

Abstract

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The foraging patterns of large herbivores will affect their impact on structures and functions of ecosystems and on human use of natural resources. The foraging patterns are affected by a multitude of factors, e.g. forage availability, environmental conditions and herbivore density. Furthermore, the importance of these factors has been suggested to vary over temporal and spatial scales. The impact from large herbivores will affect the management actions to fulfil socio-political policies (e.g. regarding damage to forests) and the harvest quotas could be decided from monitoring of animal numbers and damage. However, wildlife managers are often faced with a choice of several available monitoring methods, at varying cost and precision. The aim of this thesis was to improve our understanding of: 1) factors governing the foraging patterns of large herbivores and thereby also the impact on the ecosystem; and 2) performance of survey methods in relation to monitoring cost. The study was performed in south-central Sweden, and moose (*Alces alces*) in boreal forest was used as a model system. The results suggest that herbivore foraging decisions are scale-dependent. The significance of moose density effects, site productivity and diversity among forage species on the foraging pattern varied from feeding patch to landscape level. On the plant level, browsing pressure and moose preference for groups of certain species varied significantly. On the stand level, moose preference for certain habitats varied according to variation in snow conditions. Furthermore, the distribution of forage types (e.g. field and shrub layer) differed between the habitats and the browsing on the different layers of forage will therefore vary according to environmental conditions. The browsing pressure was also dependent on forage availability and herbivore density. Moose density in Sweden is mainly regulated by hunting. The hunting quotas rely on more or less accurate monitoring methods. The ability to reach management goals generally increased with monitoring effort, but a combination of two relatively inexpensive monitoring methods also produced successful management outcomes.

Keywords: aerial survey, *Alces alces*, browsing, damage, deer, environmental variation, foraging, forest, harvest, hunters' observations, herbivore, pattern, pellet group count, monitoring, *Pinus sylvestris*, preference, scale dependence, spatial, temporal

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The moose is singularly grotesque and awkward to look at. Why should it stand so high at the shoulders? Why have so long a head? Why have no tail to speak of?

Henry David Thoreau (1817–1862)

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by Roman numerals:

- I. Månsson, J., Kalén, C., Kjellander, P., Andrén, H. and Smith, H. 2007. In press. Quantitative estimates of tree species selectivity by moose (*Alces alces*) in a forest landscape. *Scandinavian Journal of Forest Research*
- II. Månsson, J., Andrén, H., Pehrson, Å. and Bergström, R. 2007. Moose browsing and forage availability – a scale-dependent relationship? *Canadian Journal of Zoology* 85:372-380
- III. Månsson, J. Temporal variation in moose browsing intensity and habitat preference in relation to forage availability and snow conditions. *Manuscript*.
- IV. Månsson, J., Hauser, C., Andrén, H. and Possingham H. Monitoring and harvest of moose - the cost of management success. *Submitted Manuscript*.

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Introduction

An organism's foraging pattern is its decision about where and what to eat. Those decisions affect the animal's fitness (Moen, Pastor & Cohen, 1997) but also the structure and function of ecosystems and the human use of natural resources (Gill, 1992; Jefferies, Klein & Shaver, 1994; Healy, 1997; Augustine & McNaughton, 1998; Danell et al., 2006). Organisms are not equally important for the structure and function of ecosystems. Large herbivores have been pointed out as keystone species and are thereby characterised as organisms with a high "impact factor" (Danell et al., 2006). Much of the concern about large herbivore impact relates to damage to forests and agricultural crops (Gill, 1992, 2006; Putman & Kjellander, 2003). However, there is also concern about the impact of browsing on rare tree species and cascade events (Angelstam et al., 2000; Berger, Stacey & Johnson, 2001). A multitude of factors such as forage availability, predation risk, snow condition, interaction with other herbivores, shelter from harsh weather, and human impact affect the foraging patterns of large herbivores (Senft et al., 1987; Pierce & Peek, 1984; Grover & Thompson, 1986; Morrison et al., 2003). Furthermore, the importance of these factors varies in time and space, for instance because of changes in socio-political policies, natural fluctuations or factors acting differently at different scales (Senft et al., 1987; Lavsund, Nygren & Solberg, 2003). Thus, foraging pattern by a large herbivore is clearly a synthesis of decisions concerning the intrinsic state of the animal, seasonality, interspecific interactions and environmental factors. Problems regarding foraging patterns, impact on ecosystems and management of large herbivore are obviously complex and the need for greater knowledge about the integrated components within the management of large herbivores has been highlighted (Decalesta, 1997).

The aim of this thesis was to improve our understanding of foraging patterns and browsing pressure on the tree and shrub layer. Knowledge about these problems is often closely linked to management issues. I have included studies on interactions between forestry and deer but also a study about the ability to reach management goals by using different monitoring strategies. For this purpose I have used the moose, (*Alces alces*), in the boreal zone in Sweden as a model system. The thesis is focused on moose browsing patterns during the winter period. This period is of particular interest in Sweden as browsing damage and economic loss to forestry occur mainly during the winter, as the moose winter diet is dominated by twigs from commercially important conifer species, primarily Scots pine, (*Pinus sylvestris*) (Cederlund et al., 1980; Gill, 1992).

At present, the moose is one of the most widespread and important large herbivores in the boreal zone (Franzmann & Schwartz, 1997; Baskin & Danell, 2003; Lavsund, Nygren & Solberg, 2003). The moose has been considered as a keystone species because of its major impact on plant species composition and height development of young trees (Angelstam et al., 2000; Berger, Stacey & Johnson, 2001). In Sweden, most of the concern about moose impact in the forest ecosystem has been about browsing pressure and locally severe damage to economically important forest trees, primarily Scots pine (Lavsund, 1987;

Lavsund, Nygren & Solberg, 2003). However, concern about the impact of moose browsing on rare deciduous tree species and cascade events has also risen recently (Angelstam et al., 2000; Persson, Danell & Bergström, 2000).

In Sweden, there are conflicting interests between different stakeholders, most clearly between hunters and foresters. The foresters experience large losses due to browsing damage whereas hunters prefer a large population for high harvest yield (Lavsund, Nygren & Solberg, 2003). Swedish moose management aims to combine a high yield from the moose population and simultaneously minimise forest damage (Kalén, 2005), which means that the moose population size has to be balanced with the regional quantity of forage to reach economic sustainability (Kjellander, 2007). This can be achieved by either adjusting the size of the moose population or the availability of forage (Hörnberg, 2001a). Any attempt to manage a game species for high yield while, at the same time, minimising browsing damage to forests requires a thorough understanding of population dynamics, foraging patterns and performance of management tools.

The following definitions apply to this thesis:

Browsing pressure: Severity of browsing; proportion of twigs being removed. Compared to current monitoring of forest damage in Sweden, this term includes all browsing of available shoots and not only those directly affecting future timber quality, i.e. top shoot browsing, bark stripping and stem break

Browsing intensity: Same as browsing pressure.

Damage: Browsing-induced reduction of timber quality and/or growth, with potential economic loss for the forest owner. The current monitoring of forest damage registers the proportion of trees with top shoots browsed, stem breakage or bark stripping, i.e. only effects that reduce timber quality.

Deer: Any member of the Cervidae family, i.e. also includes moose.

Field layer: the herb and dwarf shrub layer. In this study, the latter mainly consists of bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), heather (*Calluna vulgaris*).

Preference: Choice of a particular resource (tree, habitat etc) by an animal in relation to availability of the resources.

Shrub layer: In a stratified forest structure, the layer of the woody plants shorter than the trees that form the canopy. In clear-cuts and young forest stands (i.e. no canopy) all shrubs and saplings make up the shrub layer.

Selectivity: Same as preference

Browsing risk

Changes in forage availability and plant species composition within the ecosystem occur due to natural (fire, storms) and human-induced (timber harvest) disturbances. Such changes will affect the impact from deer, as the distribution and composition of the forage changes. It has been demonstrated that browsing intensity correlates with deer density and availability of forage, e.g. young trees of

Scots pine (Decalesta, 1997; Hörnberg, 2001a). However, such relationships have limited value for predicting how or in what way changes in forage species composition will affect browsing patterns, as different species have different preferences (Bergström & Hjeljord, 1987; Moser, Schütz & Hindenlang, 2006). To make predictions more robust, models need to consider both availability and preference for different tree species. By using a selectivity index for certain tree species, predictions of future herbivore impact might be improved. Such knowledge would make it possible for forest owners to take preventive actions (e.g. creating supplemental forage of preferred species or by protecting economically important plantations by fencing, etc) and thereby reduces future economic loss due to intensive browsing. Bergström & Hjeljord (1987) reviewed some 70 papers on moose preferences for different tree species. Although the relative ranking among tree species was fairly consistent - rowan (*Sorbus aucuparia*) > willows (*Salix spp.*) > aspen (*Populus tremula*) > juniper (*Juniperus communis*) > birch (*Betula spp.*) > Scots pine > alder (*Alnus glutinosa*) > Norway spruce (*Picea abies*) - no attempts were made to estimate a quantitative selectivity index for the browsed species. By incorporating absolute differences in preference among forage species into models that predict browsing pressure, I argue that the predictability and generality will improve compared to models that only include herbivore density and forage availability.

Spatial scales

In experiments conducted in artificial stands, Danell, Edenius & Lundberg (1991a) found that food selection by a large herbivore occurs primarily at the tree level. Therefore, a food item (e.g. tree or shrub) is believed to be the fundamental patch unit at which the intake rate by the herbivore should be optimised (Åström, Lundberg & Danell, 1990). Many of the earlier studies of herbivores and foraging patterns have focused on smaller spatial scales, i.e. habitat patches and single trees (Figure 1) – for review see Hobbs (2003). However, the knowledge about trade-off mechanisms at larger spatial scales is still insufficient (Hobbs, 2003; Weisberg & Bugmann, 2003). Understanding animal distribution and foraging requires a multi-scale approach because there may be a different set of trade-off mechanisms at different spatial scales creating complex heterogeneity in animal or resource distribution in both time and space (Senft et al., 1987; Forbes & Theberge 1993; Johnson, Parker & Heard, 2001; Fortin et al., 2003). Forage biomass is proposed to be a consistently important factor determining foraging patterns and herbivore distribution at all scales (Senft et al., 1987). At a small scale (plant community level), Senft et al. (1987) hypothesised that foraging response to forage availability and quality should be overmatching (i.e. a disproportionately large foraging response to a change in dietary reward (Figure 2). At larger scales (landscape and regional) the response pattern to forage biomass should be matching (i.e. a proportional change in dietary reward) (Senft et al., 1987). Along with forage availability, other environmental factors such as predation risk, snow condition, interaction with other herbivores, shelter from harsh weather and human impact, have been proposed to affect the foraging patterns and distributions of large herbivores (Pierce & Peek, 1984; Grover & Thompson, 1986; Morrison et al., 2003) and therefore influence higher-order decisions. The multiple underlying

mechanisms affecting the foraging decisions are hard to separate, especially when spatial and temporal scales get coarser and more potentially confounding variables may be involved (Hobbs, 2003). However, the role of spatial scales and different factors affecting foraging decisions is important knowledge for an overall understanding of animal distribution, impact on the ecosystem and to facilitate comparison between studies (Turner et al., 1989; Hobbs, 2003).

