EFFECTS OF MOOSE DENSITY ON TIMBER QUALITY AND BIODIVERSITY RESTORATION IN SWEDEN, FINLAND, AND RUSSIAN KARELIA

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ABSTRACT: A long history of forest use and management in Sweden has promoted conifer-dominated forests at the expense of deciduous trees such as *Populus tremula*, *Salix caprea*, and *Sorbus aucuparia*. Moose (*Alces alces*) are a key species both with respect to the maintenance of biodiversity associated with these deciduous trees and to the production of good quality Scots pine (*Pinus sylvestris)* timber. For biodiversity there is a need to restore the deciduous forest component, which is also the preferred food of moose. If the moose/preferred food ratio is too high and hence browsing on the preferred tree species too intensive, this restoration can be difficult. To study the interactions between the abundance of preferred moose food, moose density, and damage to trees, it is necessary to include landscapes with a broader combination of food abundance and moose density than found just in Sweden. This is necessary as the landscape and management situation in Sweden is rather homogeneous, with the same policies concerning forestry and moose management having been implemented. To cover a wide range of relevant factors, a study covering 8 landscapes in Sweden, Finland, and Russian Karelia was carried out in autumn 1998. Damages on both preferred trees and Scots pine in pine-dominated stands were correlated to moose density. Damages were most severe in Sweden, intermediate in Finland, and least in Russian Karelia. Moose winter densities ranged from 1.7/km^2 in Sweden to 0.2/km^2 in Russia. The cover of preferred foods (*Populus/Salix/Sorbus*) increased 13-fold from Sweden to Russia. As a consequence, the proportion of severely damaged and dead individuals of the preferred species increased 36-fold from the least to the most affected landscape. Similarly, damages on Scots pine in pine-dominated stands ranged from 57% in Sweden to 7% in Russian Karelia. Unless damage by moose is reduced in Sweden in the landscapes that we studied, it is doubtful that deciduous vegetation can be maintained, thereby affecting biodiversity. Communication with stakeholders is essential if this socio-economic problem is to be resolved. One feasible model may be co-management case studies based on a holistic landscape view and objective inventory of perceived problems among all stakeholders.

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All species are not equally important for the structure and dynamics of an ecosystem (Westman 1990). Some may affect the structure and function of the ecosystem, whereas others do not. The former are often called key-stone species (Estes *et al.* 1982, Simberloff 1988). Today, moose (*Alces alces*) are the major browser in boreal forests. To formulate management rules in forestry, it is especially important to study how key-stone species are affected by forest structure and composition, at both the stand and landscape level, as well as how the key-stone species affect the ecosystem.

In Sweden, moose have increased dramatically during the last 50 years due to lack of natural mortality and increased amounts of young forests providing a good food supply (Strandgaard 1982, Cederlund and Bergström 1996). In the boreal forest on the Fennoscandian shield, there are 2 coniferous tree species, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and 5 main deciduous tree species attaining a DBH of 20+ cm, silver and white birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*), sallow (*Salix caprea*), and rowan (*Sorbus aucuparia*). These species are preferred as winter food throughout the range of moose. According to Ahlén (1975), moose prefer the species mentioned above in the following order: *Populus tremula*/*Salix caprea*/*Sorbus aucuparia* > *Betula* spp. > *Pinus sylvestris* > *Picea abies*.

Browsing on Scots pine is of great concern to foresters and has resulted in research on how to balance the interests of foresters, hunters, and the general public. The consumption of Scots pine has increased dramatically with increasing moose densities (Hultkranz and Wibe 1989) and the damage locally can be severe (Lavsund 1987). The high browsing pressure on Scots pine suggests that other, more preferred tree species may also be affected. This could lead to reduced diversity of deciduous trees. In an evaluation for certification of the economic, environmental and social aspects of forest management (Rhubes *et al.* 1996), the effects of moose on trees were evaluated as problematic both within the economic and environmental perspectives. Browsing by large herbivores on deciduous trees was considered so serious that the"forest company's certificate was conditioned by a requirement to develop policies and functional methods to adjust the browsing to a level that does not threaten the biodiversity dependent on old deciduous trees.

