FORAGING ON NORWAY SPRUCE AND ITS POTENTIAL ASSOCIATION WITH A WASTING SYNDROME IN MOOSE IN SWEDEN

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ABSTRACT: We studied a sudden occurrence of moose (*Alces alces*) browsing twigs and stripping bark of Norway spruce (*Picea abies*) that coincided temporally and spatially with a moose wasting syndrome in southern Älvsborg County in southwestern Sweden from 1990 to 1992. Spruce is a low preference forage for moose across Sweden and reports on its use are limited. This study reports on the importance of spruce as moose forage and its qualitative value relative to other more commonly used moose browse species in this region. Rumen contents from moose collected in autumn contained low proportions of spruce twigs (1.5-2.3%), and only 2 animals (n = 155) had spruce bark in the rumen. Generally, there was little browsing damage on spruce, although damage was severe in local areas. Spruce contained low concentrations of macroelements (crude protein, calcium, magnesium, potassium, and phosphorus) and trace elements (aluminum, cadmium, cobalt, copper, iron, manganese, and zinc), thereby minimizing this as a possible explanation for moose browsing. We used *in vitro* dry matter disappearance (IVDMD) as a measure of digestibility of spruce bark and twigs, and found no differences between spruce trees that had been bark stripped by moose and a control group of undamaged specimens. In addition, average IVDMD values of 14-25% dry matter of spruce bark were considerably lower than those found for more commonly used moose browse species in Sweden. We discuss these results with respect to the potential mechanisms underlying moose bark stripping of spruce. We cannot confirm that a potential linkage between foraging on spruce and a wasting syndrome in moose exists, and suggest that further research in this area is warranted.

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Key words: bark stripping, IVDMD, moose, Norway spruce, wasting syndrome

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Norway spruce (*Picea abies*) has been found to rank lowest on preference lists of moose (*Alces alces*) in Sweden, and reports of its use as forage are limited (Cederlund *et al.* 1980, Bergström and Hjeljord 1987). Reports of occasional twig browsing and bark stripping by cervids (with the latter damages generally being more visible) have come from the southern and central regions of Sweden (Lavsund 1987). During the past decade, researchers have documented rather intensive cervid browsing, primarily by roe deer (*Capreolus capreolus*) but also moose, red deer (*Cervus elaphus*), and fallow deer (*C. dama*), on up to 50% of newly planted and naturally regenerated spruce saplings (Bergström and Bergqvist 1997).

Researchers have reported moose browsing damage on spruce in other regions of Fennoscandia, including Norway (bark stripping; Furulund 1977) and Finland. In Finland, local cases of stripping on mature spruce trees occur annually, although the phenomenon is rare and little research concerning this problem has been done in either

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Finland, Norway (Faber and Edenius 1998), or Russia (Kuznetsov 1987). In the Republic of Estonia and other parts of the Baltic states, moose cause considerable damage to spruce (Randveer and Heikkilä 1996, Faber and Edenius 1998). In North America, where moose densities are generally considerably lower than in Sweden, moose rarely browse on spruce (*Picea* spp.) (Murie 1934, Peterson 1955, Peek 1974, Renecker and Schwartz 1998), although in one recent study, tame moose consumed significant amounts of spruce (Lautenschlager *et al.* 1997).

In our study area, many forest owners reported more extensive browsing of spruce, especially through bark stripping, and the County Forestry Board surveyed the range of browsing damage (Axelsson 1990). Seven of 13 forest districts reported that spruce were damaged by moose, and one district documented over 30 damaged spruce stands. Damage occurred throughout the year with slightly more damage occurring during winter months. From a forestry perspective, bark stripping accounted for the most serious damage (Axelsson 1990).

Browsing damage to spruce in our study area was spatially and temporally linked to the occurrence of a previously unknown moose wasting syndrome (Rehbinder *et al.* 1991, Stéen *et al.* 1993). More than 1,500 animals have been found with symptoms, and many have died (Frank 1998). Many hunters and foresters assume that these two occurrences likely were concomitant, which lead to the formulation of 2 main hypotheses for explaining this behavior (Cederlund *et al.* 1994): (1) that the dense moose population in southern Älvsborg County overbrowsed its natural food base and switched to less preferred spruce forage, and because spruce is not nutritious, moose became malnourished; and (2) that the wasting syndrome triggered moose to browse on spruce which might contain one or more specific elements required by moose affected by the disease. Initial studies targeted copper (Cu) as an element of interest in this context, since decreasing concentrations of this element have been found in moose livers from this region (Frank *et al.* 1994, Frank 1998). The second explanation is related to environmental conditions, especially the well-known high acidification mainly due to anthropogenic sources in this region (Brodin 1993). Cederlund *et al.* (1994) suggest that high acidification may leach out various trace elements in moose forage deeper in the soil where they become unavailable for uptake by plant roots.

The present study is part of a larger project that examines the moose wasting syndrome (Cederlund *et al.* 1994). Our goal was to determine the importance of spruce, both in terms of quality and quantity, as forage for moose. A broad approach was taken to test several explanations relative to bark stripping of spruce by moose, rather than concentrating on possible relationships between this behavior and the moose wasting syndrome.