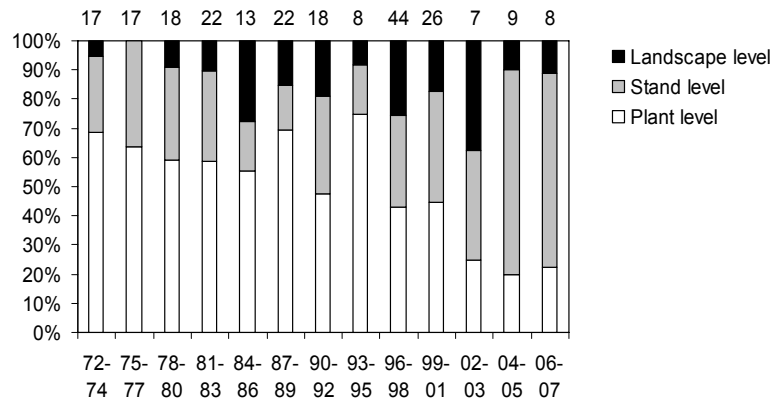


Figure 1. To get an overview of the distribution of research conducted on different spatial scales concerning deer foraging choice, I surveyed the last 25 years of all journals included in the CAB abstracts database (successor organisation to Commonwealth Agricultural Bureau). I searched all fields for “(moose or roe deer) and (browse or forage)” and noted the number of studies conducted on foraging and habitat choice at each specific spatial scale. The papers were divided by reading the abstract and using Johnson’s (1980) classification of habitat selection i.e. second-order selection (larger than home range – classified as landscape level) third-order selection (usage of various habitat within the home range – classified as stand level) and fourth-order selection (feeding of different food items – classified as plant level).

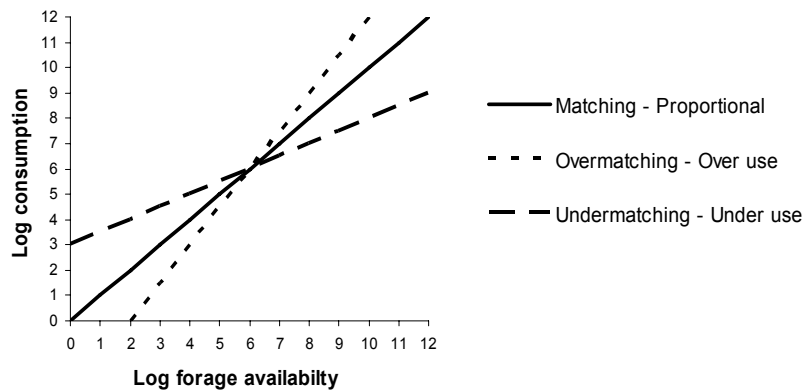


Figure 2. The principle of proportional and unproportional relationship between consumption and forage availability. In a proportional relationship the consumption doubles as forage availability doubles, which results in a slope of 1 in a log-log plot.

Temporal scales

Herbivores prefer habitats with high forage availability within the landscapes (Bergström & Hjeljord, 1987; Langvatn & Hanley, 1993; Mysterud et al., 1999). However, there may be temporal variation in preference for certain habitats due to variations in forage availability and density of animal (Maddock, 1979; Palmer & Truscott, 2002). For example, different habitat types may provide different types of forage (e.g. in field layer, shrub layer) and as the forage availability changes the herbivore's habitat preference will also change. Environmental conditions can affect the availability of food species; for example, alternative forage in the field layer may be completely unavailable after a heavy snow fall, and thereby affect the animal's preference for certain habitats (Cederlund et al., 1980). Such changes in food availability and herbivore distribution are therefore likely to affect browsing pressure on the shrub layer, as alternative forage (e.g. in the field layer) may vary from total absence to abundant. Such temporal variation in browsing pressure has been indicated by an annual variation in moose damage to Scots pine, and snow condition has been suggested as one underlying factor (Kjellander, 2007). The amount and composition of forage are clear factors affecting the browsing pressure (Moser, Schütz & Hindenlang, 2006), but factors affecting browsing pressure also include herbivore density, tree species composition and previous browsing (Decalesta, 1997; Bergqvist, Bergström & Edenius, 2003; Gill, 2006; Vehviläinen & Koricheva, 2006). A change in forage composition and availability, as a result of insect outbreaks, storms, fire, browsing, snow conditions or forestry actions, will therefore affect the herbivore distribution and browsing pattern (Weixelman, Bowyer & Ballenberghe, 1998; Taillon, Sauvé, & Cote, 2006). In order to understand the effects of deer browsing on ecosystems, not only spatial scales should be considered but also the temporal variation in moose distribution, density and browsing patterns.

Monitoring and management of moose in Sweden

Knowledge about relations between herbivore density, forage availability and browsing pressure, in time and space, allows a management goal to be set for the deer population. Two of the most central elements of moose management in Sweden consider the damage to forestry and the net increase in the moose population for harvest. Therefore a typical management goal could be defined as an optimisation problem with an interval between an upper moose population size limit (N_{max}), for example to avoid severe damage to forestry, and a lower limit (N_{min}), for example to keep a harvest quota at an acceptable size for hunters. This is certainly the case for populations ranging across large areas and where the management objective differs between several landowners and managers. However, the management of the moose population demands reliable monitoring methods to ensure that decision-making achieves the management goals (Wennberg DiGasper, 2006). Monitoring methods provide feedback on whether or not goals are currently being achieved, and also provide information to assist management and ensure that goals will be met in the future. In Sweden, aerial surveys, direct observations (hunters' observations) and pellet group counts have been used for that purpose (Lavsund, 1975; Haagenrud et al., 1987; Ericsson &

Wallin, 1999; Persson, 2003; Wennberg DiGasper, 2006). However, the methods differ according to reliability (accuracy and precision) and cost (Fuller, 1991; Ericsson & Wallin, 1999; Mayle, Peace & Gill, 1999; Barnes, 2001; Campbell, Swanson & Sales, 2004; Smart, Ward & White, 2004). The combination of variation in reliability and the state of the population also allows the use of a state-dependent monitoring system. The ability to combine monitoring methods in a cost effective and accurate manner requires more knowledge about performance and costs of each monitoring strategy. Studies comparing accuracy in wildlife monitoring methods seldom take into account the costs (but see Smits, Ward & Larsen, 1994; Campbell, Swanson & Sales, 2004). For a comprehensive understanding of moose management, an evaluation of the management success in relation to monitoring methods used and costs is therefore necessary.

Objectives

I. Browsing risk

The aims of Paper I were to establish a relative ranking order and a quantitative selectivity index of seven tree species, which are regularly browsed by moose. The quantitative selectivity index predicts the risk for the different tree species of being browsed by moose. Statistical methods developed in habitat utilisation studies at the home range level were used, by using the biomass consumption and forage composition of the tree species.

II. Scale-dependent browsing pattern

Focusing on forage availability and absolute biomass consumption by a large herbivore, Paper II aimed to describe the relationship between forage availability and browsing and to test whether this relationship is scale-dependent. The relationship between forage availability and absolute consumption was investigated to see if the relationship was proportional or not. The behaviour of the relationship is fundamental to understanding the distribution and foraging ecology of herbivores. Furthermore, a positive relationship was predicted between absolute consumption and forage availability, forage species diversity, site productivity and herbivore density.

III. Temporal variation in browsing

The two first papers focused on browsing pattern at different spatial scales, from the plant level (Paper I) to the landscape level (Paper II). The aim in Paper III was to study temporal variation in browsing pressure from a large herbivore. Browsing and preference of three different habitat types in relation to variation in forage availability, herbivore density and snow conditions was studied over ten years. I expected that forage abundance and herbivore density would be good predictors for browsing pressure, but that environmental variability, i.e. snow conditions, may add annual variation to this pressure. Finally, I tested whether an overall change in herbivore density in the area would result in different habitat specific

density changes, or if the densities changed in the same way in all habitats (young forest < 30 years, old forest > 30 years and mires).

IV. The cost of management success

Papers I, II and III produced information about the relationship between a large herbivore and browsing pressure in the forest landscape (primarily browsing on the economically important Scots pine). From these results and earlier studies we can predict goals for the herbivore population size in relation to acceptable browsing pressure. Paper IV therefore aimed to evaluate the performance, i.e. ability to reach the goal, and to estimate the cost of moose management actions in relation to use of different monitoring strategies (Table 1). A combination of field data from empirical surveys and simulations was used to estimate variance and accuracy in aerial surveys, pellet group count and hunters' observations.

Table 1. Description of the sixteen monitoring strategies used in the simulation process.

Number	Strategy
1	No monitoring, with a harvest of 400 individuals taken annually
2	Perfect knowledge of February population size
3	An aerial survey is conducted each year
4	Pellet group counts are conducted each year
5	Hunters' observations are recorded each year
6	An aerial survey and a model prediction are combined each year
7	Pellet group counts and a model prediction are combined each year
8	Hunters' observations and a model prediction are combined each year
9	Pellet group counts and hunters' observations are combined each year
10	An aerial survey is conducted every 4 th year, with model predictions each other year
11	An aerial survey is conducted every 4 th year, with pellet group counts each other year
12	An aerial survey is conducted every 4 th year, with hunters' observations each other year
13	An aerial survey is used in the first year; otherwise: * If $950 < \bar{N}_t < 1050$, then hunters' observations are used. * If $850 < \bar{N}_t < 950$, or $1050 < \bar{N}_t < 1150$, then pellet group counts are used. * If $\bar{N}_t < 850$ or $\bar{N}_t > 1150$, then aerial surveys are used.
14	An aerial survey is used in the first year; otherwise: * If $S.D.(N_{t-1}) \geq 200$, then an aerial survey is used. * If $S.D.(N_{t-1}) < 200$, a model prediction is used.
15	An aerial survey is used in the first year; otherwise: * If $300 < \bar{N}_t < 500$, $700 < \bar{N}_t < 900$ or $1100 < \bar{N}_t < 1300$, an aerial survey is used. * For all other \bar{N}_t , pellet group counts are used.
16	An aerial survey is used in the first year; otherwise: * If $350 < \bar{N}_t < 450$, $750 < \bar{N}_t < 850$ or $1150 < \bar{N}_t < 1250$, an aerial survey is used. * For all other \bar{N}_t , pellet group counts are used.