The objective of this study is to contribute to the development of methods to assess how landscape composition with respect to browse species and browser abundance affects levels of damage both in terms of wood production and maintenance of forest biodiversity. The 2 most urgent problems in Sweden are as follows: (1) bark stripping, stem breakage, and broken apical shoots on young Scots pine which are no longer developing into high-quality saw-logs at an acceptable rate: currently, the cost for this damage is larger than the cost for all other biodiversity management activities carried out by large forest companies (R. Friberg, StoraEnso, *pers. comm.*); and (2) the numbers of adult deciduous trees of aspen, sallow and rowan cannot be restored at a sufficient rate to maintain deciduous forest biodiversity: this problem is exemplified by the importance of the lichen community with *Lobaria pulmonaria* (Nilsson *et al.* 1995) and the bird community with white-backed woodpecker (*Dendrocopos leucotos*) as their focal species (Martikainen *et al.* 1998), both of which require old deciduous trees, which are preferred by moose.

To study the relationship between damage to trees, moose density, and habitat quality, it is necessary to include landscapes with a broader combination of tree species composition and moose density than found in Sweden alone. This is essential, as landscape management in Sweden is rather homogeneous, with the same forestry and cervid management policies applied throughout the country. This has lead to small differences in moose abundance across Sweden when compared to the variation among boreal landscapes in Fennoscandia in general (Danilov 1987, Nygrén 1987).

In summary, we wanted to describe the variation in moose damage to young trees across wide gradients of both moose densities and food abundance at the landscape scale. This study reports a novel approach to this problem by studying the full range in variation of moose densities and tree species compositions found in 3 forest countries on the Fennoscandian shield.

STUDY AREAS

Because moose density is a variable in this study, sampling had to be carried out at the scale of a local moose population, i.e., in an area on the order of magnitude of 1,000 km^2. Hence, the landscape is the main unit of replication. We studied 4 landscapes in Sweden and 2 each in Finland and Russian Karelia (Table 1). Collectively, all landscapes comprise a gradient in moose abundance and moose food density, including a wide range of the variables we studied. To avoid variations caused by climate and forest ecoregion, all landscapes selected were located in the same boreal forest and boreal climate region (Ahti *et al.* 1968, Tuhkanen 1984; Fig. 1). In all landscapes forest management is based on clear-cutting practices.

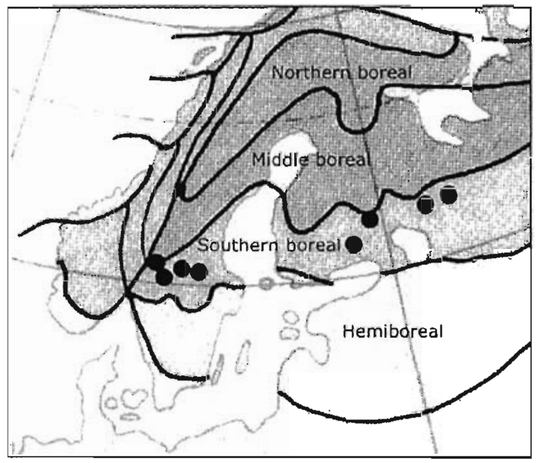

Fig. 1 Map of Fennoscandia with the location of the 8 landscapes where this study was conducted.

METHODS

Moose Density and Habitat Use

To obtain data on relative moose density figures which are independent of the density estimates provided by forestry and hunting organizations, and to get an index of local use by moose for each forest stand, moose pellet groups were counted in 100 m^2 plots at 50 m intervals along the sampling triangle (i.e., 6 plots for each young forest stand). To ascertain if pellet counts relate to moose density, the average number of pellet groups was correlated to current density estimates received from surveys in the

Table 1. Locations of the landscapes studied, and their moose density per km^2. Data on moose were provided by local hunters, STORAENSO Forest Co. staff in Sweden and Finland, and by Danilov (*unpubl.*).