STUDY AREA

Southern Älvsborg County

The study was done in Älvsborg County (57°47'N, 13°07'E) in the hemiboreal forest zone (Ahti *et al.* 1968) of southwestern Sweden (Fig. 1). Study areas were established in 1989 when work began on moose wasting syndrome (Cederlund 1990, Sand and Cederlund 1992) and our work was initiated in 1990. Most data were collected in area A, but data from 2 additional sampling areas (B and C) were collected for comparative purposes (Fig. 1). Area A was chosen initially because incidences of moose with wasting syndrome and the greatest amount of spruce damage, occurred there. Area B had incidences of moose wasting syndrome, but no spruce damage, and area C was designated as a control area, be-

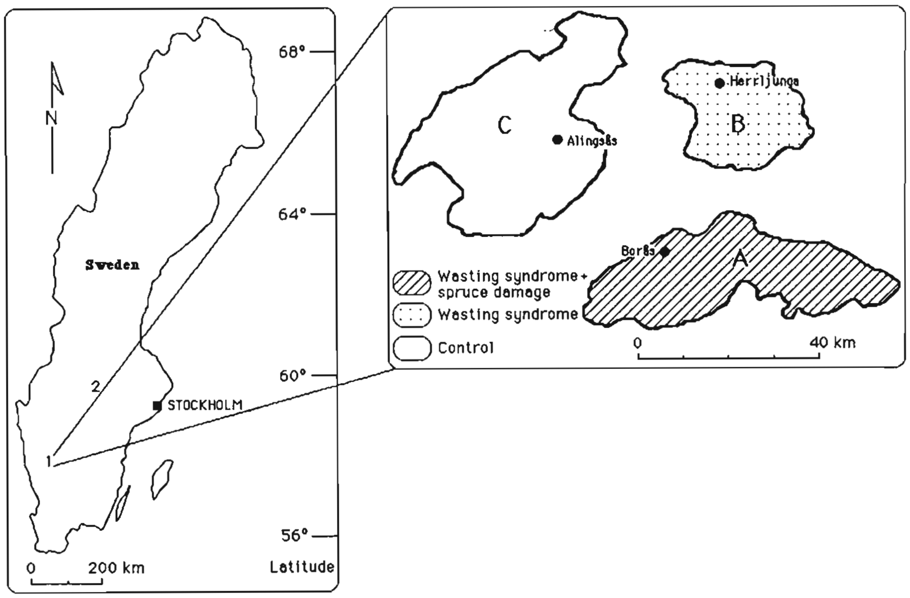

Fig. 1. Location of the main study area in southern Älvsborg County (1) and Grimsö Wildlife Research Area (2), Sweden, and of sampling areas A, B, and C in southern Älvsborg County.

cause no wasting syndrome or spruce damage was observed there.

In order to determine study area characteristics, the 3 sampling areas were included in a 1992 nationwide survey concerning moose and their environment called 'Balanserad Älgstam [Balanced moose population]' (Bergström *et al.* 1995). Within areas A, B, and C, one representative survey plot of 6,300 ha was described and surveyed in spring 1992. Percent cover, used as a measure of forage availability, of 12 moose browse species was calculated for each survey plot. Based on these surveys, Pehrson and Faber (1993) and Sand *et al.* (1995) described the sampling areas and compared these in greater detail. The sampling areas were highly fragmented forested lands interspersed with agricultural fields, with elevations 25-260 meters above sea level (Pehrson and Faber 1993). The forests were mainly composed of Scots pine (*Pinus sylvestris*) and Norway spruce mixed with deciduous trees such as silver birch (*Betula pendula*) and pubescent birch (*B. pubescens*), aspen (*Populus tremula*), and willow (*Salix* spp.). The proportions and age distribution of various forest types within the 3 sampling areas were measured (Table 1). Forest productivity, expressed as m^3 forest growth/ha/yr, ranged from 7.7 in area C to 8.7 in areas A and B (Sand *et al.* 1995).

Climate is typical of inland, southcentral Sweden. The mean winter temperature for December through March is -1.7°C with lows seldom below -25°C. The mean summer temperature from May through August is 13.7°C with highs seldom exceeding 30°C (Sand *et al.* 1995). Snow cover is present typically from mid-December to mid-March with a mean depth of 17 cm. Mean monthly summer precipitation from May through August is 75 mm (Sand *et al.* 1995). Mean annual density of moose in winter, after hunting, during the times of the study was 0.97/km^2 in area A, 1.32/km^2 in area B, and 0.82/km^2 in area C (Sand *et al.* 1995).

Grimsö Wildlife Research Area

For comparative purposes, we relate the moose data from Älvsborg County to

Table 1. Percent of various forest types found in sampling areas A, B, and C in southern Älvsborg County, Sweden.

	Area A			Area B			Area C		
Forest type	Young forest[1]	Other[2]	Total	Young forest	Other	Total	Young forest	Other	Total
Scots pine	2.9	2.6	2.6	22.0	19.3	19.7	26.5	30.4	30.0
Norway spruce	71.4	65.0	65.8	41.5	47.2	46.3	38.2	27.0	28.3
Mixed conifer	2.9	12.0	10.8	17.1	17.9	17.8	29.4	31.6	31.3
Mixed conifer/deciduous	14.3	6.0	7.1	12.2	6.0	6.9	—	4.9	4.4
Deciduous	8.6	14.5	13.8	7.3	9.6	9.3	5.9	6.1	6.1

[1] Young forest is defined as forests whose main stems have a mean height of 0.5 - 5.0 m
[2] Other are forests with main stem mean heights > 5.0 m

those from a better known population at Grimsö Wildlife Research Area (GWRA, Fig. 1), an area also included in the 'Balanserad Älgstam' project, in southcentral Sweden. Also, by the time the present study was initiated in southern Älvsborg County, moose showing signs of the wasting syndrome had become evident in the control area C, further emphasizing the need to include data from GWRA. Briefly, the GWRA consists mainly of a fairly homogeneous coniferous forest dominated by pine and spruce, with an admixture of deciduous trees, mainly birch and aspen; the latter are relatively sparse due to intensive forest management favoring conifers. Elevations at GWRA range from 75-150 m a.s.l. and mean forest productivity within the area is 6.9 m^3 forest growth/ha/yr (Sand *et al.* 1995). Climate at GWRA is comparable to southern Älvsborg County, but since the GWRA lies further north the winters are slightly longer with mean winter temperatures of -4.2°C and mean snow depths of 30 cm, whereas mean monthly summer precipitation is 65 mm (Sand *et al.* 1995). For a more detailed description of GWRA see Cederlund *et al.* (1980), Sand *et al.* (1995), and Faber and Thorson (1996). Mean annual density of moose in winter, after hunting, during the study period was 1.12/km^2 (Sand *et al.* 1995).