The moose species and moose population development in Sweden

The moose has a circumpolar distribution (Bergström & Hjeljord, 1987; Franzmann & Schwartz 1998; Baskin & Danell, 2003) in the boreal forest (Odum, 1983). It is the largest living member of the deer family, Cervidae (Putman, 1988). It is a solitary living species, but moose commonly form temporary groups during winter (Sweanor & Sandegren, 1985) and the home ranges overlap (Cederlund & Sand, 1992). The mean yearly home range within my study area is 25.9 km² for males and 13.7 km² for females (Cederlund & Sand, 1994). The species is not defined as territorial but frequently shows agonistic behaviour to other individuals within close vicinity (Sweanor & Sandegren, 1985). The European moose (*A. a. alces*, L. 1758) is one of eight existing subspecies and occurs in north-western Europe and Russia (Baskin & Danell, 2003; Hundertmark et al., 2003).

A moose needs approximately 3-6 kg twigs (dry weight) per winter day (Hjeljord, Sundstøl & Haagenrud, 1982; Baskin & Danell, 2003). Twigs from trees and shrubs dominate the forage of moose in northern Europe during winter, while leaves of woody species and herbs dominate the summer diet (Cederlund et al., 1980; Bergström & Hjeljord, 1987). Based on the feeding style, the moose is classified as a concentrate selector (Hofmann, 1985). The feeding style is closely reflected in a simple gut structure (small rumen, short papillae, and short retention time) and moose therefore demands a relatively high nitrogen level in the diet. The moose undertake seasonal migrations (northern Sweden) and their behaviour is adapted to select habitats, plant species and parts of the plants to meet the nutritional requirements (Bergström & Hjeljord 1987; Putman, 1988). Cederlund et al. (1980) found that Scots pine was predominant in the rumens of moose during the winter, making up > 55% of the January-February browsed material. Birch was frequent in the moose rumens during the whole year, particularly from June through September. The availability of forage shifts in time and space and the amount of available forage can change rapidly due to snow, forestry, fire and storms (Loranger, Bailey & Larned, 1991; Weixelman, Bowyer & Ballenberghe, 1998). During winter periods of scarce snow, field layer species such as bilberry and heather can make up a significant proportion of the rumen content (Cederlund et al., 1980). The Swedish moose population increased from the 1920s and peaked in the early 1980s (approximately 450 000 individuals in the summer of 1983). Several factors have been proposed for the dramatic growth of the Swedish moose population during 1970s, e.g. altered forest management, lack of natural predators, regulated hunting and decreased competition from free-ranging livestock (Cederlund & Markgren, 1987). Intensive forest management has been proposed as the main factor and, for example, the positive effects of clear-cutting on moose populations have often been emphasised (Cederlund & Markgren, 1987).

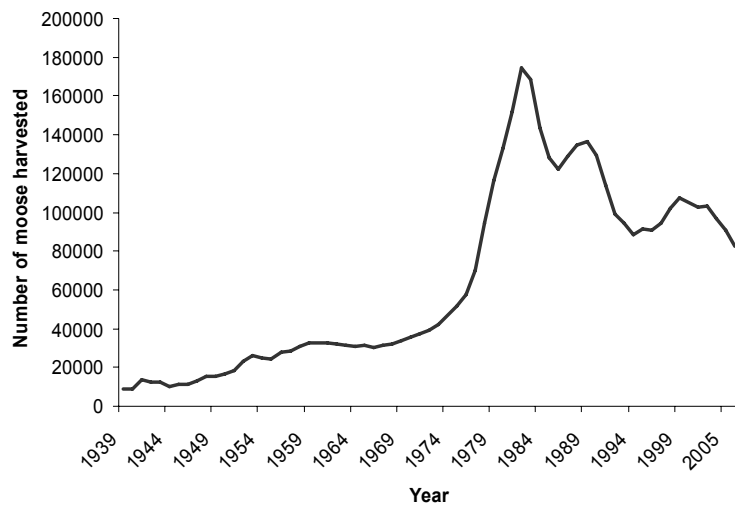


Figure 3. Number of moose harvested in Sweden 1939-2006 (Swedish Association for Hunting and Wildlife Management 2007).

In contrast to the natural situation it has been claimed that modern forestry (large clear-cutting areas) provides moose with a constant supply of high quality forage over longer periods, thus keeping the population growth at a high level (Cederlund & Markgren, 1987). In Sweden, areas of young forest areas increased threefold during the 1960s and 1970s. The moose population has decreased since the peak in the 1980s but is still numerous and the hunting bag in 2006/2007 in Sweden was 82,000 animals (Figure 3), (Lavsund, Nygren & Solberg, 2003; Swedish Association for Hunting and Wildlife Management 2007). High browsing pressure from moose and subsequent severe damage to economically important forest trees (particularly Scots pine) is still an important issue in Sweden although the moose population has decreased since the peak of the 1980s (Lavsund, Nygren & Solberg, 2003). Today the moose population is still decreasing but the expected response, i.e. a decrease in browsing pressure in young forest stands, has not yet occurred. One proposed explanation to the lack of response is a simultaneous decrease or negative trend in the amount of forests in early succession stages (Lavsund, Nygren & Solberg, 2003). In Sweden the main cause of mortality of moose is hunting (about 95 % of the adult mortality according to Cederlund & Bergström (1996)). About 30-40 % of the pre-harvest moose population is harvested every year (Rönnegård et al., submitted manuscript).

Study area

The data was collected from two overlapping study areas located in the southern boreal forest of south-central Sweden (59°84'N, 15°48' E; Figure 4). The study was initiated at the Grimsö Wildlife Research Area in 1996. In order to study scale-dependent browsing, the study area was enlarged in year 2004. The enlarged

area covered an area of 1,000 km² (Figure 4). Within this area, Grimsö Wildlife Research Area (140 km²) is located in the southwest (Figure 4). In Papers I and III, data was only collected within the Grimsö Wildlife Research Area. In Paper II, data was collected in the larger area while Paper IV was based on empirical data from both.

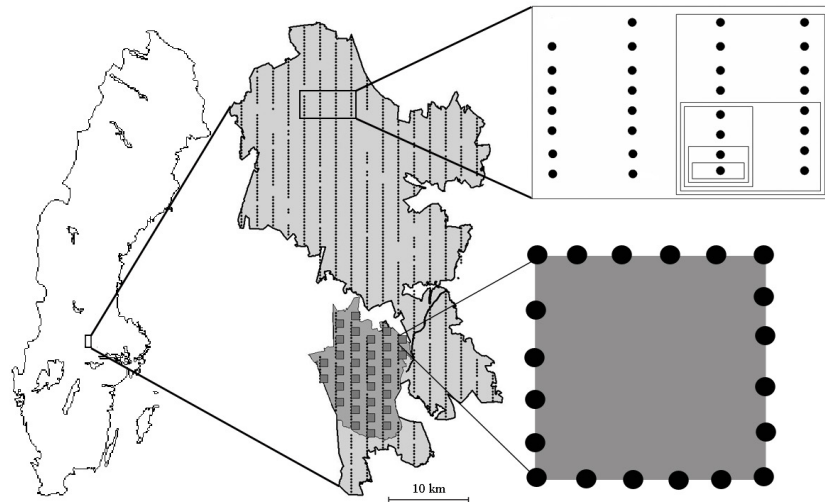


Figure 4. Location of the study area in south-central Sweden (left). Grimsö Wildlife Research Area (darker grey) and distribution of sites (1x1 km squares) with study plots along the perimeter (bottom right). The distribution of sampling plots, linear transects, within the enlarged study area (middle) and also an example of how the 6 different spatial scales were obtained (top right).

The area is dominated by forest (75%) mixed with mires (12%), lakes and rivers (7%) and other land-cover types (6%). Sveaskog, a state-owned forest company, is the dominating land owner within the study area. The forest is intensively managed for timber and pulp. The forest consists of a mosaic of fairly even-aged stands of various ages. The stands are regenerated through clear-cutting followed by planting or natural regeneration, and the rotation period is about 70-100 years. Stand size ranges from 0.5 to 64 ha, with a mean size of about 6 ha. The dominant tree species are Norway spruce and Scots pine, which are mixed with deciduous tree species, such as birch (*Betula pubescens*, *Betula pendula*), aspen, rowan and goat willow (*Salix caprea*). The field layer is dominated by bilberry, lingonberry, heather and common hair grass (*Deschampsia flexuosa*).

The moose density in Grimsö Wildlife Research Area has been estimated by pellet group counts and aerial surveys during the study period and has varied between 0.7-1.4 moose / km² from 1997 to 2006. The roe deer (*Capreolus capreolus*) density has varied between 1.9-3.0 roe deer / km² and has been decreasing since the start of the study period (Pehrson & Månsson unpubl.). The mean moose density in the enlarged area was estimated by a pellet group count (2004) to 1.7 moose / km² and the roe deer density was < 2.0 roe deer / km² (Pehrson and Månsson unpubl.). Mountain hare (*Lepus timidus*) and brown hare (*Lepus europaeus*) are two other herbivores also present in the area.

Hunting was the most important mortality factor in the moose population. In 2003, a wolf territory was established that partly overlapped with the study area. The wolf territory was located in the south-eastern part of the area, and covers approximately 20 percent of the larger area and 35 percent of Grimsö Wildlife Research Area.

Methods

Sampling plots

Grimsö Wildlife Research Area – Papers I, III and IV

In 1996, a total of 32 sites (1x1 km) were systematically distributed within the Grimsö Wildlife Research Area. The ambition was to have 20 circular sampling plots evenly dispersed along the perimeter of each 1x1 km site (Figure 4). Each year between 1996 and 2006, a total of 600 (556 in 1996) sampling plots were surveyed at the end of the winter period. In Paper III, only plots located in productive forest stands (annual tree growth $> 1 \text{ m}^3 \text{ year}^{-1} \text{ ha}^{-1}$) and mire were included and therefore the sample size was somewhat reduced. In Paper I, one of the 32 sites was excluded because of the sample size was too small (8 plots).

The enlarged study area – Papers II and IV

The 1162 sampling plots were systematically distributed along transects using a hand-held GPS compass. The distance was 2 km between transects and 400 m between the centres of the plots within transects (Figure 4). The plots were monitored between 15 April and 18 May 2004, just after snowmelt and before the start of the plant growth period.

