scots pine and willow habitats are widely used by moose in northernmost Scandinavia (Pulliainen et al. 1968). Selecting marshland with willow species or Scots pine dominated areas is greatly dependent on the snow conditions (Gebczynska and Raczynski 1984).

The population density of moose in winter ranges may greatly exceed the average density calculated on larger areas. The yearly change between summer and winter ranges is one of the reasons for high browsing pressure on some forest areas (Sweanor and Sandegren 1986, Lääperi 1990). Habitat quality and moose density are considered to be basic factors when determining the biological and economical carrying capacity (Bergström and Hjeljord 1987).

The intensive utilization of pine in young planted Scots pine stands may prevent stand development in areas repeatedly used by moose in winter (Löyttyniemi and Piisilä 1983, Löyttyniemi and Lääperi 1988). In this sense suggestions have been made about adjusting moose population densities to better correspond to the food resources in young stands.

The aim of this study is to determine factors that may affect moose browsing on Scots pine in young stands of high-density winter ranges, and to evaluate the effect of browsing on stand development in relation to food availability and carrying capacity. Moose damage and feeding habitat selection are studied in relation to the tree species composition in young pine stands and the characteristics of the surrounding forests. The characteristics of forests typical of areas with different moose winter densities are analysed in order to obtain information of winter habitats.

2 Material and methods

Field sampling. The field data were collected in 1991 in southern Finland in the area of Uusimaa-Häme Forestry Board District (60°00'–61°00' N, 23°30'–26°30' E). The study areas were moose winter ranges that had had a considerably higher than average moose density (over 1 moose/km² forested area) during the previous five years (Uusimaa Game Management District and Uusimaa-Häme Forestry Board District). The average density in the study area during 1987–1991 was 0.57 moose/km² forest land. A total of 36 randomly selected young Scots pine stands were inspected. The stands had been established ten years earlier by planting.

A systematical line-plot method was used in measuring moose feeding in the plantations (cf. Lääperi and Löyttyniemi 1988). The size of the plots was 40 m² and the distance between the lines and plots 20–30 m depending on the size of the stand. The number of inspected plots was 347 (1,388 ha). All saplings over 50 cm high were counted in the study. The twigs eaten by moose over the whole plot area were counted. The diameter of the bites on pines was measured on one half of the plot area and on deciduous trees over one quarter. The results were calculated separately for each plantation.

The forest site type was determined on the basis of the ground vegetation (Cajander 1909). There were two types in the data: the *Vaccinium vitis-idaea* type (VT) (17 stands) and the *Vaccinium myrtillus* type (MT) (19 stands). The former is a dryish and the latter a moist forest site type and both are commonly planted with Scots pine. The total number of faecal pellet groups was counted.

Biomass estimations. The biomass available for moose on saplings of different size was measured on unbrowsed trees at height intervals of 0.5 m from 0.5 m to 2.5 m. These heights were chosen in accordance with the average heights of the young stands studied. The twig diameter/weight method (Telfer 1969) was used in the biomass consumption calculations.

In order to estimate the biomass available for moose, the maximum bite diameter was first determined for all the tree species. This was done with respect to the all bites found in the area, excluding the thickest ones if the trees were obviously only occasionally browsed. The diameters used when taking small branches for the estimations were: Scots pine 9 mm, birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.) 8 mm, aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.) and willows (*Salix* spp.) 8 mm, grey alder (*Alnus incana* L.) and juniper (*Juniperus communis* L.) 5 mm. Norway spruce (*Picea abies* L.), which was rare and not used by moose in the area, was not included in the study. Very rarely occurring species such as *Frangula alnus* Miller were also excluded.

Biomass available for moose. The following regression equations were calculated for the available biomass of each tree species in the young stands (y = dry weight kg, x = height m):

		Biomass (g) per tree (mean ± S.E.)
Pinus sylvestris	log y = –6.0356 + 3.7475 log x (r = 0.967, p = 0.002, n = 6)	416 ± 10
Betula pendula	log y = –5.1443 + 3.0298 log x (r = 0.990, p = 0.001, n = 5)	53 ± 1
Betula pubescens	log y = –4.0712 + 2.5232 log x (r = 0.967, p < 0.001, n = 7)	39 ± 1
Sorbus aucuparia	log y = –3.8123 + 2.3277 log x (r = 0.973, p = 0.005, n = 5)	14 ± 1
Populus tremula	log y = –4.1418 + 2.5528 log x (r = 0.963, p = 0.009, n = 5)	22 ± 1
Salix spp.	log y = –5.4000 + 3.1853 log x (r = 0.976, p = 0.024, n = 4)	22 ± 1
Juniperus communis	log y = –8.8993 + 5.3660 log x (r = 0.956, p = 0.044, n = 4)	122 ± 10
Alnus incana	log y = –3.1612 + 1.8704 log x (r = 0.998, p < 0.001, n = 6)	14 ± 1

Table 1. The classifications used in describing forested areas from satellite images. Scrub land = low productive (0.1–1.0 m³/yr), waste land = low productive (< 0.1 m³/yr).

