

Dissertationes Forestales 233

Resource selection of moose *Alces alces* at multiple
scales – from trees, plantations and home ranges up to
landscapes and regions

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Academic Dissertation

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ABSTRACT

The Moose is a valuable game animal in Fennoscandia but also the most severe pest in forest plantations. In this thesis, I examined factors that affect the habitat selection of moose and moose damage at multiple scales.

At the plot level, browsing increased with an increasing number of artificially regenerated pines and deciduous trees taller than pines. The damage risk was the highest in plantations with heavy soil preparation.

Moose summer home ranges had more fertile sites than the overall study area. Within summer ranges moose, selected non-pine-dominated habitats and mature forests and avoided human settlements. Winter ranges contained more pine-dominated plantations and other young successional stages, more pine dominated peatland forests and less human settlements and agricultural fields. Within winter ranges, moose used more non-pine-dominated plantations and mature forests and less human-inhabited areas than expected. At the home range level, there were no significant differences between sexes, but within home ranges males and females used different habitats during both seasons.

The occurrence of damage in nearby landscape decreased the probability to find a landscape without damage and predicted an increase in the number of damaged plantations. Increased food-cover adjacencies of mature forests and plantations increased damage. An increasing proportion of inhabited areas and the length of connecting roads decreased the number of damage at the landscape sizes of 1 km² and 5 km².

Moose-damaged stands were concentrated in SW and eastern Lapland in Peräpohja Schist Belt and Lapland's Greenstone Belt with nutrient-rich bedrock. There was less damage in landscapes with an abundant amount of pine-dominated thinning forests. Moose damage plantations were located more on fertile bedrock and soils than undamaged ones. Regenerating Scots pine on fine-grained soils derived from nutrient-rich rocks and naturally occupied by Norway spruce might increase damage risk.

Keywords: *Alces alces*, habitat selection, home range, moose, moose damage risk, resource selection.

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I made the final decision to put these articles together about a year and a half ago, when we were in the middle of preparing article **IV** about moose damage, bedrock and soil. It nicely complemented two articles that had been published earlier and the one that was also under preparation, which finally became article **III** in this thesis. Thus, this thesis is not a result of a rigorous dissertation project, but I still find that together these articles fulfil an idea that I have had in mind for a thesis – to assess moose resource selection at several levels of scale.

I am grateful to many people that have contributed to this thesis either as co-authors or in any other ways. First of all, I would like to thank prof. Kari Heliövaara, who was my supervisor and whose encouraging messages like "Kyllä se tästä!" (No problem, we will be handle it!) and "Hyvä me!" (So good we are!) always delighted my day. Thank you, Kari, also for managing so many bureaucratic steps that were required to accomplish all the formal studies and finalise the last steps of this dissertation.

My sincerest thanks also to my pre-examinators prof. Pekka Niemelä and prof. Lars Edenius, two highly distinguished researchers of moose ecology. I was really happy to have you as my pre-examinators. I certainly agree with your constructive criticism about some of the additions that you suggested to be made to improve the thesis. Being restricted to the limitations of the data at hand, I hope that I could at least partly assess some of those issues. In the end, the responsibility of the final contents of this thesis remains mine.

I was also happy to get one more distinguished moose researcher, Dr., Doc. Sauli Härkönen, to consent to be my opponent. Thank you, Sauli, for taking the effort! I know your days are full with real-world game problems, but perhaps it is invigorating sometimes to recall issues from the academic world. I hope that at least some of the issues in this thesis give insight to further development to real-world moose management as well.

I am grateful to my co-authors, here in the order of appearance (as they say in movies): Prof. Eero Helle and M.Sc. Samuli Heikkinen in article **II**. Eero, I was always impressed by your jovial but still assertive way of leading the moose-collaring project. And, certainly not least, being patient with our reporting. Samuli, your efforts of calculating so many moose home ranges with the techniques that were available at that time are venerable. Not to mention the pleasant and easy-going co-operation between us during all the steps of writing this article.