Forage availability – Papers I, II, III

Forage availability was estimated in 20-m² plots as cover of living parts of tree species projected onto the horizontal plane within the height range 0.3 to 3 m (Hörnberg, 2001b). Forage availability was estimated in 1996, 2001 and 2006 in Grimsö Wildlife Research Area, and in 2004 in the enlarged area. The species recorded were rowan, willows, aspen, Scots pine, silver birch, downy birch and juniper. To create an index of total forage availability, the percentage cover of all species was summarised for each plot (i.e. forage availability can total $> 100\%$ within a plot).

Browsing pressure (Papers I, II, III) and Consumption index (Papers I, II)

An index of browsing pressure was estimated as the proportion of the total amount of previous year's shoots consumed within the 20-m² plot. Bites, only those recognised as being from the immediate-past dormant season, were recorded. The

bark tissue beneath “fresh” bites was conserved during winter (by low temperature and dormancy) and could therefore be easily distinguished from old bites from previous years.

An index of absolute consumption of browsed biomass was estimated as:

$$C = \sum_{i=1}^I (B_i F_i) \quad (1)$$

Where C is absolute consumption, B is browsing intensity (proportion of browsed twigs) and F is forage availability (percentage cover) for species *i*, and I is the total number of species considered.

The method used to estimate forage availability and browsing followed the methodology of Bergström et al. (1995). These estimates were strongly related to more precise, but considerably more time-consuming, techniques ($r = 0.7-0.9$ across common tree species and areas).

Selectivity index and preference rank (Paper I)

A general model for selectivity among food items is (e.g. Chesson, 1978; Greenwood and Elton, 1979) usually described as:

$$u_i = \frac{v_i \alpha_i}{\sum_{i=1}^I v_i \alpha_i} \quad (2)$$

where u_i is the utilised proportion of food item *i* (here based on consumption index), v is the selectivity parameter, α is the available proportion of food item *i* (based on forage availability index), and *I* is the total number of species considered (rowan, willows, aspen, Scots pine, downy birch, juniper, and silver birch). The key tasks when studying selectivity are to acquire an estimate of v for each food item (tree species) and to test for differences between them.

By rearranging expression 2, and following Aitchison’s (1986) method to solve constraints in normal distributions of unit totals, an expression to test difference in selectivity between two food items can be achieved:

$$x_i = \ln \left(\frac{v_i}{v_d} \right) \quad (3)$$

Preference ranks were obtained by two resource selection analyses – Johnson (1980) and Aebischer, Robertson & Kenward (1993). Results from Johnson’s rank test and Aebischer’s compositional analysis was obtained by using PREFER (Pankratz, 1994) and RSW (Leban, 1999) software, respectively. The two analyses were complemented by a randomisation test since the data set includes several

missing values for both the use and availability. Missing values in the log ratios were here replaced with the mean values of the non-missing log ratios. The differences in selectivity between specific food items were tested by randomisation, using 999 permutations, so the smallest obtainable level of probability was $p=0.001$.

Pellet group counts (Papers II, III, IV)

A moose density index was estimated by counting the number of pellet groups within a 100-m² plot (5.64 m radius). The size of the plot was chosen in order to avoid problems with sparse frequency of pellet groups and to avoid overlooking pellet groups (Neff, 1968; Lavsund, 1975). Pellet groups from the preceding winter, including 10 or more single pellets and with the centre of the pellet group within the plot, were counted. The first year (1996) of survey did not include pellet group counts. The plots were cleaned in the preceding autumn, except in Paper II, where pellet groups were aged by colour and position in relation to the litter and old vegetation (Neff, 1968).

Site productivity and forage diversity (Paper II)

For each plot, a site productivity index (the annual tree growth in m³ year⁻¹ ha⁻¹) was obtained from the landowner's digitalised database of stand characteristics (stand level).

A forage diversity index, Shannon-Wiener (Krebs, 1999), was calculated for the tree species (rowan, aspen, birch, juniper, pine and willow) at each spatial scale. Norway spruce was not included in the diversity index.

Hierarchical spatial scales (Paper II)

In Paper II, the study area was systematically divided into 30 grid cells, with each grid cell containing at least 32 sampling plots. The grid cells were then divided into smaller spatial scales aiming to have 32, 16, 8, 4, 2 and 1 plot included at the different scales (Figure 4). The sample size (n) for each spatial scale was 30, 60, 113, 233, 399 and 627. The different scales covered an area from the plot level (20 m²) to the size of annual home ranges of moose in the area (mean yearly home range size 25.9 km² for males and 13.7 km² for females; Cederlund & Sand 1994). An average value was calculated for each of the measured parameters (consumption, forage availability, forage diversity, site productivity and moose index) at the different scales.

Snow condition and stand age estimation (Paper III)

In Paper III, I used an index of number of days with a snow layer > 0.1 m to test if snow condition affected moose habitat preference. Snow data was obtained from the Swedish Meteorological and Hydrological Institute (SMHI).

Three different habitat types were used in the analysis (young forest < 30 years, older forest > 30 years and mire). The productive forest stands were categorised by age. The forest stand age was obtained from the dominating landowner's forest data base (GIS-based), and the age for 33 stands was complemented by field estimation 2006.

Population model (Paper IV)

In Paper IV a primary management goal was set to maintain the moose population at a density of 1.0 moose/km² after harvest. Given that managers cannot maintain the population at precisely this level, we consider the population size to be acceptable if it was between 800 and 1200 individuals in a management area of about 1000 km². A stochastic population model was used to describe changes in the actual population size from year to year, with a growth rate that varies annually:

$$N_{t+1} = \max\{0, N_t \times \lambda_t - H_t\}, \quad (4)$$

where N_t is the population size in year t , λ_t is the stochastic growth rate in year t , and H_t is the number of moose harvested in year t . The annual growth rate (mean and year-to-year variation) for a moose population was taken from two long-term studies (Grimsö Wildlife Research Area in Sweden, 33 years (Rönnegård et al., submitted manuscript) and Nordland in Norway, 27 years (Solberg & Sæther, 1999)). In the population model, growth rates were assumed to be independent and identically distributed normal random variables with mean $\mu_\lambda = 1.4$ and standard deviation $\sigma_\lambda = 0.1$.

The harvest strategy (Paper IV)

A harvest strategy was designed that aimed to drive the population to the acceptable range of population sizes (between 800 and 1200). When the population is estimated to be unacceptably high, the harvest rate is increased, and the harvest rate is decreased when the population is estimated to be unacceptably low. Four different harvest rates were used, depending on the estimated population size - 0%, 28%, 40% and 52%.

Census methods (Paper IV)

Different combinations of aerial survey, pellet group count, direct observations and population model prediction were used to evaluate the costs of management tools in relation to the ability to reach a management goal (Table 1). Aerial

surveys have probably been the most accepted and one of the most frequently used method for monitoring moose population densities and trends in Sweden (Haagenrud et al., 1987; Wennberg DiGasper, 2006). However, the method is costly and demands trained personnel, and good snow and weather conditions (Timmerman, 1974; Mayle, Peace & Gill, 1999; Barnes, 2001). Two other methods used to estimate the Swedish moose population are pellet group counts (Lavsund, 1975; Persson, 2003; Wennberg DiGasper, 2006) and direct observations (hunters' observations), (Haagenrud et al., 1987; Wennberg DiGasper, 2006). These two methods differ from aerial surveys in that they result in an indirect measure, i.e. an index of the number of animals. The transformation from this index to absolute numbers and densities is often considered to be an additional step that introduces further uncertainty to the estimates (Neff, 1968; Andersen, Hjeljord & Sæther, 1992; Ericsson & Wallin, 1999; Solberg & Sæther, 1999). The accuracy in the method has been discussed (Fuller, 1991; White, 1992; Fuller, 1992) but several studies have also shown realistic estimates and consistency in trends and densities between different independent methods (Neff, 1968; Mandujano & Gallina, 1995; McIntosh, Burlton & McReddie, 1995; Barnes, 2001). Hunters' observations have been used within moose management for more than 20 years in Fennoscandia (Finland, Sweden and Norway), (Timmerman, 1974; Haagenrud et al., 1987; Jaren, 1992; Ericsson & Wallin, 1999; Solberg & Sæther, 1999). Hunters are asked to report their moose observations, the number of active moose hunters, and the time spent on hunting moose during the first week of the hunting season. This method has shown significant correlation with deer densities estimated using other census techniques (McIntosh, Burlton & McReddie, 1995; Solberg & Sæther, 1999; Ericsson & Wallin, 1999). Furthermore, the census method is very cheap as moose hunters contribute voluntarily. In addition to the three census methods (aerial survey, pellet group counts and hunters' observations), the population model offers extra information on likely population size. For example, imagine that you observe an increase in population size from last year to this year that cannot reasonably be explained by reproduction alone. You might conclude that last year population size was under-estimated, or that it was over-estimated this year. You might weigh your conclusion against the knowledge that one survey method was less accurate than the other.

Results and discussion

I. Browsing risk

Tree species were not used proportionally to their availability and, based on the Johnson (1980) ranking, the following relative preference rank order was established rowan > willows > aspen > juniper > silver birch > downy birch > Scots pine. The preference rankings were similar for the two resource selection analyses, Johnson (1980) and Aebischer, Robertson & Kenward (1993), except that rowan and aspen switched places. The randomisation test gave somewhat different rankings compared to the Johnson (1980) rankings. Rowan switched

place with willows, and juniper switched place with silver birch. The rankings produced in the randomisation test need careful interpretation, since differences in log ratios between some species could not be tested, due to missing values (e.g. rowan and juniper never occurred in the same site, so the difference in preference for them could not be established when either of them was used as the denominator). A selectivity index was established, but only three species groups could be significantly separated (1) downy birch and Scots pine, (2) juniper and silver birch, (3), willows, rowan and aspen. The final values of selectivity, using group 1 as an index group, showed that rowan, willows, and aspen were 14 times more likely to get browsed compared to a group consisting of Scots pine and downy birch, while juniper and silver birch were 3.5 times more likely to be browsed than Scots pine and downy birch. Since the most preferred species were the least abundant, the general application of the index between specific areas should be treated with caution, as it may indicate that herbivore preference depends on plant species composition, as also indicated in Broman (2003). However, the large difference in the browsing risk shows that the forage species differs in value to the moose. This highlights the importance of including a forage value (preference) to models aiming to predict browsing pressure, i.e. the availability of certain forage species should be weighed against the species forage “value”. I argue that the predictability will improve compared to models that only include herbivore density and forage availability. Even though the pine attained a “low-rank” preference index among species, 3.6 % of previous year’s shoots were browsed and, from a forest owner’s point of view, there is still an annual risk of damage. The Swedish Forest Agency has proposed a reduction in the moose population in order to reduce damage to young trees of Scots pine (Ingemarson, Claesson & Thuresson, 2007). However, an alternative measure would be to create and provide moose with alternative forage in areas not used for forest production (e.g. along small roads in forests and areas beneath power lines). This study points out that the least abundant tree species are the most preferred and, from that perspective, management should therefore concentrate on increasing the abundance of these preferred forage species.