	Area	Areal proportion	Tree volume		
	ha	%	m³/ha	m³	%
Forest land	X		X		
Scrub land	X		X		
Waste land	X		X		
Open regenerated area		X	X		
Seed tree stand		X	X		
Small seedling stand		X	X		
Advanced seedling stand < 4 m		X	X		
Advanced seedling stand > 4 m		X	X		
Young thinning stand		X	X		
Old thinning stand		X	X		
Matured stand		X	X		
Shelterwood stand		X	X		
Age classes of stands (20 years intervals)			X		
Scots pine			X	X	X
Norway spruce			X	X	X
Birch			X	X	X
Deciduous trees			X	X	X

Characteristics of the winter range forests. The forest areas having been occupied by a varying number of moose were studied by using the data based on forest maps. The landscape in the whole area is a mosaic of forest and agricultural land. It was not possible to determine moose densities reliably in small parts of forest areas. The size of studied forest areas varied between 1500–3500 ha. They were divided into three classes according to the moose population in the winter: 1. no or very few observations, 2. 0.5–1.0 moose/km², 3. 1.0–2.0 moose/km². The densities were based on winter countings for the five previous years made on the ground simultaneously for each forest area in March (Uusimaa Game Management District, unpublished). The yearly density estimations had been used in moose management in the area for a long period.

A sample of 33 forest areas was taken randomly from each moose density class. A 2 × 2 km square was chosen in each area and marked on the map. Because disturbances such as main roads and settlements greatly affect the distribution of moose populations (Repo and Löyttyniemi 1985, Heikkilä and Raulo 1987), the squares were marked in such a way as to maintain maximum distance from possible disturbance sources.

Ground sample plots of the National Forest Inventory, satellite images from 1986 and 1988, digital map data and boundaries of the squares were applied in the processing. The data were processed by the National Forest Inventory project. The methodology has been described by Tomppo (1991, 1993).

It was not possible to distinguish the proportion of different tree species in the youngest stands. Species other than Scots pine evidently occurred in only small proportions, because this species is clearly the most popular one used in forest regeneration (Central Forestry Board Tapio 1975–1981).

The variables used to describe the characteristics of forested areas included both areal proportions and tree volumes in different kinds of stand (Table 1).

Statistical analyses. The Student t-test was used when comparing mean values, with arcsin transformation for proportions. Linear regression analyses were used in studying the relationships between browsing and stand characteristics. Analysis of variance and the pairwise t-test with Bonferroni significance level were used when analysing the characteristics of forest areas. BMDP programs were used.

3 Results

3.1 Biomass consumption by moose

Browsing of different tree species. The total biomass utilized by moose averaged 101 kg/ha (± 19 S.E.), which was 12.8 % of the total available biomass. Scots pine had been used more than other species (Table 2). The moose had browsed silver birch more than pubescent birch. The proportion used was also higher for the former species (15.9 % ± 4.6 S.E. vs. 7.7 % ± 2.4 S.E., t = 2.03, p < 0.05). The proportional use of Scots pine (9.8 %) did not differ significantly from that of birches.

The total twig biomass had been reduced considerably in two (6 %) of the stands, over 60 % of available biomass having been consumed. In these stands the biomass consumption on Scots pines was over 60 % (Fig. 1). In other cases the consumption of pine and birch remained mostly below 20 % of the available biomass.

The deciduous tree species preferred by moose (aspen, rowan and willows) were intensively utilized. In 39 % of the stands these species had been overbrowsed. Their height growth was inhibited due to the continuous browsing on the yearly growth. They had often turned into low bushy trees incapable of recovery. Rowan was overbrowsed in 54 % and aspen in 35 % of the stands where they occurred. The corresponding proportion for willows was 13 %, and willows proved to be better able to compensate for browsing than rowan and aspen. Juniper was, on the average, relatively lightly utilized compared to the other species.

The consumed biomass of pine was positively correlated with birch consumption (r = 0.67, p < 0.001, n = 36), whereas no correlation was found between other deciduous trees and pine. Also the used proportion of pine biomass increased as the consumption of birch increased (r = 0.77, p < 0.001, n = 36). However, the use of pine was not found to increase significantly along with the increase of birch consumption in 24 stands, where birch density was lower than 3000 trees/ha.

Neither the consumed biomass nor the proportional use of pine did correlate significantly with the consumption of rowan, aspen, willows and juniper. However, the number of browsed Scots pines was significantly greater in 13 stands where over 80 % of the biomass of these species had been removed, compared to less consumed stands (848/ha ± 158 S.E. vs. 458/ha ± 82 S.E., t = 2.43, p < 0.05). The difference in pine biomass removed was however not significant (86 kg/ha ± 27 S.E. vs. 52 kg/ha ± 21 S.E., t = 1.36, p = 0.18). The average height of birch and the amount of birch biomass used were similar in both cases.