METHODS

Rumen Content Analyses

To determine forage types chosen by moose and to calculate the quantitative portions of each food type in the diet, we collected 111 rumen samples (area A, n = 37; B, n = 36; C, n = 38) during the autumn 1990 hunting season from October through December, and 62 rumen samples from 44 healthy moose and 18 moose diagnosed with the wasting syndrome, from area A in autumn 1991. Samples were frozen until analysis. Each sample consisted of about 0.75 L thoroughly mixed rumen content. Thawed material was rinsed with tap water through a 4-mm sieve. Rumen items in the sieve were identified to species; i.e., Scots pine, Norway spruce, common juniper (*Juniperus communis*), and oats (*Avena sativa*), or were assigned to one of the following categories: deciduous browse including birch, willow, and aspen; dwarf shrubs including heather (*Calluna vulgaris*) and *Vaccinium* spp.; grasses and herbs; and unidentified plant parts. The identified material was dried 48 h at 50°C and weighed with 0.1 g precision. The results are expressed as percent dry matter in the sample. This method was used on a much larger sample of moose by Cederlund *et al.* (1980), and shown to give a representative view of the quantitative composition of the diet from rumen contents.

Browsing Damage

In order to assess the approximate extent of total damage to conifers by moose, a survey was made of recent and accumulated damage in areas A, B, and C within each 6,300 ha survey plot as part of the 'Balanserad Älgstam' surveys. In the spring of 1992, sampling plots within all young (mean height of main stems 0.5-5.0 m) coniferous stands (Table 1) were surveyed. Damage was categorized on a scale of 0-2 according to the following:

Recent damage (previous winter):

0 = undamaged tree; needle loss < 50% on the 6 uppermost whorls of branches,

1 = needle loss 50-90% on the 6 uppermost whorls of branches; terminal shoot browsing; stem breakage, diameter at breakage point < 20 mm; bark stripped stem < 50% girdled,

2 = bark stripped stem > 50% girdled, or needle loss > 90% on the 6 uppermost whorls of branches; stem breakage, diameter at breakage point > 20 mm.

Accumulated damage (all damage irrespective of age), as above with following additions:

1 = damaged main stem diverging < 10 cm from original stem; lateral shoot with diameter < 10 mm damaged at base of main stem,

2 = multiple damage in main stem diverging < 10 cm from original stem; damaged main stem diverging > 10 cm from original stem; multiple lateral shoots damaged at base of main stem; lateral shoot with diameter > 10 mm damaged at base of main stem; forked main stem; multiple main stems, or tree dead; repeated terminal shoot browsing.

Nutrient Development in Moose Summer Browse

We collected samples of current-growth bilberry (*Vaccinium myrtillus*), silver birch, and Norway spruce shoots every other week during the growing period and once monthly otherwise, during the summers of 1991 and 1992 from 5 locations within area A. We used methodology adopted at GWRA for long-term monitoring of nutrient development in moose browse species (Å. Pehrson, *unpubl. data*). The samples were then immediately oven-dried after collection at 50°C for at least 48 h to achieve stable weight. After drying, these were milled to pass through a 0.5 mm sieve. We used this same drying procedure for all plant samples collected for nutrient analysis and for determining *in vitro* dry matter disappearance (IVDMD). The samples were analyzed at Grimsö Wildlife Research Station for concentrations of the macroelements calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), and total nitrogen (N) content using near infrared reflectance (NIR) technique (Inframatic 8620, Perten Instruments AB, Huddinge, Sweden) calibrated against a modified Micro-Kjeldahl analysis (P, N) and atomic absorption spectrophotometry (Ca, Mg, K). Concentrations of macroelements were expressed as percent dry matter. Crude protein (CP) was estimated as 6.25 x N concentration.

Trace Element Concentrations in Moose Browse

In order to detemine if bark contained higher concentrations of trace elements than twigs, samples of twigs within moose browsing height (about 1-2 m), together with bark from the stem of the same trees, were collected from 3 plant species at GWRA in January 1993. Samples were taken from rowan (*Sorbus aucuparia*), willow, and spruce, and from 5 trees at each of 5 locales within an area of 100 ha. For a comparison between moose browse in Älvsborg and GWRA, we collected bark samples from the same 3 species at 5 - 8 locales scattered over the southern part of Älvsborg County in November 1992. In addition, we sampled spruce bark from 2 areas, one with moderate amounts of bark stripping damage and one without, in early May 1992 within area A in Älvsborg. The area without damage had been limed in autumn 1990 due to high acidification. All bark samples were taken from 5 trees within each area, and included the outer and inner bark into the wood.

Trace elements analyzed were aluminum (Al), cadmium (Cd), cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn). The analyses were performed by the Chemistry Laboratory at the National Veterinary Institute (SVA, Uppsala, Sweden) using DCP-AES direct current plasma-atomic emission spectrometry technique (Frank and Petersson 1983, 1985). All concentrations of trace elements were expressed in parts per million (ppm) on a dry matter basis.