II. Scale-dependent browsing pattern

This study provided an insight into scale-dependence in factors affecting large herbivore browsing patterns. Scale-dependence is a fundamentally important topic in ecology since it determines whether results can be generalised over different spatial scales. Three lines of evidence were found that supported scale-dependence in the browsing patterns of a large herbivore (the moose):

1) The partial contribution of four independent variables (forage availability, moose index, site productivity and forage diversity) included in a multiple regression model explaining food consumption by moose, changed at the different spatial scales (Figure 5). Consumption of forage was positively related to forage availability at all spatial scales. However, the proportion of total variation explained by forage availability was largest at intermediate scales (Figure 5). The variation explained by moose index decreased with increasing scale and, in

contrast, the relative importance of site productivity increased with spatial scale (Figure 5). Relative importance of forage diversity in the model showed no consistent pattern, but reached its highest value on the second-largest scale tested.

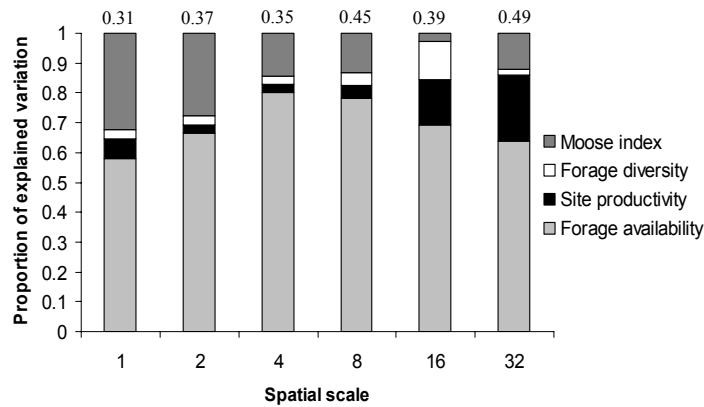


Figure 5. Multiple regression explaining forage consumption by moose at 6 different spatial scales in south-central Sweden. Proportion of the total variance explained by the four explanatory variables. The total variance explained (R^2) is given above the bars.

2) The explanatory variables in the selected models (Akaike’s Information Criterion) changed at larger spatial scales. According to the model selection, model ID 1 (using the same variables as in the multiple regression) was ranked highest for the four smallest spatial scales, whereas the top-ranked models at the two largest spatial scales differed (Table 2). The importance of forage availability in the model was further highlighted, as it was included in all AIC-selected models (ID 1-5) irrespective of scale (Table 2). Two models (ID 4, 5) without moose index were selected, but only at the two largest spatial scales (Table 2). However, the top-ranked model (ID 2) at the largest scale included moose index.

3) The relationship between browsing and forage availability changed at the different spatial scales. The absolute consumption was not significantly different from proportional use (matching) of forage availability at the three largest spatial scales. At the three smallest spatial scales, the increase in consumption was significantly lower than expected from a proportional use of forage, as the slope in the log-log relationship was significantly < 1 ($p < 0.001$). Thus, plots with high forage availability were under-used (undermatching) as compared to plots with low forage availability. Differences in the relationships at different scales indicate that different factors affect decisions of herbivores at different scales. This study therefore supports the hypothesis that different factors contribute to foraging decisions at different scales (cf. Senft et al., 1987). This study focused on variables that have been shown to affect the foraging patterns of a large herbivore, either directly (forage availability) or indirectly (site productivity and forage species diversity). As predicted, forage diversity (Westoby, 1974; Pulliam, 1975) and site productivity (Danell et al., 1991b) were two important factors, in addition to forage availability and herbivore density, in explaining foraging pattern of moose. However, the best models in the study explained approximately 50% of the

variation and apparently other factors also affect foraging patterns. In addition to the variables included here, several other factors have been proposed to affect the foraging pattern by large herbivores, e.g. cover, predators, hunters and snow conditions (Peterson & Allen 1974; White, Felle & Bayley, 2003; Edwards 1983; Whittaker & Lindzey, 2004).

To sum up, forage availability seems to be an important factor affecting foraging decisions of moose, irrespective of scale. Therefore, land-use practices that affect forage distribution may have an effect on spatial distribution of moose and subsequently on their impact (e.g. forest damage and biodiversity). According to model selection procedures, the AIC and the proportion of total variation explained by different independent variables affect foraging decisions differently at different spatial scales. Furthermore, the relationship between consumption and forage availability changed from under-utilisation at small scales to proportional use at the home range level. Thus, for a comprehensive understanding of moose browsing in relation to food resources, a multi-spatial scale approach is necessary.

Table 2. Models explaining moose browsing at different spatial scales in south-central Sweden, ranked according to $\Delta AICc$ values (shown in parentheses after rank)

Model ID	Model				Spatial scale					
	F	M	S	D	1 Plot	2 Plots	4 Plots	8 Plots	16 Plots	32 Plots
1	X	X	X	X	1 (0)	1 (0)	1 (0)	1 (0)	2 (2.21)	4 (2.82)
2	X	X	X		2 (0.81)	2 (0.96)	2 (0.19)	3 (2.08)		1 (0)
3	X	X		X			3 (1.40)	2 (0.98)		
4	X	X		X					1 (0)	3 (1.50)
5	X	X	X						3 (2.57)	2 (0.18)

Note: Variables are forage availability (F), moose density (M), site productivity (S), and forage diversity (D). The table includes models with $\Delta AICc < 2$ at any scale. If a model had a $\Delta AICc < 2$ at any scale, then the $\Delta AICc$ and rank are also given at the other scales up to $\Delta AICc < 4$.

III. Temporal variation in browsing

Understanding temporal variation in habitat selection and browsing intensity by large herbivore is fundamental because of their large impact on the ecosystem. The impact to the ecosystem by deer has been discussed previously (Decalesta, 1997; Danell et al., 2006). My study supported the importance of a joint function of forage and herbivore density in predicting impact (Decalesta, 1997). In my study, the browsing pressure on a forage species that dominated the diet of a herbivore was predicted by forage availability and moose density. Thus, the overall browsing pressure on Scots pine increased with increasing density of moose and decreased with forage availability of Scots pine over the study period (Figure 6). Hörnberg (2001a) also showed the importance of not only focusing on the herbivore density but rather the combination of density and the current forage

situation. However, variation in environmental conditions will complicate predictions and interpretation of browsing pressure on young trees, as this pressure is dependent on available alternative forage (Moser, Schütz & Hindenlang, 2006). The availability of alternative forage (field layer species) in my study was dependent of an environmental factor (snow) that varies annually and therefore creates uncertainty in predictions of impact of moose on young trees. The browsing pressure on downy birch and silver birch (the most important forage species for moose after Scots pine) were not significantly related to either moose density or forage availability. The difference in ability to predict browsing pressure among the species might be explained by the importance of Scots pine in moose winter feed, making up more than 55% of the total diet compared to the two birch species, which comprise 6-17% of the winter diet (Cederlund et al., 1980).

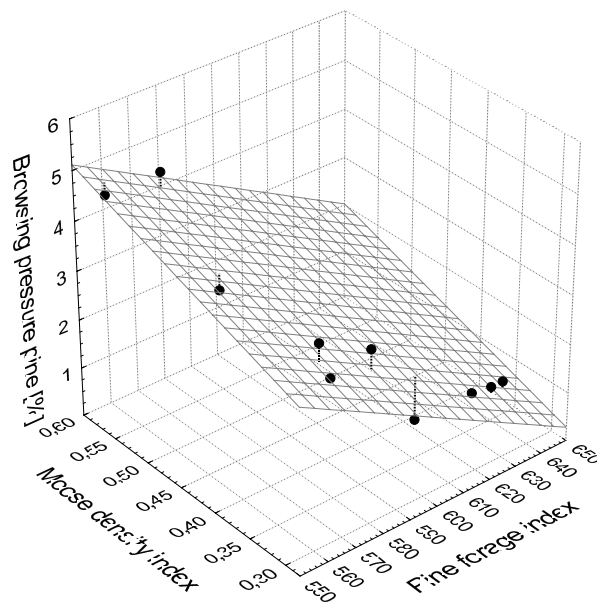


Figure 6. The relationship between annual moose browsing pressure on Scots pine (proportion of shoots being browsed), moose density index (mean moose pellet groups per plot) and Scots pine forage index (Σ [mean forage cover in habitat*area of habitat, km²]). $Browsing\ pressure\ (pine) = 18.9 - 0.0309 * \{pine\ forage\ index\} + 5.44 * \{moose\ density\}$.

Habitat-specific browsing pressure on Scots pine was also positively related to habitat-specific herbivore density (Figure 7). Moose density was always higher in young forest plantations compared to mire and old forest (Figure 7), but the rate of increase between browsing pressure and moose density was similar in all three habitats (Figure 7). There was also a significant difference in forage availability in the shrub layer species between the different habitat types. Most forage (Scots pine, downy birch, silver birch and total forage) was found in young forest plantations < 30 years (Figure 8). Consequently, this study also showed that large herbivores prefer patches with high forage availability, which corresponds with

earlier studies in boreal, nemoral and grassland systems (Senft et al., 1987; Bergström & Hjeljord, 1987; Morellet & Guibert, 1999; Frank, 2006; Moser, Schütz & Hindenlang, 2006).

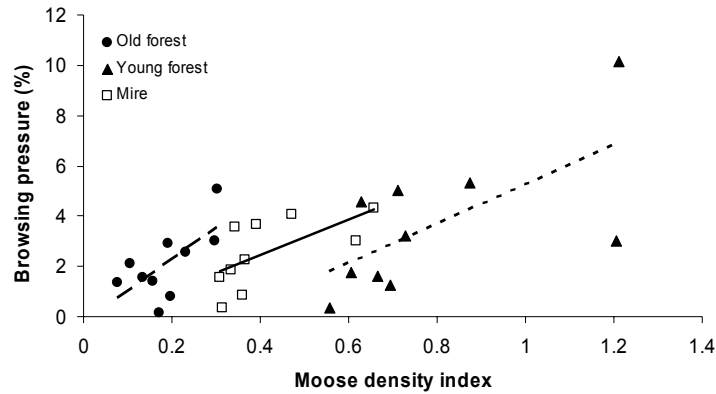


Figure 7. The relationships between annual habitat-specific moose browsing pressure on Scots pine and habitat specific moose density index. The forest habitat was classified into young forest < 30 years and older forest > 30 years.