Consumption in relation to browse availability and stand characteristics. The average total biomass available for moose was greater on the VT type than on the MT type (Table 2). This was due to the significantly greater biomass of Scots pine in the former type. The availability of deciduous tree species was consistently higher on
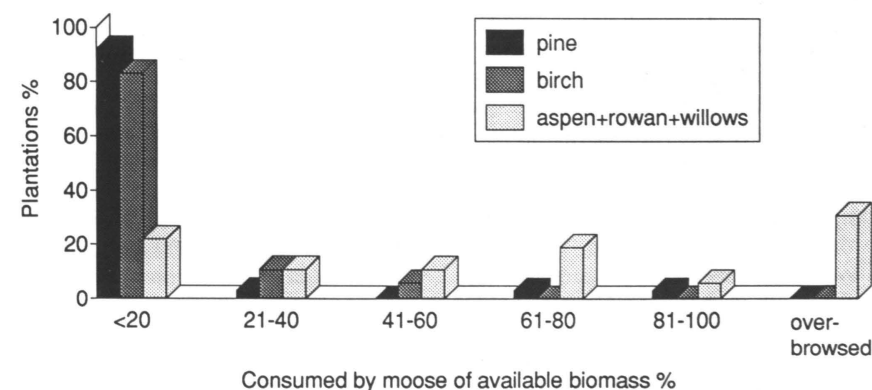

Fig. 1. Twig biomass consumed by moose out of the total biomass available in different tree species in young Scots pine stands of high-density moose areas (1–2 moose/km²).

Table 2. The average height, stand density, available and consumed biomass (± S.E.) in forest types of experimental young stands. VT = *Vaccinium vitis-idaea* type. MT = *Vaccinium myrtillus* type. Level of significance : o = < 0.10, * = < 0.05, ** = < 0.01. Different letters = significant difference between tree species (p < 0.001) (t-test). N = 36.

Tree species	Height m		Trees/ha		Available biomass kg/ha		Consumed biomass kg/ha		Total average consumption kg/ha
	VT	MT	VT	MT	VT	MT	VT	MT	
Pinus sylvestris	175 ± 12	171 ± 8	3117 ± 376	1579 ± 147 **	1203.5 ± 176.2	694.2 ± 162.2 *	41.7 ± 13.9	84.1 ± 28.5	64.1 ± 16.6 a
Betula pendula	165 ± 14	201 ± 17	1030 ± 280	1261 ± 359	47.2 ± 12.3	80.0 ± 24.8	7.6 ± 2.8	6.9 ± 2.7	7.3 ± 1.9 b
Betula pubescens	171 ± 13	168 ± 10	1267 ± 265	1567 ± 305	52.7 ± 11.4	66.1 ± 14.7	1.8 ± 0.6	5.2 ± 2.5	3.6 ± 1.4 bc
Sorbus aucuparia	104 ± 7	110 ± 09	708 ± 132	1734 ± 366 *	7.4 ± 2.0	29.4 ± 14.1 o	8.5 ± 3.6	23.2 ± 7.3 o	16.3 ± 4.4 abd
Populus tremula	118 ± 11	127 ± 15	398 ± 92	667 ± 184	4.8 ± 1.4	12.6 ± 4.7	3.9 ± 1.5	5.3 ± 1.9	4.7 ± 1.3 be
Salix spp.	98 ± 7	121 ± 10	142 ± 42	397 ± 104 *	1.4 ± 0.7	11.0 ± 3.5 *	0.1 ± 0.05	7.7 ± 3.8 *	4.1 ± 2.1 be
Alnus incana	169 ± 18	203 ± 22	83 ± 21	258 ± 113	0.5 ± 0.2	1.7 ± 0.8	0.3 ± 0.2	0.5 ± 0.3 o	0.4 ± 0.2 ce
Juniperus communis	108 ± 6	118 ± 10	80 ± 16	90 ± 34	8.4 ± 2.9	5.4 ± 2.0	0.8 ± 0.4	0.8 ± 0.7	0.8 ± 0.4 cd
Deciduous trees	149 ± 10	152 ± 9	3495 ± 489	5509 ± 619 *	122.2 ± 18.5	206.0 ± 42.5 o	23.0 ± 5.8	49.5 ± 11.3 *	37.0 ± 6.8
In total	156 ± 6	160 ± 8	6612 ± 514	7088 ± 609	1325.7 ± 177.9	900.3 ± 156.8 *	64.7 ± 14.2	133.6 ± 31.9 *	101.0 ± 18.8
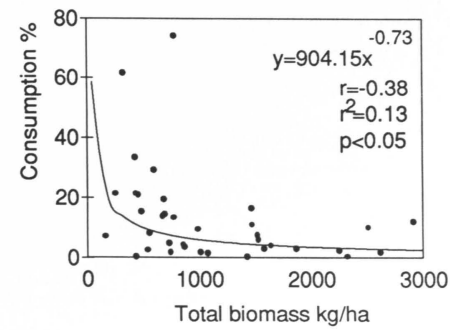
Fig. 2. Proportion of total biomass consumed by moose in young Scots pine stands.

Fig. 3. Proportion of total twig biomass (± S.E.) consumed by moose in young Scots pine stands on dryish (VT = *Vaccinium vitis-idea* type) and moist (MT = *Vaccinium myrtillus* type) forest sites (t = 2.52, p < 0.05). Biomass consumed of Scots pines (t = 1.79, p = 0.08), respectively.

the MT type. The availability of rowan and willows was significantly greater on the MT type. The biomass availability of the overbrowsed, preferred tree species was underestimated in some cases, because they produced new shoots but were not able to increase height. There were no significant differences in the average height of the tree species between forest types.