Country	Landscape	Latitude/ Longitude	Moose density
Sweden	Höljes summer	60.7/12.6	1.2
Sweden	Höljes winter	60.9/12.4	1.7
Sweden	Säfsnäs	60.2/14.2	1.1
Sweden	Larsbo	60.2/15.4	1.0
Finland	Imatra	61.4/28.5	0.45
Finland	Ilomantsi	62.6/30.8	0.25
Russian Karelia	Kaskesnavolok summer	61.5/33.3	0.15
Russian Karelia	Kaskesnavolok winter	61.8/33.5	0.35

different landscapes. Because most of the moose-related damage on trees and shrubs occurs during winter, only winter densities (i.e., post-hunting period) were used.

Tree Species Composition in Young and Old Forest

Within each landscape 20 pair-wise sampling units were distributed systematically. Each sampling unit consisted of 2 habitat types; young 1.5 - 4 m tall Scots pine stands suitable for winter browsing, and old (>60 yr) forest stands. The sampling units were spread out evenly in the selected landscape and were located in the centre of stands larger than 3 ha. At each sampling unit in young forests, 3 circular plots of 100-m^2 (5.64 m radius) were placed at the corners of an equilateral triangle with 100-m sides (3 plots/sampling unit). To assess vegetation both from the point of view of moose food and of the individual tree, young trees were measured both as the vertically projected summed cover of each individual tree in percent, and the number of individuals per unit area.

To get an overview of the composition of trees in old forests, being the natural seed source for the recruitment of seedlings after logging, the basal area was assessed using a half size column relascope. The sampling points were placed at the corners of an equilateral triangle with 100-m sides in the old forest stands located nearest to each sampled young forest.

Browsing Damage

At each site, Scots pine, Norway spruce, silver birch, white birch, rowan, aspen, and sallow were measured and browsing damage was assessed. Damage on Scots pine, spruce, and birch was defined according to the National Board of Forestry guidelines as a reduction in the quality of the future saw-logs caused by broken tops or cambium damage. Damage on aspen, sallow, and rowan was defined as the inability (all long-shoots browsed or dead) of a tree to grow to a size where it is no longer susceptible to damage. This conservative method was used to ensure that moose damage was determined unambiguously.

For the economically important species such as Scots pine, Norway spruce, and the birches, only individuals taller than 50% of the upper height of the stand canopy were assessed. The reason we chose to assess only these dominant trees is that due to selective removal of individuals occurring below this level during silvicultural cleaning, they are unlikely to be recruited into the population of trees that will form the future stand. By contrast, all individuals of aspen, rowan, and sallow were measured as they are not actively removed during silvicultural practices, and potentially can grow to adult trees irrespective of their present size.

Moose browsing damage on pine, spruce, and birch was divided into different types, only taking into account damage that affects the quality of the future saw log. Each tree was classified using the following criteria: not damaged (A), bark stripping (B), stem damage in the form of a fork, bayonet or stick (C), other damage (D), or tree is dead caused by moose (E).

Browsing damage on rowan, aspen, and sallow were measured as the proportion of long shoots browsed during the lifetime of the tree. Trees were classified in 5 groups: not browsed (0), <50% of long shoots damaged (1), >50% of long shoots damaged (2), all long shoots damaged (3), or tree is dead caused by moose (4). The height of 1 random individual of each species was measured in each of the stands.

To ensure a sufficient sample size of rowan, aspen, and sallow, damage was assessed both at the corners of the sampling triangle and along a 4-m wide band-transect between the sites in each sampling unit. The total area of this sampling was

(4x3x100)+(3x100)=1,500 m^2 at each of the 20 young forest stands in a landscape.

RESULTS

Moose Population Densities

The trend differs during the past 15 years in each country. In Sweden, the moose population declined by 50% from the peak of the early 1980's to the present densities of 0.8-1.1/km^2 (Cederlund 1996, Faber 1997). In Finland the density has been more stable during the past 15 years and the present density is 0.3-0.4/km^2 (Nygrén 1987). In Russian Karelia the density has also been stable, but at an even lower level of 0.1-0.3/km^2 (P. Danilov, *unpubl. data*).