In vitro Dry Matter Disappearance Analyses

In order to determine and compare the apparent digestibility of spruce and pine foliage, we ran IVDMD trials modified after Tilley and Terry (1963). Our IVDMD method was originally developed at the Swedish University of Agricultural Sciences (SLU) for energy determinations in grass hay by den Braver and Eriksson (1967), and is described completely by Pehrson and Faber (1994). This procedure has been used at GWRA for studies on the digestibility of browse in moose and roe deer (Cederlund and Nyström 1981, Pehrson and Faber 1994). A total of 12 separate categories of foliage samples were collected in December 1991 and used as IVDMD substrate; 6 samples of spruce twigs and bark from Älvsborg County (Table 2), and 6 samples of twigs and bark from spruce and pine at GWRA (Table 3). Four IVDMD trials were run, 2 in January/February 1991 in Älvsborg County using rumen inocula from 3 moose harvested there, and 2 at GWRA in February 1991 using rumen inocula from 4 moose harvested there. We present IVDMD results in terms of percent dry matter.

Statistical Analyses

We compared differences in rumen contents between sampling areas with Kruskal-Wallis tests and differences between healthy and sick moose with Mann-Whitney *U* tests. A Chi-square test compared amounts of spruce and pine damage done by moose, and a Kruskal-Wallis test tested changes over time in CP content in bilberry, silver birch, and spruce. We tested for differences in trace elements using Mann-Whitney *U* tests and Wilcoxon signed-rank tests. The IVDMD values were compared using a Mann-Whitney *U* test. Statistics were computed using StatView™ SE+^{Graphics}(Abacus Concepts, Inc., Berkeley, CA).

RESULTS

Rumen Content Analyses

There were some differences in food choice by moose in autumn 1990 with respect to quantities of the 8 browse species/categories among the 3 sampling areas (Table 4), with area C differing considerably from areas A and B in 2 main respects (Table 4). Moose in area C consumed about 4 times more pine than moose from areas A and B but only about half as much deciduous browse. Grasses/herbs and spruce twigs compose only a small portion of the autumn diet of moose from all areas, and spruce bark was not found in any of the rumen samples. There were no differences in browse consumption between sex or age classes of the moose.

Table 2. Mean *in vitro* dry matter disappearance (IVDMD) in percent dry matter (± SD) of bark and twigs of Norway spruce (*Picea abies*) from southern Älvsborg County, Sweden, tested using moose inocula from Älvsborg and Grimsö Wildlife Research Area.

Sample	Älvsborg moose[1]	Grimsö moose[2]
Norway spruce (< 15 yrs old) twigs trees previously stripped by moose	27.9±2.4	27.6±0.7
Norway spruce (< 15 yrs old) twigs previously unstripped trees	27.3±3.1	27.5±1.3
Norway spruce (< 15 yrs old) bark trees previously stripped by moose	23.2±3.8	23.3±2.5
Norway spruce (< 15 yrs old) bark previously unstripped trees	21.6±2.9	23.2±2.1
Norway spruce (> 45 yrs old) bark trees previously stripped by moose	17.5±4.2	16.1±0.6
Norway spruce (> 45 yrs old) bark previously unstripped trees	18.6±3.1	18.2±1.5

[1] Means presented are based on results of inocula from 3 moose shot in Älvsborg and replicates of $n = 4$; i.e., 4 *in vitro* tubes per sample and moose

[2] Means presented are based on results of inocula from 4 moose shot within Grimsö Wildlife Research Area, and replicates of $n = 4$; i.e., 4 *in vitro* tubes per sample and moose

Table 3. Mean *in vitro* dry matter disappearance (IVDMD) in percent dry matter (± SD) of bark and twigs of Norway spruce (*Picea abies*) compared to Scots pine (*Pinus sylvestris*) from Grimsö Wildlife Research Area, Sweden, tested using moose inocula from Grimsö and southern Älvsborg County.

Sample	Älvsborg moose[1]	Grimsö moose[2]
Scots pine (< 20 yrs old) twigs previously unstripped trees	28.3±2.1	28.0±1.2
Scots pine (< 20 yrs old) bark trees previously stripped by moose	21.7±2.7	23.9±2.9
Scots pine (< 20 yrs old) bark previously unstripped trees	26.5±1.0	28.1±2.6
Norway spruce (< 20 yrs old) twigs previously unstripped trees	26.7±4.4	25.7±1.3
Norway spruce (< 20 yrs old) bark previously unstripped trees	24.8±2.9	26.1±1.2
Norway spruce (> 60 yrs old) bark previously unstripped trees	14.2±2.8	15.9±1.9

[1] Means presented are based on results of inocula from 3 moose shot in Älvsborg and replicates of $n = 4$; i.e., 4 *in vitro* tubes per sample and moose

[2] Means presented are based on results of inocula from 4 moose shot within Grimsö Wildlife Research Area, and replicates of $n = 4$; i.e., 4 *in vitro* tubes per sample and moose

Table 4. Mean percent dry matter (± SD) of different plant species and categories of browse in rumens of healthy moose harvested during the 1990 autumn hunt in southern Älvsborg County, Sweden.

Browse species/category	Area A $n=37$	Area B $n=36$	Area C $n=38$	P Value[1]
Scots pine (*Pinus sylvestris*)	10.2±16.8	9.88±15.5	42.3±30.0	0.0001
Norway spruce (*Picea abies*)	1.52±4.97	2.30±7.16	1.79±6.42	0.23
Common juniper (*Juniperus communis*)	0.01±0.05	1.36±4.73	3.93±11.9	0.009
Deciduous	47.4±33.5	42.9±34.0	23.2±24.1	0.003
Dwarf shrubs	37.5±29.7	19.9±24.9	25.6±24.0	0.02
Grasses/herbs	2.56±5.39	5.44±14.9	0.64±1.54	0.008
Oats (*Avena sativa*)	0	16.5±31.1	0.98±6.06	0.0001
Unidentified plant parts	0.81±3.43	1.79±6.57	1.51±5.22	0.23

[1] Kruskal-Wallis test

All moose consumed both deciduous browse and dwarf shrubs (Fig. 2), and within area B and C nearly all moose consumed pine, even though, in area B, this species comprised only about 10% of the diet. Approximately 20% (areas A and C) and 40% (area B), respectively, of moose ate spruce browse (Fig. 2), even though it was of little importance quantitatively (Table 4). More than half the moose in areas A and B ate grasses and herbs.