The moose had utilized a smaller proportion of the biomass, the greater the total available biomass (Fig. 2). The consumed biomass was greater on the MT type than on the VT type (Fig. 3). A relatively high proportion of the available Scots pine biomass was removed on the MT type. The consumed pine biomass per tree was greater on the MT type than on the VT type (53 g ± 19 S.E. vs. 16 g ± 6 S.E., t = 2.10, p < 0.05, df = 34). The total pine biomass removed per stand was also relatively great on the MT type. No significant difference was respectively found between per-tree availability (392 g ± 61 S.E. vs. 446 g ± 76 S.E.); thus other factors such as stand density and tree species composition were more important in relation to the differences found in utilization of pine saplings. Deciduous trees were more used in the MT type, accordingly with their availability.

The number of Scots pine saplings browsed by moose was the higher, the greater the availability of the two most commonly occurring tree species, silver birch and pine (Table 3). The biomass of these two tree species was intercorrelated with the total biomass availability. The availability of silver birch alone explained 21 % of the variation (r = 0.45, F = 8.82, p < 0.001), which explained browsing better than in combination with pubescent birch. The two birch species were also intercorrelated. Neither the densi-
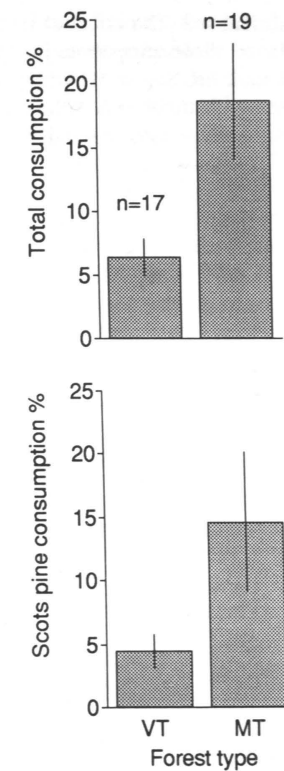
ty nor the biomass availability of deciduous species other than birch explained the browsing of pine.

The biomass removed by moose from the Scots pines increased as the proportion of spruce-dominated stands in the surrounding forests increased (Table 3). Spruce-dominated stands alone explained 11 % of the variation (r = 0.33, F = 4.14, p < 0.05). In addition, the consumption of pine increased with increasing available pine biomass. Also the biomass removed from deciduous browse species increased as their availability increased (r = 0.49, r² = 0.24, p < 0.01).

The average size of the studied young stands was relatively small (1.7 ha ± 0.3 S.E.), and there was no relationship between the consumption by moose and stand size.

Faecal pellet groups. The number of moose pellet groups/ha was significantly correlated with

Table 3. The effect of stand characteristics on moose browsing on young Scots pines (multiple regression analyses). Availability = biomass kg/ha. Stands % = proportion of the stands in the surrounding forests. Variables: X_1 = Silver birch availability, X_2 = Scots pine availability, X_3 = spruce stands %, X_4 = young stands %.

Number of browsed pines/ha

	Regression coefficient	T-value	P-value
Silver birch availability	0.48	3.35	0.00
Pine availability	0.34	2.40	0.02

$R = 0.57$, $R^2 = 0.32$, $F = 7.90$, $P = 0.002$
Regression equation: $Y = 209.8735 + 0.0027556 X_1 + 0.00022655 X_2$

Pine consumption kg/ha

	Regression coefficient	T-value	P-value
Spruce dominated mature stands %	0.38	2.47	0.02
Pine availability	0.35	2.26	0.03

$R = 0.48$, $R^2 = 0.23$, $F = 4.88$, $P = 0.014$
Regression equation: $Y = -48183.45703 + 1166.3877 X_3 + 0.04642 X_2$

Number of pine stem breakages/ha

	Regression coefficient	T-value	P-value
Silver birch availability	0.78	7.35	0.00
Young stands %	−0.26	−2.44	0.02

$R = 0.80$, $R^2 = 0.63$, $F = 28.65$, $P = 0.000$
Regression equation: $Y = 16.33656 + 0.0021483 X_1 - 3.66528 X_4$

Pine stem breakages %

	Regression coefficient	T-value	P-value
Silver birch availability	0.64	5.39	0.00
Spruce dominated mature stands %	0.27	2.27	0.03

$R = 0.75$, $R^2 = 0.56$, $F = 21.20$, $P = 0.000$
Regression equation: $Y = -5.03352 + 0.000084234 X_1 + 0.09360 X_3$

the consumed biomass of deciduous saplings ($r = 0.56$, $r^2 = 0.31$, $p < 0.001$), but not with the amount of consumed Scots pine. The abundance of pellet groups increased as the summed proportion of young successional stages (open areas, seed/shelter tree stands, young stands) in the vicinity of the plantations increased ($r = 0.50$, $r^2 = 0.25$, $p < 0.01$). Neither the availability of Scots pine and deciduous saplings in the plantations nor the proportion of spruce-dominated forests in the surroundings were correlated with the pellet group density.

3.2 Stem breakages

The proportion of stems broken by moose on Scots pines was significantly higher in the MT type ($9.5 \% \pm 3.4$ S.E.) than in the VT type stands ($1.9 \% \pm 0.6$ S.E.) ($t = 2.10$, $p < 0.05$). In the MT type stands stem breakage was relatively abundant, 160/ha ± 71 S.E. vs. 63/ha ± 25 S.E. in the VT type ($p = 0.21$).