As there are temporal changes in moose density in each country, and our assessment of moose damage measured the cumulative damage over several years, we calculated the average moose density over a time period equalling the average stand age (13 yrs) of the landscapes studied. Results from recent moose population surveys in the 8 landscapes showed a strong decrease in moose population density from Sweden to Russian Karelia (Table 1). In the Swedish landscapes, these average moose densities ranged from 1.0 - 1.7/km^2, in the Finnish 0.25-0.45/km^2, and in Russian Karelia 0.15-0.35/km^2 (Table 1).

The variations in moose densities among the 8 landscapes were closely correlated to the pellet group counts made in young forest stands (r^2=0.74, t=4.18; P=0.006; Fig. 2).

Species Composition in Old Stands

The total basal area of old trees in Sweden, Finland, and Russia was not significantly different (Table 2). By contrast, large differences were found in the species composition among the 3 countries. The amount of the 3 most preferred species namely rowan, aspen, and sallow, are also those most important for deciduous forest biodiversity and increased from 0.6% in Sweden and 0.4% in Finland to 6.9% in Russian Karelia.

Species Composition in Young Stands

The average total vertical cover of young trees in Sweden, Finland, and Russian Karelia was between 55 and 60%, and not significantly different. However, large differences were found in the species composition among the different countries (Table 3). The amount of the 3 most preferred

Table 2. Basal area (mean ± SD m^2/ha) of trees in old forest stands adjacent to the sampled young forest stands in Sweden, Finland, and Russian Karelia.

Tree species	Sweden (n=80)	Finland (n=40)	Karelia (n=40)	ANOVA F; P-value
Sorbus aucuparia	0.04±0.14	0.004±0.03	0.12±0.24	5.56;0.005
Populus tremula	0.08±0.42	0.08±0.17	1.5±1.7	33.48;0
Salix caprea	0.02±0.10	0.01±0.05	0.10±0.19	7.79;0.0006
Betula spp.	1.3±1.7	1.5±2.2	6.4±4.3	52.15;0
Picea abies	13±7.3	7.2±6.6	12±5.8	9.69;0.0002
Pinus sylvestris	9.3±7.4	14±9.3	4.5±5.7	15.16;0
Alnus incana	0.03±0.12	0.04±0.19	0.36±0.92	7.16;0.001
Larix decidua	0.02±0.17	0	0.004±0.03	0.50;0.61
All	24±5.5	23±4.6	25±5.3	2.39;0.09