Predictions and interpretations of studies concerning deer damage towards both commercial tree nurseries and forests are complicated, as browsing pressure varies between years even though the herbivore population has been fairly stable (Conover & Kania, 1995; Bergström & Edenius, unpubl. in Kjellander, 2007). This was clearly illustrated in a large scale and long-term study (1992-2001) in northeastern Sweden (Bergström & Edenius, unpubl. in Kjellander, 2007). In that study, annual variation in snow condition, forage quality and length of plant growth period were discussed as potential explanatory factors to the annual variation in browsing damage to young pine forest stands. In my study the browsing pressure on Scots pine increased with moose density and the number of days with a snow layer deeper than 0.1m. Furthermore, the preference for certain habitat types varied between years and this variation was also explained by the snow variable (significant for old forest and young forest but weaker for mire ($p=0.06$; Figure 9). Availability of field layer species varies in relation to the snow layer (about 3/5 of the available bilberry forage is covered by a 0.1 m snow layer, as the mean height of bilberry plant was 16.9 ± 0.37 S.E. (own data from 1996-2003). Environmental conditions (e.g. snow, droughts) have been pointed out as factors affecting spatial heterogeneity in distribution, habitat preference and diet of large herbivores (LeResche & Davis, 1973; Cederlund et al., 1980; Cederlund, 1982; Morellet & Guibert 1999; Morrison et al., 2003; de Garine-Wichatitsky et al., 2004). Field layer species like bilberry and heather were more common in moose rumens during winter periods of scarce snow, and constituted up to 40 % of the moose diet during these periods (Cederlund et al., 1980). Thus, it is most likely that the ultimate cause of variation in habitat preference and browsing pressure is the differences in forage availability between habitats and diet shifts (Tremblay et al., 2005; Moser, Schütz & Hindenlang, 2006).

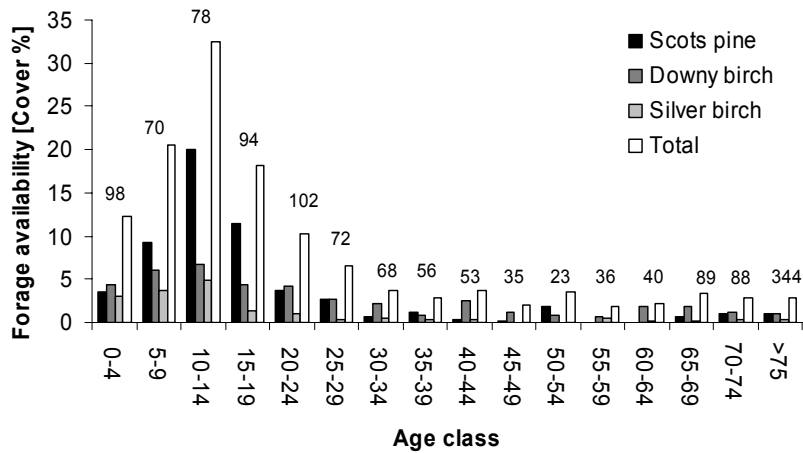


Figure 8. Forage availability for 16 different age classes of productive forestland. Forage availability and stand age was estimated in the same plots 1996, 2001, and 2006. Sample size for each age class is given above the bars ($n_{\text{total}}=1446$).

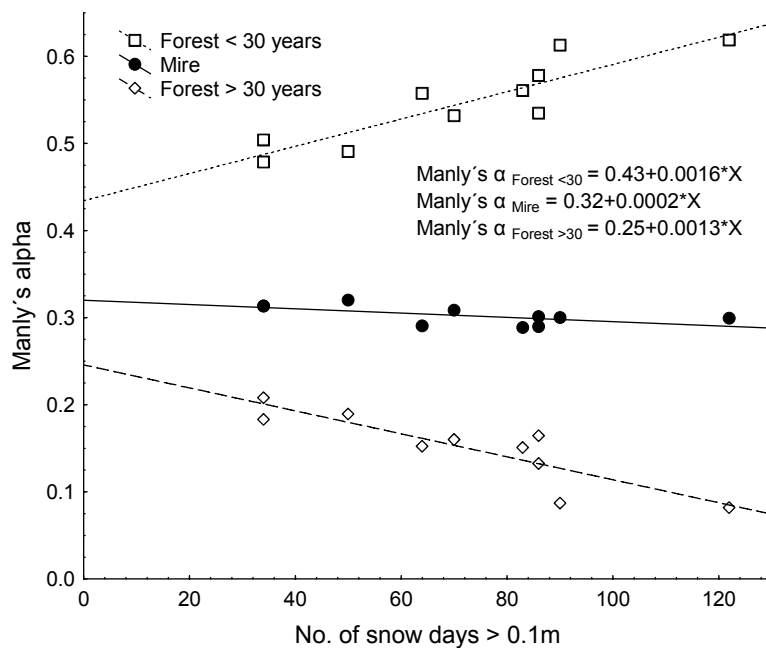


Figure 9. The relationships between moose habitat preference (Manly's alpha) and snow condition (number of days with a snow layer > 0.1 m). The forest habitat was classified into young forest < 30 years and older forest > 30 years. Note that the preference indices for the three different habitats are not independent of each other, because the proportions total one.

There were no significant relationships between moose habitat preference (Manly's alpha) and overall moose density index for any of the three habitat types ($p > 0.54$ in all three cases). Furthermore, the relationship between habitat-specific

density and overall moose density was not significantly different from a proportional relationship for any of the three habitats. The proportional relationship also indicates density independence in habitat selection. This result contradicted that of Kie & Bowyer (1999), who showed a density-dependent habitat preference for white-tailed deer. A proportional pattern between overall density and habitat specific density is also easier to handle within wildlife management because an effort to halve the animal density, as for example in young forest stands (where the most serious economic damage occurs), means that management has to halve the overall herbivore density.

IV. The cost of management success

Three measures of moose management performance were used in this study – how often the population was of desirable size, annual variation in harvest, and time before the population was of undesirable size for the first time. The general pattern was that better management performances were achieved with increasing monitoring costs (independent of used evaluation criteria). The number of years the moose population was within the management goal ($800 < N < 1200$) varied between 7.4 and 14.6 years, and was positively related to the cost of the monitoring strategy used (Table 3 and Figure 10). Annual aerial survey (strategy 3) was one of the best methods with regard to proportion of time within the management goal. However, the simulations indicated that a combination of two relatively cheap monitoring methods could significantly improve management performance at a relatively low cost. A combination of two methods is rare within the Swedish moose management; 23% of the Swedish moose management units (MMU) had utilised two different monitoring methods within management, but they are probably seldom combined (Wennberg DiGasper, 2006). Hunters' observation is the most common monitoring method, and was used in 54% of the Swedish MMU (Wennberg DiGasper, 2006). However, by combining hunters' observations with pellet group counts (strategy 9) the proportion of years within the management interval increased from 0.60 to 0.73. Thus, a combination of pellet group counts and hunters' observations every year performed equally to the annual aerial survey with regard to proportion of time within the management goal (Table 3).

Perfect knowledge

Given perfect knowledge of the moose population size in February and the given harvest strategy, the moose population was, on average, within the management goal for 16.2 years (± 2.6 years) out of 20. This uncertainty is due to the fact that the census is conducted post-harvest and pre-reproduction. The mean yearly growth rate was $\lambda = 1.40$ (± 0.10 st. dev.), which was based on two long-term moose studies from Scandinavia (27 years, Norway, Solberg & Sæther, 1999; 33 years, Sweden, Rönnegård et al., submitted manuscript). Obviously reproduction varies considerably between years and the performance in management actions will depend on this variation. Thus, monitoring strategies conducted after the reproduction and before hunting season, e.g. distance sampling that achieves both density, reproduction (e.g. juveniles/female) and sex structure (Buckland et al.,

2001), is to be preferred for improving management performance. However, the monitoring methods currently used are not applicable during the summer period.

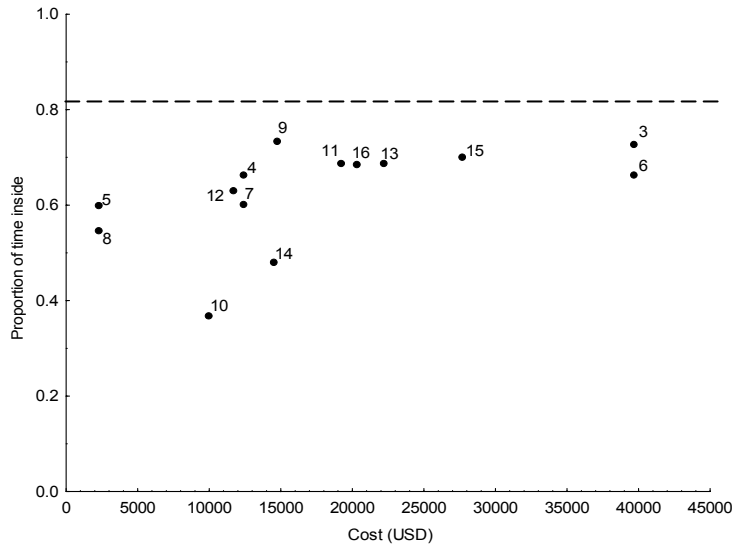


Figure 10. The relationship between proportion of time within the moose management goal and annual cost for the survey. Included monitoring strategies: 3-16 (Table 1). The dashed line indicates performance with perfect knowledge of moose population in February (i.e. Strategy 2).

Time to first occasion outside management goal

By managing the moose population with a constant harvest of 400 moose (assuming a constant deterministic population growth for the starting population of 1,000) it took an average of 4.5 years before the moose number was unacceptably low ($N < 800$) or large ($N > 1200$) for the first time (Table 3). On the other hand, it took on average 6.3 years before the population was of undesirable size for the first time when there was perfect knowledge of the moose population in February (Table 3). The best monitoring strategy, in terms of the first occasion when the population size was outside the management goal, was the combination of pellet group count and hunters' observations each year (strategy 9). By using that approach, it took on average 5.7 years before the population was either too large or too small for the first time (Table 3).

Harvest

The sustainable deterministic harvest was 400 (1000 pre-reproduction population size and mean $\lambda = 1.40$). The mean yearly harvest, calculated using different monitoring methods, varied between 376 and 394 and was negatively related to monitoring cost. Annual aerial surveys (strategy 3) followed by annual pellet counts and annual hunters' observations (strategy 9; Table 3) had the lowest inter-year variation in harvest. The variation in harvest decreased when model prediction was included in the monitoring strategy (Table 3).