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Article **IV** was also a result of excellent co-operation among my co-authors: Dr. Teija Ruuhola, Dr. Juho Matala, M.Sc. Seppo Nevalainen and Mr. Vesa Nivala. None of us being a geologist, there were quite many issues that we had to solve when writing this paper. My special thanks to you, Teija, for sorting out complex issues of geological terms and processes. They were invaluable, as were your other efforts, too!

Article **III** was inspired by an idea to put together large data of moose damage and habitat data that were available. In addition to my co-authors, my thanks go to the staff of the National Forest Inventory that has always been helpful in providing data for our

disposal in many projects: Prof. Erkki Tomppo, Dr. Matti Katila, Dr. Sakari Tuominen, M.Sc. Antti Ihalainen and M.Sc. Jouni Peräsaari.

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The data in articles **I**, **II** and **III** were partly collected and analysed with grants from the Ministry of Agriculture and Forestry. The compensated moose damage data in articles **III** and **IV** were collected with the kind help of many people in the Forest Centre. Luonnonvarakeskus (Luke) granted me a project to accomplish this thesis.

Finally, my dear wife, D.A. Silja Nikula, and daughters Emma and Sara, your skills in arts and our discussions – many times philosophical – about the many facets of life have been the most important essence of my life. I am grateful to have you in my life!

Rovaniemi February 15th 2017

Ari Nikula

LIST OF ORIGINAL ARTICLES

This dissertation is based on the following three published articles (**I-II, IV**) and one manuscript (**III**). In the summary, they are referred to using their roman numerals given below. The publications are reprinted here with the kind permission of the publishers.

I Nikula, A., Hallikainen, V., Jalkanen, R., Hyppönen, M. & Mäkitalo, K. 2008. Modelling the factors predisposing Scots pine to moose damage in artificially regenerated sapling stands in Finnish Lapland. *Silva Fennica* 42(4): 587–603.

<http://dx.doi.org/10.14214/sf.235>

II Nikula, A., Heikkinen, S. & Helle, E. 2004. Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. *Wildlife Biology* 10: 121–135.

III Nikula, A. & Nivala, V., Matala, J., Heliövaara, K. Modelling the effect of habitat composition and roads on the occurrence and amount of moose (*Alces alces*) damage at multiple scales. Manuscript.

IV Ruuhola, T., Nikula, A., Nivala, V., Nevalainen, S. & Matala, J. 2016. Effects of bedrock and surficial deposit composition on moose damage in young forest stands in Finnish Lapland. *Silva Fennica* 50(3) article 1565.

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CONTRIBUTIONS OF THE AUTHORS

The following table summarizes the major contributions of the authors in articles:

	I	II	III	IV
Original idea	MH, RJ, AN, VH, KM	EH, SH, AN	AN	AN, TR, JM, SN
Materials	MH, RJ	SH, AN	AN, VN	AN, TR, SN
Modelling and analysis	VH, AN	AN, SH	AN	TR, AN
Manuscript preparation	AN, VH, RJ, MH, KM	AN, SH, EH	AN, VN, JM, KH	TR, AN, JM, SN, VN

AN=Ari Nikula, EH=Eero Helle, JM=Juho Matala, KH=Kari Heliövaara, KM=Kari Mäkitalo, MH=Mikko Hyppönen, RJ=Risto Jalkanen, SH=Samuli Heikkinen, SN=Seppo Nevalainen, TR=Teija Ruuhola, VH=Ville Hallikainen, VN=Vesa Nivala

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1. INTRODUCTION

1.1. Animal resource selection at multiple scales – theoretical background

Animals behaviour on the quest for different resources needed to fulfil energetic, as well as other nutritional needs, cover, rest and others, is not random, but based on several criteria (Owen-Smith et al. 2010). Due to temporal changes in the amount and quality of the resources, the criteria may change or have different importance in time periods that vary from diurnal to seasonal changes. The criteria for selecting resources also vary spatially and have different levels at which decisions are made. Knowing the quantitative and qualitative criteria, as well as temporal and spatial variation in these criteria, is the prerequisite for disciplines like wildlife management, conservation biology, pest management and controlling invasive species.