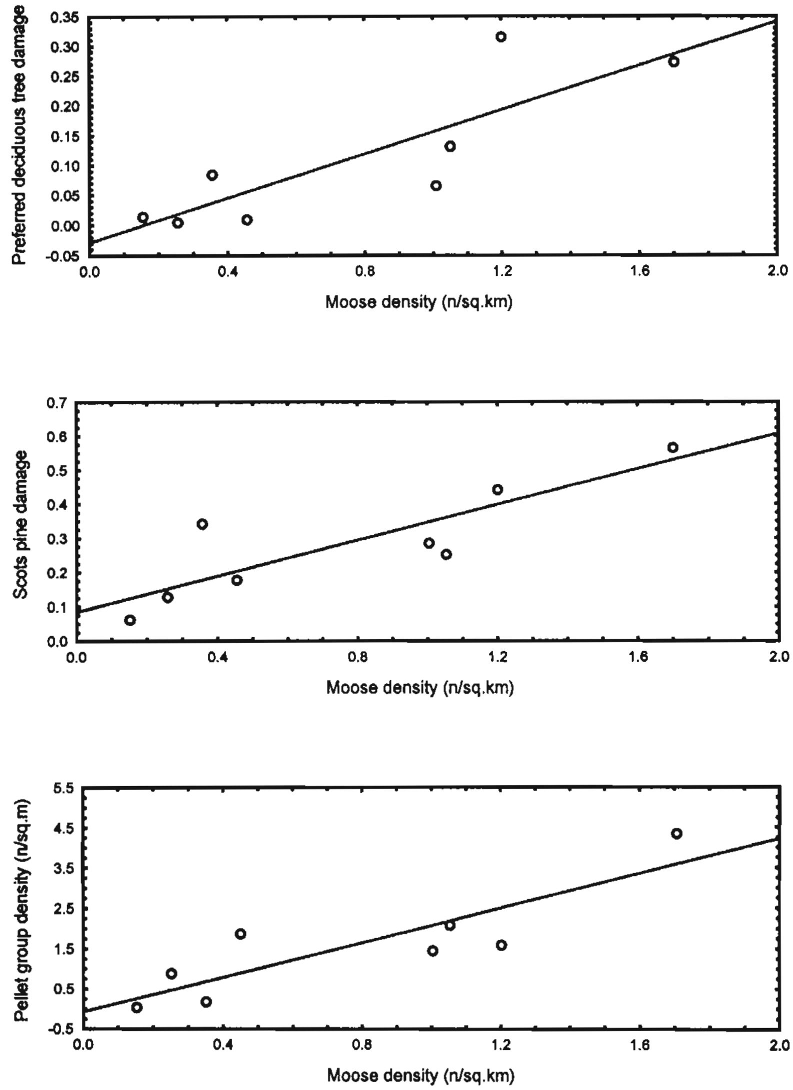

Fig. 2. Relationships between moose density and the density of pellet groups in young forest, as well as the proportion of damaged Scots pine in pine dominated stands and damaged preferred deciduous trees.

species; rowan, aspen, and sallow increased from 1.6% in Sweden to 4.2% in Finland and 18.6% in Russian Karelia. By contrast, coniferous species declined from 39% in Sweden, 38% in Finland, and to 21% in Russian Karelia. For birch there was no trend.

Damage to Scots Pine

In this analysis only pine-dominated stands (>1,800 pine/ha) were included. The reason is that stands with a low amount of pine could show an irrelevantly high proportion of damaged pine in spite of a low total damage level measured as the density of trees damaged.

When comparing the damage on Scots pine, it was found that there was a significant difference between the 8 landscapes (1-way ANOVA, F = 4.15, P = 0.003). Further, when comparing these damages to the differing moose densities across the 8 landscapes (Table 1), there was a strong positive relationship ($r^2 = 0.75$, $t = 4.21$, $P =$

Table 3. Vertically projected cover (mean percentage ± SD) of tree species in young forest in Sweden, Finland, and Russian Karelia.

Tree species	Sweden (*n*=80)	Finland (*n*=40)	Karelia (*n*=40)	ANOVA *F*;*P*-value
Sorbus aucuparia	0.71 ± 0.98	1.9 ± 3.1	3.9 ± 6.0	11.2;0.00003
Populus tremula	0.45 ± 3.0	1.5 ± 3.5	10 ± 11	33.9;0.00000
Salix caprea	0.41 ± 0.96	0.87 ± 1.2	4.7 ± 4.2	50.5;0.00000
Betula pendula	3.5 ± 6.5	6.6 ± 6.3	4.7 ± 4.1	3.62;0.02889
Betula pubescens	12 ± 10	5.6 ± 8.6	16 ± 13	10.6;0.00005
Picea abies	13 ± 11	3.8 ± 5.6	9.2 ± 7.3	11.9;0.00002
Pinus silvestris	21 ± 15	34 ± 14	11 ± 10	28.8;0.00000
Pinus contorta	4.8 ± 12	0	0	6.37;0.0022
Larix decidua	0.08 ± 0.36	0	0.025 ± 0.16	1.16;0.32
Alnus incana	0	0.3 ± 1.10	0.02 ± 0.10	4.31;0.015
All	56 ± 18	55 ± 16	60 ± 1	1.38;0.25

0.006; Fig. 2).

Damage to Preferred Species

The proportion of severely damaged rowans declined steeply from 22% in Sweden to 1% in Finland, and 1% in Karelia. The damage on aspen and sallow showed a similar pattern. The proportions of severely damaged aspen were 30% in Sweden, 1% in Finland, and 8% in Karelia. For sallow, the proportions were 14% in Sweden, 0% in Finland, and 4% in Karelia (Table 4). We attribute the observation that damage to preferred species was higher in Russian Karelia than in Finland to the fact that one of the Karelian landscapes was a regional winter range while none of the Finnish landscapes was of that type.