State dependency

The state-dependent monitoring strategies (strategies 13-16; Table 1) did not differ significantly from other strategies in any of the performance measures used (Table 3). Restricting the states that triggered expensive monitoring decreased the cost significantly while maintaining almost equal performance (compare strategies 15 and 16). Strategy 16 (aerial surveys and pellet counts) had the best performance of the state-dependent monitoring strategies for all three performance measurements (time within the management goal, inter-year variation in harvest and time to the first year outside the management goal; Table 3). Aerial surveys were on average used 56% of the time in strategy 16, and so this strategy was the most expensive state-dependent monitoring strategy (compare strategies 13-16 in Table 3).

With the exception of variation in harvest, the use of model prediction in combination with other monitoring methods, surprisingly, did not improve management performance. A survey will tell us something about the population recruitment for that year, but the survey also incorporates a measurement error. By including a model prediction, extra information about the credibility of the observed growth rate (λ) and reduced effect of the measurement error would be obtained. However, the model predictions sometimes make the opposite mistake, i.e. surveys suggesting an extreme growth rate (high or low) occur less frequently because model predictions assume that extreme changes are due to measurement errors. This results in an inappropriate harvest rate, and the continual use of model prediction means that year after year, true population size was repeatedly underestimated (or repeatedly overestimated). On the other hand, without modelling we do not rely on the previous year's population estimate, and so there is equally likely to be an overestimate or underestimate of the population each year, and the harvest 'mistakes' will even out over the years.

The lack of age and sex structure in the simulation of the moose population and the transformation of indices (hunters' observations and pellet group counts) to population size are probably the most significant limitations in the simulation process. These two factors may affect the relative differences between the monitoring strategies. Including age and sex structures in the moose population might increase the probability of predicting the annual variation in reproduction and therefore reduce the risk of undesirable population size. Thus, monitoring methods that provide information about sex ratios in the population, like aerial surveys and hunters' observations, should perform relatively better than pellet group counts if age and sex structure were included.

Table 3. Management performance and cost for the sixteen monitoring strategies. Mean and standard deviation (within brackets).

Monitoring strategy	Proportion of time inside interval	Proportion of time N<800	Proportion of time N>1200	Annual harvest	Within-run S.D. (Harvest)	Cost (USD)	First year outside (800, 1200)
1	-	-	-	-	-	-	4.5 (±2.6)
2	0.81 (±0.11)	0.11 (±0.10)	0.08 (±0.08)	394	89	-	6.3 (±4.1)
3	0.73 (±0.17)	0.18 (±0.15)	0.09 (±0.10)	390	133	39700	5.7 (±3.8)
4	0.66 (±0.17)	0.22 (±0.17)	0.12 (±0.11)	388	159	12400	4.6 (±3.3)
5	0.60 (±0.17)	0.28 (±0.18)	0.12 (±0.11)	379	182	2300	3.8 (±2.8)
6	0.66 (±0.17)	0.21 (±0.17)	0.13 (±0.13)	389	113	39700	5.5 (±3.8)
7	0.60 (±0.18)	0.24 (±0.19)	0.16 (±0.14)	390	130	12400	4.5 (±3.3)
8	0.55 (±0.19)	0.28 (±0.22)	0.17 (±0.17)	389	143	2300	4.4 (±3.3)
9	0.73 (±0.14)	0.17 (±0.14)	0.10 (±0.10)	392	136	14700	5.7 (±4.1)
10	0.37 (±0.20)	0.40 (±0.24)	0.23 (±0.19)	376	194	9900	4.0 (±2.8)
11	0.69 (±0.15)	0.21 (±0.17)	0.10 (±0.10)	386	152	19200	5.2 (±3.6)
12	0.63 (±0.18)	0.26 (±0.18)	0.11 (±0.10)	380	170	11700	4.4 (±3.3)
13	0.69 (±0.15)	0.21 (±0.15)	0.10 (±0.10)	384	152	22200 (±3400)	5.1 (±3.3)
14	0.48 (±0.19)	0.32 (±0.23)	0.20 (±0.18)	383	164	14500 (±500)	4.3 (±2.8)
15	0.70 (±0.15)	0.19 (±0.15)	0.11 (±0.10)	390	145	27700 (±2800)	5.4 (±3.8)
16	0.69 (±0.15)	0.21 (±0.15)	0.10 (±0.10)	385	150	20300 (±2800)	5.0 (±3.6)

Note: The following measures of management performance were used:

* Proportion of time that true population size is unacceptably low (N < 800) or high (> 1200)

* Standard deviation in harvest within a run

* Mean annual cost of monitoring

* Proportion of years in which each monitoring method is used

* The first year in which true population size is unacceptable (N < 800 or N > 1200)

Conclusions and management implications

This thesis shed light on the importance of including forage availability, preference of forage species and the distribution of forage in the landscape in addition to herbivore density when predicting herbivores' foraging patterns and impact on the ecosystem (Figure 11). Forage availability and composition is dependent on forestry actions, natural disturbances and environmental factors and varies over time and space. Furthermore, environmental conditions can affect the forage availability, for instance snow can affect availability of alternative forage in the field layer. The density of moose in Sweden is mainly dependent on harvest but in some areas also affected by predation from bear and wolf. The harvest quota relies on more or less imprecise management tools such as monitoring damage or population size. Thus, moose management can change the animal density, both due to implemented socio-political policies but also due to imprecise tools. Obviously, the factors that affect herbivore density and forage availability vary at both the temporal and spatial scale and are integrated to the foraging patterns and also affect the impact on the ecosystem. Managing for deer impact on the ecosystem requires knowledge about all these components at different temporal and spatial levels.

At the plant level, there was a large variation in moose preference for certain tree species. Since the most preferred species were the least abundant, one should be cautious about the general applicability of the index between areas, as it may indicate that preference depends on plant species composition. However, in this study, simple field measures were used that can easily be applied within management to quickly get an overview of the herbivore-forage situation in certain areas. Apparently, a pine and a rowan differ a lot in value to the moose and such information should be used in models predicting spatial distribution and availability of forage. Preference indices for certain tree species might also be valuable knowledge when creating supplemental forage by habitat management aimed at improving the conditions for such preferred species. Habitat management has been discussed as an alternative strategy to decreasing the number of moose in Sweden. The availability of forage affects the distribution of large herbivores and consumption of forage over several spatial scales, ranging from single feeding patches to the home range level. Therefore, all kinds of land-use practices that affect forage distribution will also affect herbivore distribution and browsing pattern. However, the relationship between forage and consumption is somewhat different at different spatial scales. Scale-dependence highlights the importance of careful comparison between studies but also problems with general application of models predicting herbivore browsing impact on forests over different spatial scales. In this study, browsing pressure on trees was predicted by knowledge about forage availability and moose density. However, annual variation in snow depth will complicate predictions and interpretation of browsing pressure on the shrub layer. This is because browsing pressure in young pine stands is dependent also on available forage in the field layer (e.g. bilberry and heather). The field layer varied in availability and might become unavailable during winters with deep snow.

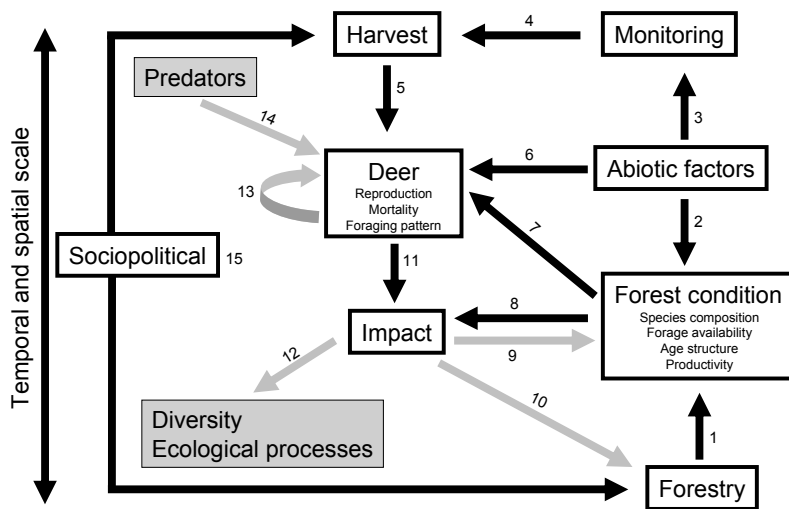


Figure 11. In this thesis I have dealt with interactions and components affecting deer impact on the ecosystem and deer management. Naturally, only a sample of interactions and components affecting the system was included. In this flow chart, modified from Decalesta (1997), illustrating ecosystem management, I illustrate the interactions included in this thesis in a general approach. Black arrows indicate the interactions included in the study; indirectly (literature) or directly (my results) while grey arrows indicate interactions not studied here. Unfilled boxes are components that were included in the thesis, while grey boxes were components not included.

1. Forestry affects the forest composition, e.g. tree and age composition. *Papers I, II and III (Lautenschlager et al., 1997).*
2. Weather conditions affect the forest, e.g. storms, droughts generating fires. *Paper III (Lautenschlager et al., 1997).*
3. Weather conditions steer the choice of monitoring methods, e.g. snow. *Paper IV (Timmerman, 1974).*
4. Harvest quota is determined from more or less precise monitoring estimates. *Paper IV (Ericsson & Wallin, 1999).*
5. Deer harvest will affect the population density. *Paper IV (Lavsund, Nygren & Solberg, 2003).*
6. Abiotic factors affect reproduction and mortality of deer. *Paper IV (Solberg & Sæther, 1999; Rönnegård et al., submitted manus).*
7. Forest condition, e.g. distribution of forage, will affect deer foraging pattern *Papers II and III (Bergström & Hjeljord, 1987).*
8. The forest condition will affect the impact from deer (e.g. browsing pressure is dependent of species composition and forage availability). *Papers I, II and III (Hörnberg, 2001a).*
9. The impact from deer can affect species composition and forage availability (*Gill, 2006*).
10. The impact will affect forestry, e.g. economic losses. *Paper IV (Ingemarsson, Claesson & Thuresson, 2005).*
11. Deer density affects the impact on the ecosystem. *Paper III (Hörnberg, 2001a).*
12. Deer impact can change ecological processes and diversity (*Berger et al., 2001*).
13. Density dependence in deer population, e.g. effects on reproduction (*Kjellander, 2000*).
14. Predators will affect deer mortality and foraging pattern. (*Edwards, 1983*).
15. Sociopolitical policies can change forestry actions and deer management. *Paper III (Lavsund, Nygren & Solberg, 2003; Kalén, 2005).*

Management actions based on only one year of browsing pressure survey thereby run the risk of determining incorrect harvest quotas. For instance, the damage level can shift from unacceptable one year to acceptable next year even though moose density was almost the same. This highlights the importance of using a set of different kinds of monitoring methods but also the use of a running mean. The running mean is calculated by finding the mean of all the values in a “neighbourhood”, i.e. the three latest years of damage levels can be used and thereby smooth the monitoring estimates. This thesis also included a study of management tools. The general pattern was that the management performance improved with increasing monitoring costs. Nevertheless, a combination of two relatively cheap monitoring methods can significantly improve management performance at a relative low cost. However, even though we have perfect knowledge about moose numbers after the census period, uncertainty in annual growth rate will be added to the system due to annual variation in reproduction. Most of the moose monitoring methods used are conducted during winter or early spring, before the reproduction period. To improve performance, methods conducted after reproduction and before the harvest should be used, such as distance sampling. Irrespective of survey method used, the cost of monitoring moose will be small. Compared to the costs of reduced timber quality in the future and loss of income from hunting fees and meat (Mattsson, 1990; Ingemarson, Claesson & Thuresson, 2007).