One central question in herbivory is by which criteria do herbivores select their resources in landscapes with patchily distributed resources (Searle et al. 2005). It has been presented that from the herbivores perspective, the landscape can be seen as a collection of resources at different hierarchical levels, and the resources at each level determine which will be used (Senft et al. 1987; Kotliar and Wiens 1990). A theoretical framework for hierarchical resource selection was presented in the hierarchy theory, which postulates that different levels (hierarchies) of selection operate spatially and temporally at different orders of magnitudes such that they can be separated from each other (Allen et al. 1987; O'Neill et al. 1989). Each level contains a limited amount of resources/food, and by relating the amount of resources that have been used to those that were available, it can further be deducted what kind of quantitative and qualitative aggregations of resources are important for some species' ecology and biology at that certain level.

Johnson (1980) introduced the concept of the selection order, which means that the selection processes take place at four levels of hierarchy. The first order selection covers the whole geographic area where a species occurs. The second order selection covers the home range, i.e., the annual area used by an individual animal or group of animals. The third order selection takes place within home ranges and pertains to the usage of different habitat components. The smallest scale in Johnson's (1980) concept of selection orders was the fourth order selection, which includes individual food items such as plants and plant parts.

Several theories that explain mechanisms in resource selection have been developed at the smallest level of selection, i.e., at the level of plants and plant communities. Functional response has remained as a popular theoretical framework in ecological studies that assess an animals response to food resources. The concept of functional response was originally presented by Holling (1959), who first described it for predator-prey situations, but after which, functional response has been extended to herbivores as well (Spalinger and Hobbs 1992). A basic idea in functional response is that animals change their eating rate as a response to a changing amount or quality of food. Depending on the species-prey setup, the response can vary from linear to decelerating or accelerating rates (Holling 1959).

The optimal foraging theory predicts that herbivores should maximize the net rate of energy intake (or other needs) subject to various constraints (Pyke et al. 1977; Belovsky 1981a). Activities that are used for finding food cause costs, and an animal should thus either minimize the time used for searching for food or maximize the net intake of energy in a given time to get an optimal rate of costs and gains. In addition to movement costs

related to the acquisition of food, herbivores have to balance between energy contents and the nutritional quality of the food (Belovsky 1978). Therefore, herbivores have been hypothesized to favour sites with diverse composition of plant species due to the diverse set of nutrients gained from several plant species (Westoby 1974; Belovsky 1981b).

The Marginal Value Theorem (MVT) (Charnov 1976) is one optimality model that predicts the time animals spend foraging in a place, but it also predicts an optimal point when it is profitable to leave the place. The MVT theory extended the resource selection of animals by including two new components to the system: a patch and an optimality in food resource use. From a large herbivore's point of view, a patch means a plant or a collection of plants. An animal should thus consider resources outside the patch in relation to the resources left in a patch. The optimal time to leave for the next patch (giving up time) is when the intake of food drops below the average level of intake rates across all patches (giving up density) (Charnov 1976).

In addition to energy and nutrients plants contain so-called secondary compounds that are toxic to animals (Freeland and Janzen 1974). Secondary compounds are part of a plants defence system against herbivores, and the composition, as well as the amount of secondary compounds, largely varies among plant species, but also due to relative availability of carbon and nutrients available in soil for plants (Bryant et al. 1983). Also, the capability to handle these compounds greatly varies among herbivore species. In addition to direct toxic effects, the metabolism of toxic compounds requires energy which is on the cost-side of the energy budget of the herbivore. Therefore, herbivores should optimize the intake of energy and nutrients in relation to secondary compounds (Freeland and Janzen 1974).

In addition to the energetic and qualitative properties of individual plant species, the properties of other plant species also might affect the food selection of herbivores. The plant association theory predicts that the consumption of some plant species is dependent on the quality of other plant species that accompany it in the same patch (Barbosa et al. 2009). The consumption of low-quality plant species should increase when these are accompanied by high-quality species in the same patch (associational susceptibility), whereas low-quality plant species might protect higher-quality species from consumption (associational resistance). There is some evidence for associational susceptibility (Hjältén et al. 1993; Milligan and Koricheva 2013), but most of the studies have not found support for associational resistance (Danell et al. 1991; Milligan and Koricheva 2013).