When comparing the combined sum of preferred deciduous trees with all long shoots damaged (damage class 3) and dead trees (damage class 4) for the preferred species as a group, it was found that there was a significant difference between the 8 landscapes (1-way ANOVA, F = 25.19, P = 0.000). Further, when comparing these damages to the differing moose densities found across the 8 landscapes (Table 1), a clear significant positive relationship was found (r^2 = 0.71, t = 3.83, P = 0.009; Fig. 2).

Another way of expressing the strong effect by moose on the preferred tree species is to compare their average height with the maximum height of each stand in the 3 countries. While the maximum height of the trees in the stand was almost the same, there were strongly significant differences among the length of the preferred tree species (Table 5). Viewed at the scale of stands only 3.8% of the stands in Sweden (*n*=80) reached up to more than 50% of the maximum height of the stands. The corresponding figures were 18% in Finland (*n*=40) and 75% in Russian Karelia (*n*=40). As these ratios were significantly different (χ^2=73.8, P=0.001) it is clear that moose browsing affects the probability of successful maturation of the preferred tree species. In Russian Karelia most damage on rowan was caused by brown bears (*Ursus arctos*) while breaking young trees to feed on rowan berries.

Table 4. Damage (mean±SD) by moose on tree species in young forests in Sweden, Finland, and Russian Karelia. For the preferred species *Populus/Salix/Sorbus* the proportion of individuals with 100% damage to long shoots is presented. The economically important species are denoted as A = not damaged, B = bark stripping, C = stem breakage.

Tree species	Sweden (n=80)	Finland (n=40)	Karelia (n=40)	ANOVA F; P-value
Sorbus aucuparia	0.21±0.19	0.01±0.00	0.00±0.00	37.86;0
Populus tremula	0.21±0.29	0.00±0.01	0.02±0.07	17.05;0.0000
Salix caprea	0.13±0.23	0.00±0.00	0.03±0.12	8.88;0.0002
Betula pendula A	0.28±0.33	0.52±0.34	0.73±0.28	17.42;0.0000
Betula pendula C	0.71±0.33	0.46±0.32	0.24±0.26	20.74;0.0000
Betula pubescens A	0.50±0.33	0.73±0.35	0.86±0.16	19.21;0.0000
Betula pubescens C	0.47±0.35	0.25±0.34	0.13±0.16	17.01;0.0000
Pinus sylvestris A	0.55±0.26	0.72±0.18	0.63±0.31	5.54;0.0048
Pinus sylvestris B	0.08±0.10	0.00±0.01	0.00±0.01	18.38;0.0000
Pinus sylvestris C	0.25±0.21	0.15±0.15	0.31±0.29	5.05;0.0076
Picea abies A	0.87±0.23	0.85±0.24	0.85±0.23	2.96;0.1625
Picea abies C	0.02±0.09	0.01±0.05	0.07±0.11	2.94;0.0568

DISCUSSION

This study strongly suggests that moose population density is the main factor affecting the amount of moose-related damage among landscapes to young Scots pine trees, as well as the preferred species rowan, aspen, and sallow. This has also been suggested by other studies (Lavsund 1987, Bergström and Wikberg 1992) but not shown as clearly.

Several other factors also contribute to the local variation in moose browsing. For example, within the same region, or even landscape, damage can be quite different depending on whether it is a summer or a winter moose range (Sweanor 1987). Variations in snow depth and browse composition appear to be the most important factors determining moose habitat choice (Bergström and Hjeljord 1987, Kuznetsov 1987). Snow depth decreases the accessibility of food resources, reduces ability to move, and increases the energy required for locomotion (Nordengren 1997). Hence, moose are making habitat-choice decisions on different spatial scales. They may select

Table 5. Average maximum height (mean±SD) of the sampled young forest stands and average length of tree species preferred by moose.