The number of Scots pine stems broken by moose increased as the available biomass of silver birch increased (Table 3). The availability of silver birch alone explained 57 % of the variation ($r = 0.75$, $F = 44.85$, $p < 0.001$). Stem breakages were negatively correlated to the proportion of young stands in the surroundings. The proportion of broken stems was dependent on the availability of silver birch, which alone explained 49 % of the variation ($r = 0.49$, $F = 33.22$, $p < 0.001$), and on the proportion of spruce-dominated stands in the surroundings.

The number of pine stem breakages was significantly greater when the density of birch exceeded 5000 trees/ha than at lower densities (Fig. 4). Three of the stands with high birch density were in MT type and one in VT type. Stem breakages were also more abundant when the average height of birch exceeded 210 cm (average height relationship birch/pine 1.6, average height of pines 164 cm ± 14 S.E.) than in stands with shorter birches (average height relationship birch/pine 0.9, average height of pines 176 cm ± 8 S.E.)(Fig. 5). The occurrence of deciduous trees other than birch did not correlate with breakages.

Stem breakages were slightly more abundant on silver birch than on Scots pine (230/ha ± 63 S.E. vs. 114/ha ± 39 S.E., $t = 1.59$, $p < 0.10$). The proportion of broken stems was significantly higher on silver birch ($20.4 \% \pm 3.9$ S.E. vs. $5.9 \% \pm 1.9$ S.E., $t = 3.34$, $p < 0.01$).

The breakage point in Scots pine was, on the average, located below the top shoot, indicating a relatively high browsing pressure. In the eight stands where the density of pine was below 1400 trees/ha the number of stem breakages averaged 123/ha ± 62 S.E., and in the stands with a higher density 112/ha ± 48 S.E. respectively. Thus the proportion of stem breakages was significantly higher in the former stands ($10.8 \% \pm 4.8$ S.E.) than in the latter ($4.5 \% \pm 2.0$ S.E.)($t = 2.06$, $p < 0.05$), indicating a relatively high susceptibility to damage in a sparse stand.
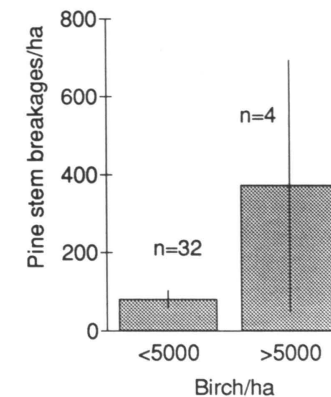

Fig. 4. Number of pine stem breakages ($\pm$ S.E.) caused by moose at different densities of birch ($t = 2.46$, $p < 0.05$, df = 34).
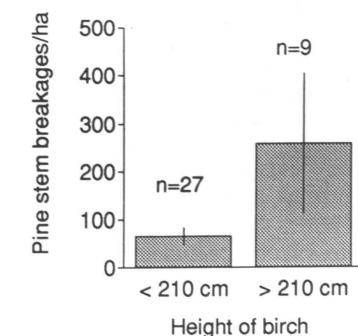

Fig. 5. Number of pine stem breakages ($\pm$ S.E.) caused by moose at different heights of birch ($t = 2.21$, $p < 0.05$, df = 34).

3.3 Characteristics of the forest stand classes

The forest areas with a high moose density were characterized by relatively high proportions of low-productive scrub or wasteland and peatlands (Fig. 6). Peatlands classified as either productive forest land or low productive land were significantly more common in high-density than in low-density moose areas.

The proportion of young stands, which are the most important food sources, out of the total area did not differ significantly between the moose density classes. The proportion of young stands (< 4 m in height) was 17–19 % of the total forest area, indicating no major effect at the different moose densities.