In addition to affecting the eating rate, changes in the amount and quality of food can affect animals behaviour at several scales, ranging from single plants and parts of plants to plant communities (Shiple and Spalinger 1995) to landscapes and regions (Senft et al. 1987). In addition to the internal structure of the patch, the spatial arrangement of the surrounding patches also affects an animal's decision to keep on feeding or moving to other patches (Searle et al. 2005). So far, most studies have been made at the plant level or at the level of plant communities, and quantitative results of functional response at levels larger than plant association are virtually lacking (Owen-Smith et al. 2010). However, the fact that large herbivores in particular change their environments in response to the changes in food resources or other conditions indicates that herbivores gain some benefit in doing so (Owen-Smith et al. 2010).

The problem of scale has received growing attention in ecological studies since 1980s (Wiens 1989; Levin 1992; Schneider 2001). One main message in the discussion of scale was that the scale should be assessed according to the question at hand. Scale is generally defined by two components: grain and extent, and they both affect our ability to make inferences about the phenomena in question (Turner et al. 1989; Wiens 1989). Grain refers

to the smallest resolvable unit of study, whereas extent is the area over which the study is made. Although, hierarchical levels in hierarchy theory (Allen et al. 1987) implicitly include the idea of different spatial and temporal scales, the terms "level" and "scale" are not synonymous. The term "level" refers to the relative ordering of a system's organization, whereas the scale refers to the resolution at which patterns are measured, perceived or represented (Turner et al. 1989). When applied to herbivores, the collection of resources can be measured by several scales (including varying grain sizes), but the levels of selection are determined by the selection processes at different levels of hierarchies (Johnson 1980).

In practice, it is not possible to separate different levels of hierarchies in ecosystems only by their physical features without defining processes which are typical to each level and which are different in their frequency or the rate of change at each level (Turner et al. 1989). Senft et al. (1987) presented that the typical levels of hierarchy for large herbivores are region, landscape and plant communities. Processes that are linked to the region level are, e.g., migration, home range selection and nomadism, as a response to the change of forage availability. At the landscape level, herbivores select their ranges by preference to plant communities or other landscape components that include qualitatively and quantitatively enough preferred food. At the level of plant communities, herbivores select plant species that, e.g., maximize the amount of food and nutrients or minimize toxic components (Senft et al. 1987).

Analytically, in order for one to be able to separate different processes at different levels of hierarchy from each other, it is a prerequisite that the amount of available food and other resources at each level can be measured as well as the use of these resources by herbivores at the same levels. In analysing the resource use of animals, the central concepts are the usage and availability of resources (Johnson 1980; Thomas and Taylor 2006). If the usage of resources is disproportional to their availability, the usage is said to be selective. Further, if the availability is made equal among resources, analytically or, e.g., by cafeteria experiments, it is analytically possible to draw conclusions about the order of preference among resources (Johnson 1980; Thomas and Taylor 2006). In order for one to be able to measure the availability and the use of resources, they have to first be defined in terms of quality and quantity, and after that, the geographic area from which these resources are measured should be delineated with criteria that have been derived from the behaviour of the species (Thomas and Taylor 2006).

Generally, when talking about scale, ecologists usually refer to the geographic extent of the study area. However, from the point of view of many ecological processes and studies regarding them, it is important to also define the grain size in relation to the process because it sets the limit for the smallest measurable targets (Turner et al. 1989; Wiens 1989). For example, in animal ecological studies, grain size should be similar to the size of units that animals base their decisions on resource use. When the grain size increases, one measurable unit includes more environmental variation, and it can mask units that are important from the animals decision-making point of view. As a result, important information that explains the process is lost (Wiens 1989). Also, the size of the study area should be adjusted according to the process in question. The size of the area where one individual makes a decision about resource use is probably different from what is needed, when studying population-level phenomena, like resource-dependent variation in population size (Senft et al. 1987; Wiens 1989).