	Sweden (n=80)	Finland (n=40)	Russian Karelia (n=40)	ANOVA $F;P$-Value
Maximum stand height (m)	3.81±1.32	3.79±0.88	3.95±1.03	0.22; 0.80
Length of preferred species (m)	0.74±0.42	1.36±0.65	2.43±0.81	106.9; 0

different areas partly because of snow depth and composition of the vegetation. Within those areas certain habitats are often selected. In a particular feeding habitat, moose use is often concentrated in certain parts and within those parts the most preferred accessible forage is chosen (Bergström and Hjeljord 1987).

The Need to Sample the Full Range of Variation

In a landscape that was altered by man a long time ago, it is difficult to appreciate the extent to which we have modified it from its past state. One major potential flaw is to not be fully aware of the total range of historic variation. For example, to differentiate species use and need of different habitat types, it is necessary to perform studies on the full range of variation found in natural landscapes, and to know whether or not the occurrence in the habitat is permanent. If necessary, results must be obtained or studies initiated in reference areas where important properties are still intact (Angelstam 1996, Angelstam *et al.* 1997).

Swedish moose densities are exceptionally high (Tankersley and Gasaway 1983, Baskin and Lebedeva 1987, Danilov 1987, Heptner *et al.* 1989, Hörnberg 1991, Käkelä *et al.* 1991), and the proportions of deciduous trees in Swedish forests are exceptionally low compared with other parts of the boreal forest. We argue that unless this is considered it is not possible to make valid studies of the effects of moose browsing and tree species composition on browsing pressure of preferred food plants by performing studies only in Sweden.

Moose Affects Future Tree Species Diversity of Mature Stands

Height measurements of rowan, aspen, and sallow showed that in only 4% of the Swedish stands do these species have a chance to become mature trees. By contrast, in Finland rowan, aspen, and sallow were allowed to follow the stand height development in 18% of the stands investigated. In Russian Karelia, rowan, aspen, and sallow generally followed the overall stand height development in all stands investigated. Hence, as long as the present high browsing pressure remains on the Swedish landscape, rowan, aspen, and sallow will probably not be able to mature at the rate required to restore deciduous forest biodiversity.

While young forest stands in both Sweden and Finland are subject to silvicultural cleaning, this was generally not the case in Russian Karelia. However, as shown by Härkönen *et al.* (1998), moose browsing in silviculturally cleaned stands was less intense than in untreated ones. As the trend in browsing intensity increased from Russian Karelia to Sweden, with increasing incidence of silvicultural cleaning, we conclude that the effect of moose density is stronger than that of differences in silviculture.

Cervid browsing and its effect on plant communities has also been discussed in North America. White-tailed deer (*Odocoileus virginianus*) and moose have been 2 of the important species focused upon by researchers and managers (McShea *et al.* 1997, Augustine and McNaughton 1998, Moen *et al.* 1998). It has been shown that there can be direct and indirect effects of white-tailed deer and moose resulting in changes in plant community composition, plant productivity, and nutrient cycling (McInnes *et al.* 1992, Pastor *et al.* 1993, Ritchie *et al.* 1998). These impacts will in turn have implications for the management of these species (Sinclair 1997). It is, therefore, important to fully understand the interrelationships between cervids and plant communities, and how cervids affect and regulate these systems (Augustine and McNaughton 1998). In a broader perspective, understanding the interactions between ungulates in general and whole ecosystems should be the ultimate goal.

Alternate Stable States?

Studies on several types of ecosystems suggest that a population can be stable at more than one mean level of population density (Sutherland 1974, Simenstad *et al.* 1978). Classically, animals (or plants) at an intermediate (lower) trophic level may escape from the "predator pit" and densities may stabilize at a higher level if predators (or if herbivores; then the "herbivore pit") are absent, or predation (herbivory) negligible.