The only differences in diet between healthy and affected moose were in the use of grasses and herbs (P = 0.006) and unidentified plant parts (P = 0.02). Although there were differences between years in healthy moose from 1990 and 1991 (Table 5), and between healthy moose in 1990 and sick moose in 1991 (grasses and herbs, P = 0.004, and unidentified plant parts, P = 0.005, respectively), there were no differences between healthy moose in 1991 and sick moose in 1991 (Table 5). However, traces of spruce bark were found in very small amounts in rumens from 2 healthy animals harvested in 1991.

Browsing Damage

Overall, there was little damage to spruce (Table 6). There were differences in recent and accumulated browsing damage to spruce between the 3 sampling areas

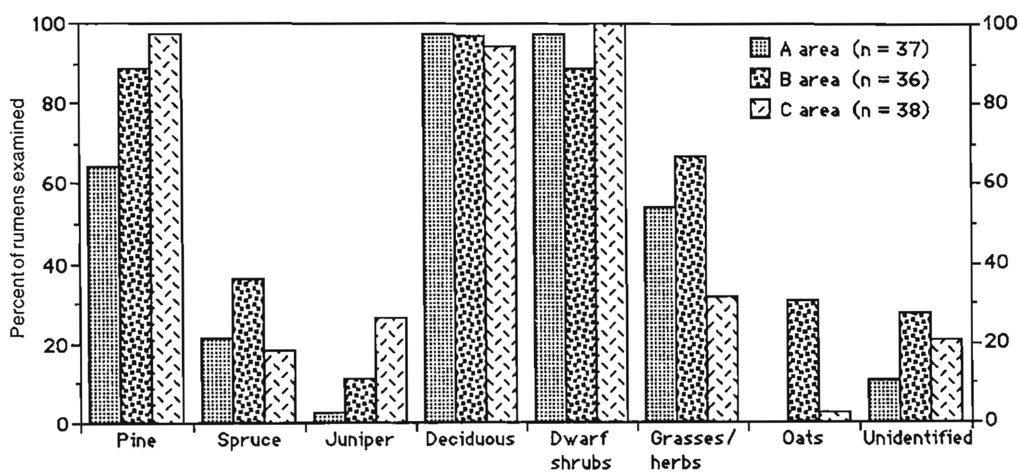

Fig. 2. Percent of moose with different plant species and categories of browse in rumens from animals harvested in autumn 1990 in southern Älvsborg County, Sweden.

Table 5. Mean percent dry matter (±SD) of different plant species and categories of browse in rumens of healthy and sick[1] moose harvested during the 1990 and 1991 autumn hunts within sampling area A in southern Älvsborg County, Sweden.

Browse species/category	Healthy moose			Sick moose[1]		
	1990 $n = 37$	1991 $n = 44$	P Value[2]	1991 $n = 18$	P Value[3]	P Value[4]
Scots pine (*Pinus sylvestris*)	10.2±16.8	12.1±18.7	0.30	17.8±27.2	0.90	0.51
Norway spruce (*Picea abies*)	1.52±4.97	1.22±3.19	0.56	1.11±4.52	0.33	0.59
Deciduous	47.4±33.5	34.6±33.3	0.04	38.1±36.1	0.70	0.14
Dwarf shrubs	37.5±29.7	42.4±32.4	0.53	31.6±34.9	0.23	0.45
Grasses/herbs	2.56±5.39	5.02±13.2	0.02	6.90±12.7	0.15	0.006
Unidentified plant parts	0.81±3.43	4.72±16.1	0.02	4.43±10.7	0.60	0.02

[1] Moose affected by a wasting syndrome
[2] Comparison of healthy moose in 1990 and 1991 by Mann-Whitney *U* test
[3] Comparison of healthy and sick moose in 1991 by Mann-Whitney *U* test
[4] Comparison of all 3 groups by Kruskal-Wallis test

($\chi^2 = 28.76$, 4 df, $P < 0.0001$ and $\chi^2 = 28.1$, 4 df, $P < 0.0001$, respectively). For pine, there were also similar differences in recent and accumulated browsing damage between sampling areas ($\chi^2 = 192.52$, 4 df, $P < 0.0001$ and $\chi^2 = 31.29$, 4 df, $P < 0.0001$, respectively).

Nutrient Development in Moose Summer Browse

Mean CP concentrations varied considerably both within ($P < 0.0007$ in all cases), and between browse species, and between 1991 and 1992 (Fig. 3). CP development in all species was highly synchronous in both years, with peaks by mid-May followed by declines with a slight delay in 1992 compared to 1991. Crude protein content was consistently higher in silver birch than in bilberry and spruce particularly in 1991.

Monthly patterns of Ca, Mg, P, and K concentrations were similar to that of CP. This is consistent with long-term patterns at GWRA (Å. Pehrson, *unpubl. data*); therefore, only mean minimum and maximum values are presented here (Table 7). In area A concentrations of Ca were highest in bilberry, lowest in spruce; Mg was only high

Table 6. Mean frequencies of percent moose damage[1] on Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) surveyed during spring 1992 within 3 sampling areas in southern Älvsborg County, Sweden.