Only certain stand characteristics showed significant differences between the moose density classes. The tree volume (m³/ha) was greater in over 4 m-high young stands in high-density moose areas than in the low-density areas (Fig. 6). The total volume of pine was higher in high-density than in low-density moose areas. The oldest stands had smaller tree volumes in moose areas than in non-moose areas.
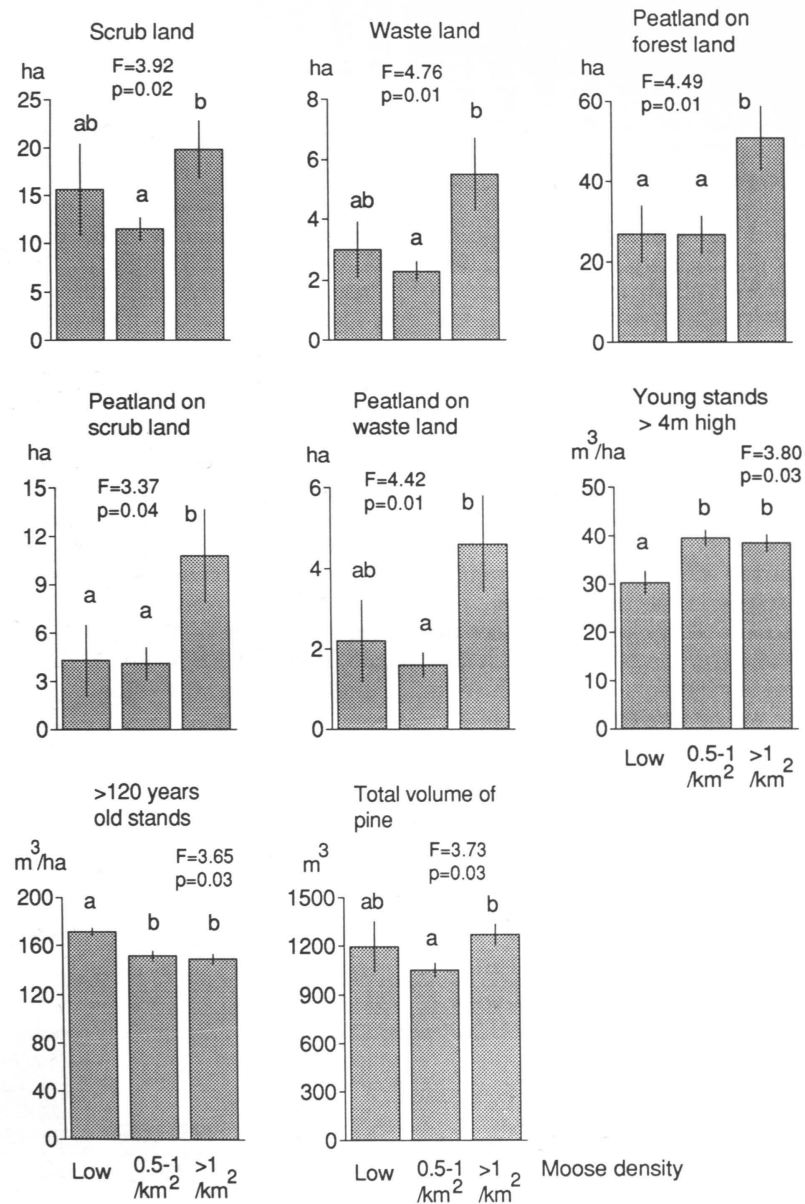

Fig. 6. Characteristics of forests growing in areas with different moose densities. Mean values ± S.E. (ANOVA, df = 2, 96, the pairwise t-test and Bonferroni signicance level of 5 %).

4 Discussion

Feeding habitat selection. The reasons why cervids choose patches in forests for feeding have mainly been studied with respect to food availability and cover aspects. Compared to the white-tailed deer, for instance, moose is more adapted to use open areas (Telfer 1970, Kearney and Gilbert 1976) and relatively large openings are used in winter (Euler 1981). Differences between subspecies of moose in the use of habitats have also been suggested, related to adaptation in the use of seral successional stages (Peek 1974). The presence of older stands is also an important component of winter habitats (Hamilton et al. 1980, Welsh et al. 1980). A major advantage can obviously be obtained in forests with different age classes and good availability of young stands of small size (Peek et al. 1976), which was typical of our study area. This is also because the winter feeding of female moose with calves is mainly concentrated on the edges of logged habitats, the older stands being important during late winter when there is excessive snow cover (Thompson and Vukelich 1981). On average, the edge effect has not been found in Fennoscandia, either in relatively small (Heikkilä 1990) or large (Andrén and Angelstam 1993) Scots pine stands.

In the present study a high frequency of mature spruce forests increased the use of pine (cf. Repo and Löyttyniemi 1985). Besides young trees, a supply of dwarf shrub forage may also determine the use of older forest stands during autumn and early winter (Hjeljord et al. 1990). The decisions made by moose in habitat choice might be related to seasonal change in the use of foraging patches.

The number of faecal pellet groups increased along with an increase of young seral stages in the surrounding forests reflecting the importance of concentrated forage availability. The occurrence of pellet groups was evidently more related to yearlong than only winter habitats (Lavsund 1975). Pine stem breakages in the present study were negatively correlated to the proportion of young stands in the surroundings, probably indicating no need by moose to concentrate in relatively mild winters accordingly with food available in saplings. The snow conditions were not found to have conclusively restricted movement (Coady 1974, Sweanor and Sandegren 1986). The maximum snow cover in the study area was less than 60 cm during the previous five years (Monthly report ...).

In the present study deciduous saplings were the more used the greater the availability. The use of pine biomass, both per hectare and proportionally, increased as the use of birch increased, probably indicating the importance of deciduous browse in feeding habitat selection (Miguelle and Jordan 1979). However, the availability of birch explained significantly the browsed number of pines but not the biomass consumption. The fact that a relatively small part of the variation is explained by site characteristics is obviously due to the large biomass of pine and its importance as winter food. The monoculture stands of pine may also be heavily used (e.g. Heikkilä and Mikkonen 1992).

Welsh et al. (1980) report that jackpine (*Pinus banksiana*) is not used, if a mixture of deciduous trees is only scarce. According to Créte (1989), the availability of deciduous saplings is the major factor affecting habitat selection compared to the availability of commonly used balsam fir. The nutritive value of birch in terms of digestibility is however relatively low (Hjeljord et al. 1982, Salonen 1982). Our results support partly the concept of the importance of a mixed diet in feeding habitat selection.