For North American conditions in general, Crête (1987) estimated that the carrying capacity of moose could exceed 20 per 10 km^2 if populations are limited by food only, but could remain at 4 per 10 km^2 when moose are preyed on by 2 predator species. The natural predators are functionally extinct in most areas of Sweden, severely reduced in Finland, but intact in most of Karelia (Danilov 1987). Sweden is close to the extreme managing principle whereby maximum sustainable harvests are achieved simply by eliminating all predators and replacing predation with human harvest (Cederlund and Bergström 1996). However, as pointed out by Ballard and Larsen (1987:599) this means "that managers might be faced with a different sort of problem, i.e., too many moose and not enough hunters to control their numbers." This is currently the problem in Sweden where few large predators remain.

Based on these experiences, it appears that to reach higher levels of deciduous shrubs per moose, it is necessary to reduce the moose density below the desired level, then let the deciduous cover escape from the "herbivore pit", and finally allow the moose density to increase to an appropriate level again.

Are Moose Overabundant in Sweden?

Whether or not moose are perceived as overabundant depends on the different perspectives of the observer. As discussed by Sinclair (1997) for white-tailed deer in North America, there are different definitions on carrying capacity, both biological and arbitrary.

Typically, timber companies would like the "timber carrying capacity" to be low, thereby ensuring that the level of damage is low. Another user of the renewable forest resources, i.e., hunters, will have another point of view with a "hunter carrying capacity" lying near the maximum sustainable yield of the population. Nature conservationists, being concerned about the viability of rare species, have suggested that high cervid numbers either degrade habitat or threaten rare plant species, therefore the "rare species carrying capacity" must be placed near, or even below, the timber carrying capacity (Sinclair 1997).

At the present moose-forage ratio, we conclude that moose are overabundant in Sweden according to both the "rare species carrying capacity" and "timber carrying capacity". However, adjusting the moose density to a lower level is also a socio-economic issue. Moose hunting is an important event for the people living in forested areas, both economically and socially. All stakeholders included in this discussion should be aware that solving the problem of overabundant moose has negative consequences.

MANAGEMENT IMPLICATIONS

There are in principle 3 ways of reducing the browsing pressure on preferred tree species: (1) to reduce moose densities; (2) to increase the amount of food; and (3) to reduce the availability of food. A reduction of the Swedish moose density to the level observed in Finland or Russian Karelia would probably reduce the browsing pressure on rowan, aspen, and sallow so that these tree species will recover and increase in size and numbers. However, if it is not politically acceptable to rapidly decrease the moose population to such a low level, other means have to be employed. We suggest that the first step should be to develop more relevant ways of expressing moose densities, which better reflect the quantitative and qualitative aspects of browse.

Browsing damage can be viewed as a ratio between the number of animals and their food resource. This clearly illustrates that browsing pressure can be influenced both by manipulating moose and its food. Using only moose population density per land area in discussions on moose and habitat management to decrease browsing damage is therefore misleading. The moose per food ratio within the range of a local moose population could be expressed in several ways with increasing precision and cost.

A first step would be to calculate the number of moose per unit area of young forests, ranging from 5 -15 years after clear-cutting. If there is information about the tree species composition in the young forest stands, the number of moose could be expressed per unit area of young Scots pine-dominated forest within browsing height ranging from 5 - 15 years. Finally, with detailed knowledge of the average height, cover, and availability of different forage species used by moose, an index could be expressed as a ratio between moose and its food resource.

The management implications for rowan, aspen, and sallow are somewhat different. Due to the low densities of the 2 most important trees for boreal deciduous forest biodiversity, i.e., aspen and sallow, management has to proceed in 2 steps. First, it is essential to protect the already established mature individuals of these species. Secondly, efforts to increase the amount of aspen and sallow should be concentrated in areas where growing conditions are suitable for regeneration and survival. Examples of such areas are stands with existing aspen clones, often found in old fertile agricultural areas in the forest landscape that can produce aspen and sallow with high abundance and rapid growth. Special care should be taken to find stands where aspen and sallow are protected naturally by steep slopes or large boulders, which reduce the availability to moose. Finally, to create conditions that allow growth and development of aspen clones and sallow that are established, these sites should be made as inaccessible as possible for moose. This could be done either by fencing or by harvesting the local moose population.

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