Both monitoring methods (aerial surveys) and browsing pressure on pine seem to be dependent on snow conditions. This indicates that a long-term change can be expected in the ability to use specific census methods and browsing pressure on forests as snow conditions change, for example, as a result of the ongoing and large-scale climate change. In most of Sweden therefore, damage is expected to decrease due to a milder climate with less snow but, at the same time, damage will probably also increase in some areas as precipitation in the form of snow is expected to increase at higher altitude.

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Swedish summary - Svensk sammanfattning

Denna avhandling tar upp olika aspekter som påverkar älgens fördelning och betesmönster i skogslandskapet. Älgens betesmönster handlar i grova drag om vad och var älgen väljer att beta. Detta val kommer i sin tur att påverka älgens framgång vad gäller fortplantning (fitness) men också människans utnyttjande av naturresurser t.ex. jakt och skogsproduktion. Det är därför viktigt med ökad förståelse vad som påverkar älgarnas fördelning och betestryck i landskapet. Utifrån denna förståelse kan vi ställa upp mål för vår älgpopulation. För att få kunskap om var i förhållande till målet vi ligger krävs uppföljningar inom älgförvaltningen i form av inventeringar. De inventeringsmetoder som idag vanligen används inom älgförvaltningen (flyginventering, spillninginventering, älgobsen) skiljer sig åt i både precision och kostnader. Denna avhandling tar därför även upp hur effektiva dagens älginventeringsmetoder är på att leda älgförvaltningen till förutbestämda mål och vad de olika metoderna kostar att genomföra.

Älgens betesmönster styrs på olika rumsliga skalor. Det kan handla om var i landskapet individen väljer att etablera sitt hemområde, vilket skogsbestånd den väljer att gå till inom sitt hemområde eller till vilken planta/växt eller t.o.m. del av växt den väljer att beta på. Min avhandling började med att fokusera på växtnivån och vilka av våra vanliga trädararter som löper störst risk att bli betade och hur stor denna risk är jämfört med älgens huvudsakliga vinterföda, nämligen tallskott. Liksom tidigare studier visat så väljer älgen i första hand att beta på rönn, asp och viden/sälg, d.v.s. den föredrar (prefererar) dessa arter. Denna grupp av arter var signifikant skild vad gäller preferens från älgens "andrahandsval" nämligen värtbjörk och en. Grovt räknat visade studien att rönn, viden och asp löpte 14 ggr högre risk att bli betad jämfört med "tall- och glasbjörksgruppen", medan värtbjörk och en löpte 3,5 ggr högre risk att bli betad jämfört med tall och glasbjörk. Denna kunskap om hur betet fördelar sig på de olika trädslagen ger oss bättre förutsättningar att kunna värdera tillgängligt foder i skogslandskapet då t.ex. tallfoder och rönnfoder tycks vara olika mycket värt. Det kan också nämnas att gran knappt utnyttjades alls av älg i det område som studien utfördes.

Den andra studien fokuserade på större rumsliga skalor. Plantnivån lämnades således för att här studera hur fyra olika faktorer (fodertillgång, markens produktionsförmåga (bonitet), mångfald av foderarter samt antalet älgar) styr älgens foderkonsumtion på sex olika rumsliga skalor. Dessa skalor sträckte sig från provytanivå (20 m²) till studieytor större än älgarnas årshemområden (1300-2600 hektar). De fyra variablerna sattes in i en multipel regressionsmodell för att förutsäga foderkonsumtion. Det visade sig att denna modell förklarade mellan 31 och 49 % av den totala variationen beroende på skala. De olika faktorerna påverkade olika mycket på de olika skalorna. Mängden foder var genomgående en faktor som styrde älgarnas konsumtion oavsett vilken skala man studerade. Allra störst andel (80%) av den totala förklarade variationen i modellen utgjorde fodertillgången på de intermediära skalorna (ytor som representerade 160-320 ha, d.v.s. inom älgens hemområde). Vidare kunde det påvisas att relationen mellan

konsumtion och fodertillgång var proportionell på de tre största skalorna, d.v.s. konsumtionen fördubblades när fodertillgången fördubblades. Däremot var relationen oproportionell på tre lägsta skalorna, och mönstret där visade att ytor med mycket foder underutnyttjades jämfört med ytor med lite foder. Tätheten av älg förklarade konsumtionen bäst på de lägre skalorna och minskade successivt när den rumsliga skalan ökade. Detta något förvånande mönster har även visats i tidigare studier d.v.s. antalet älgar och konsumerad biomassa visar tydliga linjära samband på liten skala men att mönstret inte framträder lika tydligt på större skala. Bonitet förklarade konsumtionen bäst på de två största skalorna, 17-23% av den förklarade variationen. Denna studie visar att fodertillgången till stor del påverkar älgens foderkonsumtion. Det betyder att händelser som förändrar foderfördelningen i landskapet (storm, skogsbruksåtgärder, brand etc.) även kommer att påverka älgarnas fördelning och konsumtion. Att olika variabler påverkar olika på olika skalor gör att man för bästa förståelse bör jobba med olika förklarande modeller på olika skalor. Vidare bör man vara medveten om skalberoende mönster vid jämförelser av olika studier där skalan kan variera.

De två första studierna behandlade älgens betesmönster över rummet, men olika faktorer som påverkar älgarnas bete och fördelning ändras även över tid. Den tredje studien syftade därför till att studera hur älgens val av habitat och betestryck varierar över tid när olika förutsättningar (fodertillgång, älgtäthet och snödjup) förändras. Älgtäthet och fodertillgång sattes in i en linjär regressionsmodell för att se hur väl betestrycket på tall, glasbjörk och vårtbjörk gick att förklara. Betestrycket på tall förklarades till stor del av älgtäthet och tillgång på tallfoder medan väldigt liten variation i betestryck på de båda björkarterna gick att förklara med vare sig älgtäthet och olika mått på fodertillgång (tall, glasbjörk, vårtbjörk och total fodertillgång). Relationen mellan betestryck och älgtäthet studerades även specifikt för tre olika habitattyper (skogsbestånd > 30år, skogsbestånd < 30år och myr). Det visade sig att det fanns ett positivt linjärt samband mellan betestryck och älgtäthet oberoende av habitattyp. Vidare kunde man se att frekvensen spillningshögar per provyta alltid generellt var högre i ungskogsytor (< 30 år) jämfört med både myr och skogsytor över 30 år. Myr var det habitat som hade näst högst frekvens av spillningshögar. Denna skillnad i preferens var signifikant mellan alla tre habitaten. Det fanns också en variation i preferensindex för de olika habitaten mellan olika år även om ungskog alltid var den mest prefererade habitattypen. Det visade sig att denna variation gick att förklara med antalet dagar med snödjup över 10 cm. Ju fler dagar med djup snö desto högre preferens för ungskogsytor. Mindre antal snödagar ledde till högre preferens för främst skog över 30 år och myr. Detta mönster hänger förmodligen ihop med att mängden tillgängligt blåbärsris är betydligt högre i äldre skog och mängden ljung är högst på myrar. Både blåbär och ljung är viktiga foderkomponenter under vinterperioder med lite snö och tycks enligt resultatet även styra älgarnas habitatval. Blir det mycket snö blir fältskiktet mindre tillgängligt och älgarna söker då upp skogsytor med mer tillgängligt foder i buskskiktet d.v.s. med mer foder ovan snön. Detta fördelningsmönster kommer även i förlängningen att påverka betestrycket på unga tallar, med andra ord, under vintrar med lite snö kan man förvänta sig att ett lägre betestryck på tallungskog jämfört med vintrar med långa perioder med mycket snö. I denna studie påvisades även att förhållandet mellan den totala älgtätheten i

landskapet och den specifika tätheten i de tre olika habitaten är proportionell. Detta innebär till exempel att man kan fördubbla eller halvera tätheten i ett specifikt habitat genom att halvera respektive fördubbla den totala tätheten i landskapet. Detta förhållande kan förstås förändras beroende på tätheten (under min studie varierade tätheten mellan 7 och 14 älgar per 1000 ha) och man ska vara försiktig med att generalisera resultatet utanför detta intervall. Dessutom säger inte resultatet något om risken för klumpvis fördelning av älgar inom habitaten, vilket innebär att även vid en halverad älgtäthet kan risk för ytor med älgkoncentrationer och högt betetryck förekomma.

I den avslutande studien användes en kombination av empiriska data och simuleringar för att testa hur olika inventeringsmetoder lyckades vägleda älgförvaltningen till förutbestämda mål. Det visade sig att generellt sett ökar måluppfyllnaden med kostnaden för inventeringsinsatser men att det fanns en del intressanta undantag. Bland annat visade det sig att en årlig kombination av älgobsen och spillningsinventering stod sig lika bra som årliga flyginventeringar, men kostnaden för den sistnämnda var i stort sett tre gånger så hög. Ett problem med de vanligaste älginventeringsmetoderna i Sverige är att de utförs efter eller under jakt och före älgarnas reproduktionssäsong. Detta innebär att vi inte bara måste ta hänsyn till osäkerheten i inventeringsmetodiken utan även den årliga variationen i reproduktion i älgpopulationen. Även med perfekt kunskap av älgstammens storlek före reproduktion lyckades man endast vara inom målintervallet 81 % av tiden. För att minska denna osäkerhet skulle inventeringarna utföras efter reproduktion och innan jakt för att få ett säkrare underlag för lämpligt jaktuttag.

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Prolog

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