As a selector type browser, the moose is suggested to gain benefit from high diversity of plant species, the seasonal adaptation of digest-

ing browse being well developed (Hofmann and Nygrén 1992). The importance of food quality in the use of feeding habitats of moose is emphasized by Risenhoover (1989). Saether et al. (1989) report that a higher selectivity and mobility in searching for food patches is characteristic of moose using ranges of good quality. The increase in the number of browsable stems has been reported to greatly increase the use of habitats (Créte 1977), which is advantageous for selective feeding (Vivås and Saether 1987) as well as in maximizing energy intake in winter (Schwartz et al. 1988).

In the present study rowan and aspen especially had frequently been overbrowsed (cf. Saether 1990) and their availability in part of the stands had subsequently been greatly reduced. In such stands the pines had been browsed more frequently and the biomass utilized was relatively great compared to that in other stands. The preferred deciduous trees may have played an important role in habitat selection during initial stand development, thus probably affecting the subsequent use of the stands. A good quality browse is obviously important in the autumn (Andersson 1971), when the moose feed selectively (Renecker and Hudson 1989).

Because of overbrowsing, the availability of preferred tree species was underestimated to some extent, owing to their ability to produce new shoots after browsing. The birch has been reported to compensate after stem breakage by increasing the height growth (Heikkilä et al. 1993). These effects were not possible to take into account, but they were concluded to have no significant effect on the comparisons.

Characteristics of the forest areas. The forest areas provided similar amounts of young stands irrespective of the moose density. The characteristics of core winter range areas could not be identified because distinct moose groups were not followed. Thus moose densities may be associated e.g. with the distribution of young stands at the local level. According to Ballenberghe and Peek (1971), the winter range consists of a series of intensively used areas. The winter ranges are often located relatively far from lakes and characterized by a mosaic of mature and young mixed stands (Proulx and Joyal 1981). Gentle slopes are frequently occupied (Poliquin et al. 1977, Proulx 1983). The positive effect of higher than average topography (Heikkilä 1990) may reflect the importance of good visibility (Repo and Löyttyniemi 1985). In the present study, the proportion of youngest stand classes in the surround-

ings, which indicate good visibility did not correlate with browsing but with the number of pellet groups.

In general, the determination of high-density winter yards according to the area of early seral stages seems to be difficult in forest areas subjected to small-scale, intensive management. Crête and Jordan (1982) reported that moose densities are not correlated with forage availability, obviously due to a high biological carrying capacity in their study area. In areas where the plant composition structure of used habitats is stable during the winter (Joyal and Bourque 1986), the history of forest management in a specific locality may better explain the moose areas (cf. Welsh et al. 1980). In our study the relatively high volume (m³/ha) of over 4 m high young stands in high-density moose areas may reflect their suitability during previous years.

Peatlands were significantly more common in high-density compared to low-density moose areas in the present study. Moose browsing frequently occurs in peatland forests, where the available food is relatively abundant (Peltonen 1986). Young peatland forests are obviously advantageous for moose owing to the mobilization of soil nitrogen for the plants after drainage (cf. Bryant et al. 1983). Low-productive land may also contain forage in terms of low-growing and bushy vegetation.

The differences in the stand volumes were relatively small between moose density classes. Relationships between habitats and moose could only be evaluated on relatively large areal base. In high-density moose areas the tree volume of old forests was lower than that in low-density areas. This may reflect their avoidance of habitats with a dense cover where there is scarce undergrowth. The relatively great volume of pine in high-density areas is in accordance with the results concerning the importance of Scots pine as winter food.

The moose often use the same wintering areas each year (LeResche 1974), despite a considerable decrease in food supply (Andersen 1991). The fidelity of moose in returning to previously used areas may greatly determine the use of habitats (Cederlund and Okarma 1988, Cederlund and Sand 1992), although a part of the moose population evidently does not follow distinct rules in moving. Both males and females occupy similar sites in winter (Miller and Litvaitis 1992). The size of moose groups in wintering areas is more dependent on population dynamics than on foraging factors (Sweanor and

Sandegren 1986). Measures, which promote the concentration of moose populations, such as concentration of clearcuttings, should be avoided in the forest management of the wintering areas.

Damage caused by browsing on Scots pine in relation to stand characteristics. According to the present results moose browsing is relatively intensive on moist forest type (cf. Heikuraurainen 1982, Heikkilä 1990), while Lääperi and Löyttyniemi (1988) found an inverse relationship between moose damage and soil fertility. Especially the proportional use of pine was great on the moist type, where stand density was low. The pines of the two forest types were of similar size. Thus the high pine consumption per tree on the moist type was mainly due to the low stand density. In the case of saplings growing on poor soils the effect of damage will be relatively great owing to the low growth rate of the trees (Danell, Niemelä et al. 1991). This effect could not be analysed in the present study, because the most dry sites were not included. In spite of the low growth rate, naturally regenerated Scots pine stands are often able to withstand browsing owing to the high stand density (Heikkilä and Mikkonen 1992).

Positive correlations have been found in previous studies between the density of aspen and rowan and browsing on pine (Löyttyniemi and Piisilä 1983, Lääperi and Löyttyniemi 1988, Heikkilä 1990), but not with birch. Bergerud and Manuel (1969) did not find any correlation between stem damage on balsam fir and the presence of paper birch (*Betula papyrifera*). Danell et al. (1991) reported that there is no difference in the degree of browsing on Scots pine between food patches containing only pine and those with a mixture of pine and aspen. The use of pine in relatively young seedling stands has been found to be primarily dependent on the availability of birch as well as on rowan (Heikkilä unpublished). In our study the presence of rowan and aspen had no marked effect on browsing during the period when pines are most susceptible to damage.