	Area	n	Recent 0	Recent 1	Recent 2	Accumulated 0	Accumulated 1	Accumulated 2
Norway spruce	A	688	92.4	7.0	0.6	90.8	8.4	0.8
	B	621	97.6	2.4	—	96.6	3.4	—
	C	141	100	—	—	99.3	0.7	—
Scots pine	A	93	36.6	16.1	47.3	30.1	21.5	48.4
	B	549	60.3	24.0	15.7	53.2	16.6	30.2
	C	238	97.1	2.9	—	55.0	23.9	21.1

[1] 0 = no damage, 1 = moderate damage, and 2 = heavy damage; for details see 'Browsing Damage' in Methods

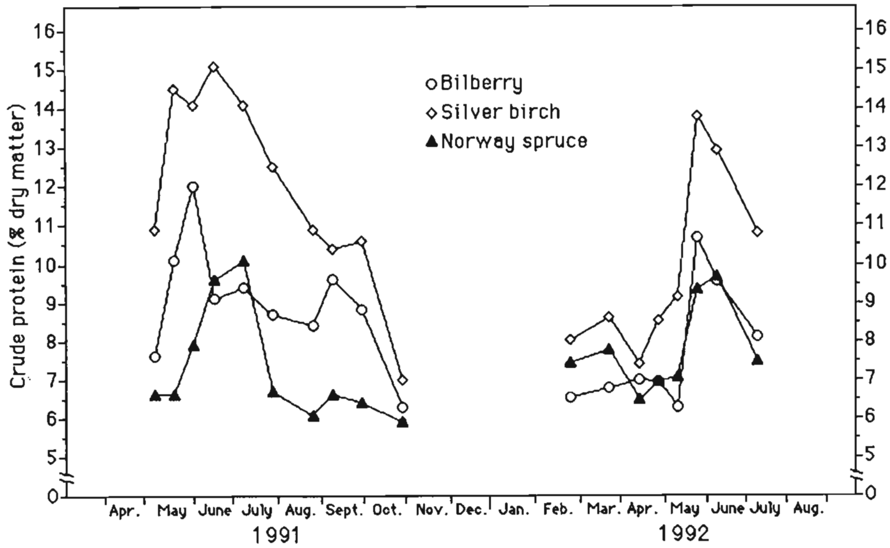

Fig. 3. Concentrations in percent dry matter of crude protein (CP) from current-growth bilberry (*Vaccinium myrtillus*), silver birch (*Betula pendula*), and Norway spruce (*Picea abies*) shoots collected during summer 1991 and 1992 within sampling area A in southern Älvsborg County, Sweden.

in silver birch; P was higher in silver birch than bilberry and spruce; and concentrations of K were highest in spruce (Table 7).

Trace Element Concentrations in Moose Browse

We found no differences between bark and twigs of rowan for any trace elements, whereas willow twigs contained significantly more Cu than did bark ($Z = -2.02$, $P = 0.04$) (Table 8). Spruce bark contained higher concentrations of all elements except Al and Mn (Table 8).

There were no large differences in any trace elements in the bark samples between GWRA and Älvsborg of the 3 browse species (Table 8). However, spruce bark from Älvsborg contained considerably higher concentrations of Cd and Co than spruce bark from GWRA. Also, rowan bark from Älvsborg contained higher concentrations of Al and Mn than rowan bark from GWRA (Table 8). Further, willow bark in southern Älvsborg County contained higher concentrations of all elements except Zn than Grimsö willow bark.

There were higher amounts of Fe in spruce bark from the area that had been

Table 7. Mean concentrations in percent dry matter ($n = 5$) of calcium (Ca), magnesium (Mg), phosphorus (P), and potassium (K) in current-growth twigs of bilberry (*Vaccinium myrtillus*), silver birch (*Betula pendula*), and Norway spruce (*Picea abies*) collected during summer 1991 within area A in southern Älvsborg County, Sweden.

	Bilberry		Silver birch		Norway spruce	
Mineral	Min.	Max.	Min.	Max.	Min.	Max.
Ca	0.45	0.85	0.25	0.58	0.18	0.35
Mg	0.08	0.15	0.07	0.20	0.06	0.13
P	0.10	0.22	0.15	0.28	0.13	0.23
K	0.33	0.60	0.25	0.75	0.43	1.05

Table 8. Mean concentrations in parts per million (ppm) dry matter (±SD) (n = 5-8) of aluminum (Al), cadmium (Cd), cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) in twigs and bark from 3 moose browse species collected in winter 1992 at Grimsö Wildlife Research Area and southern Älvsborg County, Sweden.

Element	Grimsö twigs	Grimsö bark	*P* Value[1]	Älvsborg bark	*P* Value[2]
		Norway spruce (*Picea abies*)			
Al	91±34	161±61	0.08	131±53	0.31
Cd	0.31±0.07	0.77±0.25	0.04	1.33±0.48	0.04
Co	0.15±0.05	0.25±0.14	0.04	0.53±0.38	0.24
Cu	2.58±0.55	4.44±0.72	0.04	4.56±0.89	0.77
Fe	26±10	76±38	0.04	63±28	0.46
Mn	816±270	755±222	0.69	798±513	0.88
Zn	51±10	138±54	0.04	176±57	0.14
		Rowan (*Sorbus aucuparia*)			
	Grimsö twigs	Grimsö bark	*P* Value[1]	Älvsborg bark	*P* Value[2]
Al	19±17	25±18	0.35	57±27	0.04
Cd	0.44±0.03	0.43±0.05	0.50	0.45±0.12	0.72
Co	0.20±0.05	0.13±0.09	0.35	0.09±0.03	0.36
Cu	5.74±0.51	5.32±0.76	0.14	4.77±2.16	0.07
Fe	37±1	39±10	0.69	51±14	0.07
Mn	177±47	240±81	0.14	502±220	0.02
Zn	56±11	48±16	0.69	49±23	0.72
		Willow (*Salix* spp.)			
	Grimsö twigs	Grimsö bark	*P* Value[1]	Älvsborg bark	*P* Value[2]
Al	51±34	37±20	0.22	67±29	0.08
Cd	1.17±0.10	1.12±0.45	0.50	2.65±2.08	0.02
Co	0.22±0.15	0.21±0.13	0.69	0.60±0.45	0.08
Cu	9.56±1.11	2.92±0.75	0.04	3.07±1.08	0.88
Fe	63±54	35±11	0.22	57±25	0.08
Mn	75±32	67±48	0.50	173±201	0.19
Zn	194±47	284±135	0.04	233±98	0.31

[1] Comparison of twigs and bark at Grimsö Wildlife Research Area by Wilcoxon signed ranks test
[2] Comparison of Grimsö and Älvsborg bark by Mann-Whitney U test

bark stripped than from the undamaged area (Z = -2.61, P = 0.009) (Table 9). This was concomitant to higher amounts, although not significant, of all other trace elements analyzed except Zn. At the same time, there were great variations in most trace element concentrations found in the individual samples as witnessed by the large standard deviations (Table 9).