In the present study, the amount of main stem breakage increased with the availability of birch. The occurrence of other deciduous tree species did not correlate with such damage. The effect was significant at relatively high densities of birch, as well as when birch occurred as overgrowth above pine. The occurrence of birch saplings at relatively low densities has been reported to reduce the effect of stem damage (Heikkilä 1991). In the present study the consumed bio-

mass of pine did not correlate with birch consumption at lower birch densities than 3000 trees/ha, which also supports the idea of the effect of relatively high birch stand densities only.

The palatability of Scots pine suppressed by birch overgrowth is better than that of freely growing pines (Heikkilä et al. unpublished). In our study the average differences were not as extreme, but a similar effect may have occurred in some of the saplings. It may also be easier for moose to repeatedly browse the leader shoot of pines located close to relatively high birch forage. Silver birch is faster growing and used more by moose than pubescent birch (Danell et al. 1985, Danell and Ericson 1986), and is thus able to compete with pine. Silvicultural cleaning had been done in the study area only occasionally and at a relatively early stage.

Effects of browsing in relation to carrying capacity. Moose management in Finland is based on economical rather than on biological carrying capacity (Nygrén and Pesonen 1993). This is closely connected with the reduction in wood quality caused by main stem breakage of valuable tree species. Main stem breakage has been found on approximately every second browsed sapling (Löyttyniemi and Piisilä 1983, Heikkilä 1991).

The proportion of total available biomass consumed by moose was the smaller the greater the availability. This inverse relationship between food resources and stem damage has earlier been reported in young conifer stands (Thompson 1988, Heikkilä and Mikkonen 1992, Andrén and Angelstam 1993). The functional response by moose in relation to food availability suggests an increase of total food intake and decelerating proportional use as as food availability increases (Andersen and Saether 1990, Lundberg and Danell 1990, Åström et al. 1990).

The proportion of Scots pine out of the total biomass was on average 85 %. Thus the abundance of this tree species is the most important factor in relation to the browsing effect of moose. On the average the moose had removed only a relatively small proportion of the total available twig biomass. The loss in the available biomass of Scots pine was over 60 % in 6 % of the stands. In these stands the effect of browsing had inhibited stand development due to the considerable loss in yearly growth. In addition, stem breakages considerably lowered the quality of pines in about 15–20 % of the stands. The fact that the compensatory growth of Scots pines after continuous shoot damage is relatively good (Eden-

ius et al. 1992, Heikkilä and Löyttyniemi 1992) explains the absence of dead saplings.

Our study showed a considerable loss in the biomass of the most palatable deciduous species during the initial development of young Scots pine stands. These species are rapidly overused owing to their good digestibility, relatively small available biomass and small number of twigs (Bergström and Danell 1987a, Saether 1990, Heikkilä 1991). In turn, the recovery capacity of birch is relatively good (Bergström and Danell 1987b, Heikkilä et al. 1993). The effects of continuous browsing may lead to short- and long-term structural changes in the forest ecosystem (Bédard et al. 1978, Risenhoover and Maass 1987, McInnes et al. 1992, Thompson et al. 1992). Owing to the competitive relationships found between the tree species in our study, the Scots pine stands growing on moist sites tend to change to birch-conifer mixed forest. On dry sites also an increase of spruce dominance is possible (cf. Kuznetsov 1987).

According to Brandner et al. (1990), the main effect of moose browsing on *Abies balsamea*, the main conifer species used by moose in northern America, was a reduction in tree height. This was significant at relatively high moose densities (> 2.5 individuals/km²) compared to those in our areas. At corresponding moose densities the carrying capacity, expressed in terms of annual forage production, was not exceeded in eastern Quebec (Créte 1989). The available biomass was relatively great in our areas, both for coniferous and deciduous browse. In this sense, overbrowsing by moose can be considered a problem in only part of the young stands in our high density moose areas.

Results for the areal forest stand composition indicate no great variation between the moose ranges in terms of the availability of young successional stages. The proportion of young stands under 4 m in height can be considered to be the most important food source (Parker and Morton 1978). According to the areal proportions, 18 ha of such stands were available per moose at a density of one moose/km², which was the lower limit for high-density areas. Thus a great variation is suggested between forest areas in the amount of young stands per moose.

Lavsund (1987) reports that one moose/km² means 10 % severe damage on Scots pine and two moose 25 %, respectively. This is near that was found in our study area. The resistance of forested areas to moose damage is reported to be relatively good when there are more than 30 ha of pine stands younger than 20 years old/moose (Morow 1976), which is more than in our area. The amount of damage increases rapidly at densities higher than 0.2 moose/km² (Kuznetsov 1987, Abaturov and Smirnov 1992). Direct comparisons between estimations are difficult, e.g. because the stand densities used in forest management vary considerably and moose densities may be determined on a different areal basis. Because forest areas with the highest densities are primarily susceptible to damage, the distribution of the moose population in forested areas should be monitored for management purposes.

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