In vitro Dry Matter Disappearance Analyses

There were no significant differences attributable to where rumen inocula were taken; i.e., IVDMD values for Älvsborg and Grimsö moose were similar with P >

Table 9. Mean concentrations in parts per million (ppm) dry matter (± SD) ($n = 5$) of aluminum (Al), cadmium (Cd), cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) in Norway spruce (*Picea abies*) bark collected from 2 areas in May 1992 in southern Älvsborg County, Sweden.

Element	Area with spruce bark stripping damage	Area without spruce bark stripping damage	*P* Value[1]
Al	99±44	86±18	0.40
Cd	1.13±0.31	0.92±0.16	0.35
Co	0.25±0.13	0.19±0.06	0.92
Cu	3.39±0.48	2.92±0.57	0.21
Fe	45±10	31±2	0.009
Mn	484±377	314±93	0.60
Zn	195±25	216±23	0.35

[1] Mann-Whitney *U* test

0.15 in all cases. Further, there were no significant differences in IVDMD of Norway spruce regardless of sample type (i.e., bark or twig), tree age, or if previously damaged (Table 2). Bark and twigs of both young (< 20 yrs. old) Norway spruce and Scots pine from GWRA had very similar IVDMD values (Table 3).

The lowest IVDMD values observed were for bark from mature (≥ 45 yrs. old) spruce trees (Table 2 and 3). We did not test bark from mature pine, since it is never used as forage in the southern parts of Sweden (Pehrson and Faber 1993). We found no differences in IVDMD between spruce that had been bark stripped previously and those that were undamaged (Table 2 and 3).

DISCUSSION

Our findings confirm that moose at varying densities in southwestern Sweden use Norway spruce twigs and bark as forage. However, the low proportions of spruce in the autumn diet indicates that it is not an important food. Results for Sweden are similar to North American studies, where spruce is used only sparingly as forage by moose (Murie 1934, Peterson 1955, Peek 1974, Risenhoover 1987, Renecker and Schwartz 1998).

Food choice seemed to be rather consistent within this moose population since we detected only marginal differences in the proportions of browse categories found in rumens between years and sampling areas, and between sick and healthy animals. In general, various forage types occurred in rumens in proportion to their respective coverage in the sampling areas (Pehrson and Faber 1993).

Our sampling period coincided with the autumn moose hunt, somewhat prior to the peak time of year when moose eat spruce (December-April; Axelsson 1990). Because of this, we cannot imply that spruce browsing is insignificant throughout the year. However, the low amounts of damage observed on spruce (Table 6), confirm general findings that spruce is of minor importance as moose browse. Furthermore, overall damage appears to be very low at the landscape level, but there is concern voiced by foresters (Axelsson 1990, Pehrson and Faber 1993), regarding prospects for significant economic losses at the local level due to spruce bark stripping by moose. Our earlier research has shown a similar pattern in Sweden for pine bark stripping by moose, with relatively large local impacts of minor importance at the landscape level (Faber 1996, Faber and Thorson 1996, Faber and Edenius 1998).

In an earlier paper (Pehrson and Faber 1993) we did not find any relationship between site variables for spruce stands and the occurrence of moose-induced damage. The only pattern we observed was that damage to spruce occurred on sites with the highest forest productivity. This pattern, however, was not consistent, since stands of similar site productivity could exhibit great variation in levels of damage.

Spruce has relatively low nutritional value when compared to important browse species such as birch and bilberry (Cederlund *et al.* 1980). Spruce contained lower CP and macroelement levels (except for K) when compared to these 2 species. However, concentrations of K in birch and bilberry were equivalent to those found at GWRA where spruce browsing is incidental. It is not likely that moose forage on spruce as a source of K since it is suggested that increased concentrations of K may hamper the uptake of Na (Staaland and Jacobsen 1983, Faber *et al.* 1988). Generally, the 3 studied browse species in our study area had similar or even higher concentrations of CP and the 4 macroelements analyzed, relative to those found at GWRA (Å. Pehrson, *unpubl. data*). The patterns of difference between years concerning concentrations and development of nutrients were similar between Älvsborg and GWRA, thus confirming that differences in site conditions exist between these regions in favor of Älvsborg.

It was found that spruce is comparable to pine in IVDMD, thus suggesting its value as moose forage may be comparable to pine in winter. Pine has been shown to be the important conifer component in winter diets of moose across Fennoscandia (Cederlund *et al.* 1980, Bergström and Hjeljord 1987). However, IVDMD values found here for bark from mature spruce are much lower than in other browse species investigated in southcentral Sweden using the same IVDMD methodology (Pehrson and Faber 1994, Faber 1996) and it would also indicate the unlikelihood that significant amounts of spruce were missed during botanical studies of rumen contents.

Further, we were not able to distinguish any differences in IVDMD between bark from stripped and unstripped spruce trees. Results from 2 similar collections from mature spruce stands in close proximity to GWRA that had been bark stripped by moose, revealed somewhat higher, although not statistically significant, IVDMD values for bark stripped spruce trees compared to undamaged ones (W. Faber and Å. Pehrson, *unpubl. data*). We found that in samples collected from one of these spruce stands there were significantly higher CP values in bark from stripped spruce. Likewise data from Älvsborg and GWRA show that variation between the paired samples was greater than within the paired samples (Tables 2 and 3); there was also a positive covariation of qualitative variables in the bark samples. Thus, when considering other measures of spruce in combination with its potential digestibility, we would argue that spruce, especially with regards to bark from mature trees (i.e., > 45 years old) most utilized by moose, is of lower quality than most other moose browse species available in our study area. In this context these facts lend support to our first hypothesis that spruce consumption is an indication of overbrowsing.

Few studies report on trace elements in moose forage in Sweden (Pehrson and Faber 1993, Faber and Lavsund 1999). Present results suggest that it is difficult to obtain reliable values of trace element concentrations in plant samples, because many samples are required. This is evident since our collections at GWRA within a 100 ha area showed about the same variation (Table 8) as within Älvsborg where samples were collected over the whole southern part of the county. In addition, we lack knowledge about what concentrations of the different trace elements are required for maintaining a healthy, productive free-ranging moose population. Compared to the normal requirements given for domestic sheep *Ovis aries* and cattle *Bos taurus* (National Research Council 1985, 1996), our results suggest there are insufficient amounts of essential trace elements and macroelements if moose have similar requirements. However, our data reveal that concentrations of trace elements in moose forage in Älvsborg, or in forage for any other moose populations of which we are aware, do not differ considerably from and are not lower than concentrations at GWRA. Thus, it is difficult at present to relate the wasting syndrome in moose in southern Älvsborg County to a primary deficiency of any particular trace element in moose forage (Pehrson and Faber 1993). Further, the difficulty lies in being able to elucidate which trace element(s), if any, is of significance for moose. When comparing analyses of nutrient concentrations in moose forage species, it is obvious that most variables that describe the quality of the sample in any way covariate positively (Pehrson and Faber 1993, Å. Pehrson, *unpubl. data*).

Earlier, Flynn *et al.* (1977) found indications that Cu deficiency linked to decreased Cu content in browse occurred in free-ranging moose in Alaska. Frank and colleagues (Frank *et al.* 1994, Frank 1998) have advocated secondary Cu deficiency due to elevated molybdenum (Mo) levels as a potential cause of the moose wasting syndrome in Sweden. This is based on the fact that Cu concentrations in moose livers have decreased considerably in synchrony with increased levels of Mo in southern Älvsborg County over a 10-15 year period. The mechanism triggering uptake of Mo in moose forage could be the intensified liming of forested lands, lakes, and wetlands conducted in this area, a method used to counteract ongoing acidification in this region (Frank 1996). However, Pehrson (1996) in a study performed in this region did not find any differences in concentrations of Mo and Cu in moose forage between limed and unlimed forest stands.

A number of farmers have reported that their cattle display a similar behavior (i.e., bark stripping of spruce) in the areas where spruce bark stripping by moose is prevalent (Andersson 1988, Pehrson and Faber 1993). No comprehensive study on this phenomenon has been performed but from scattered visits it was discovered that such bark stripping bouts by cattle occurred in pastures with spruce trees next to spruce stands damaged by moose. This bark stripping has been performed by both dairy and beef cattle in various stages of productivity, and in some of the pastures where cattle have grazed for decades without a single incident of such damage. In most cases farmers have experienced intensive bark stripping with extensive damages appearing where cattle had access to spruce stands. It seems unlikely, especially in light of our results regarding qualitative aspects of spruce, that highly productive livestock would benefit from consuming bark of spruce.

The question remains to be answered as to what lead both cattle and moose in patchily distributed areas of southern Älvsborg County to strip spruce bark. One could argue that any underlying mechanism may be identical for these 2 ruminant species due to similarities in the spatial and temporal distribution of spruce damages, and that perhaps other minerals or nutrients not thus far investigated may be involved. In this context, some ecotoxicologists have noted that in this region known for its textile industry, an accompanying release of organic environmental pollutants (e.g., dioxins, dieldrin, and brominated flame retardants) has potentially contaminated these same areas where spruce damage occurred. They suggest that this may in turn lead to vitamin C deficiencies in moose and cattle, and also potentially to cases of osteoporosis in moose, although the mechanisms involved in this relationship are not clearly understood. It is suggested that spruce bark may be a good source of vitamin C, and that moose and cattle consumed spruce bark for this reason (M. Lind and J. Örberg, Section of Ecotoxicology, Uppsala University, *pers. comm.*). Alternatively, it is possible that consuming spruce bark is simply a hedonic behavior that is taste-guided, as has been suggested for salt ingestion in animals (Schulkin 1991).

CONCLUSIONS

In general quantitative terms, spruce seems to be of minor importance to moose in southern Älvsborg County, and it is inferior to favored moose foods such as birch, bilberry, rowan, and pine. Bark stripping seems to be of little importance relative to the total amount of forage needed by a moose population and to the actual damage experienced. Yet the sudden increase in use, at least locally, suggests that there may be other underlying factors which may have triggered this behavior. High acidification, a wasting syndrome, and/or high moose densities leading to overbrowsing, may have separately or in combination lead to this sudden occurrence of spruce utilization. However, factors investigated in this study relative to spruce consumption do not explain why moose began foraging on spruce in recent years. On the contrary, most of our results lend support to research which indicates that spruce is a low quality forage only rarely utilized by moose in North America (Murie 1934, Peterson 1955, Peek 1974, Risenhoover 1987, Renecker and Schwartz 1998) while it ranks lowest on winter food preferences of moose across Scandinavia (Bergström and Hjeljord 1987). Further research should focus on other hypotheses for explaining the mechanisms behind this unique behavior in our study area.

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