According to the definition, resource is any biotic or abiotic factor directly used by an organism (Hall et al. 1997; Morrison and Hall 2002). From any organism's point of view, an important point is that to be a resource, it must actually be used by an organism to gain

some benefit. Resources should also be defined in a way that they can be found within the target area and be measurable (Morrison and Hall 2002). The most important resources for herbivores are food, cover and water.

Habitat is one of the basic concepts in theoretical and applied research in ecology and population biology. However, despite the habitat having a central role in studies that aim to understand, e.g., species distribution in relation to its environment, there is no unanimous definition for habitat (Morrison and Hall 2002). According to Morrison and Hall (2002), the term "habitat" is a concept and cannot be tested as such. However, there are some characteristics that can be linked to habitat. According to Morrison and Hall (2002), habitat "has spatial extent that is determined during a stated time period <...> the various components of habitats – cover, food, water, and such – are contained within this area". Thus, the definition of habitat can be expressed as the physical space within which the animal lives, and the abiotic and biotic entities (e.g., resources) that exist in that space (Morrison and Hall 2002).

However, for practical reasons, habitat has often been defined as a bounded space and synonymous to "vegetation category" or "biotope" (Dennis et al. 2003). In landscape ecology, the term patch is used in a similar context and refers to a relatively homogenous area that differs from its surroundings at the scale of landscape mosaic (Forman 1997). In reality, however, patches are seldom discrete and homogenous entities embedded in a homogenous matrix, but there is variation in both the internal structure of the patch and the level of the environment that contains the patch (Kotliar and Wiens 1990). Thus, patchiness in landscapes occurs at many scales that form a hierarchical patch structure (Kotliar and Wiens 1990). From the point of view of an animal, the smallest scale can be defined as the smallest perceivable structure of the environment, within which there is no variation that animals respond to. An upper limit, in turn, is defined by the extent of an animal's annual home range. Both the smallest scale and the extent are organism-dependent, as are the number of levels in a nested patch hierarchy that animals respond to (Kotliar and Wiens 1990). From the perspective of an herbivore, a patch can be defined as a collection of resources (e.g., food) at a given scale, the pattern of which does not change abruptly when an animal moves within the patch (Kotliar and Wiens 1990).

In this thesis and in **II – III**, the term "habitat" refers to different types of habitats (in terms of Morrison and Hall's (2002) components of habitats), i.e., different types of forests, peatlands, agricultural fields, inhabited areas and waters. From the point of view of Land Use and Cover (LUC) data used in **II-III**, a habitat is equivalent to LUC class that has been defined according to criteria in Table 1 in **II** and Table 1 in **III**.

1.2. Remote sensing and GIS enable large scale studies in ecology

A prerequisite for extending resource selection studies from the plant and plot level up to animal's home range, landscape and finally to region-wise studies are data that cover large areas. At the same time, these data have to include information that is relevant from the point of view of the study species. These data also have to provide qualitatively and quantitatively detailed information that can be linked to the resource selection process. The development of technology from the beginning of 1970s has enabled the analysis of large areas in ecological studies. The most important development has been made in remote sensing, especially satellite image-based mapping of natural resources (Campbell 2002) and the development of geographic information systems, GIS (Star and Estes 1990). Also, an

evolvement of landscape ecology increased the understanding of the metrics needed to measure the structure of the landscape that explain different processes like interactions of animals with landscapes (Naveh and Lieberman 1984; Wiens et al. 1993; Wiens 1995).

Remote sensing is the science of deriving information about the earth's land and water areas from images acquired from a distance (Campbell 2002). The launch of LANDSAT 1 in 1972 and the availability of data collected by it, especially in digital form, increased the interest to develop techniques to handle and analyse remote sensing data from the point of view of natural resource mapping (Campbell 2002). As a part of it, the usability of the satellite image data in forest inventory was studied soon after the launch of the first natural resource satellites (Iverson et al. 1989).

Also in Finland and Fennoscandia, the potential of satellite images in forest inventory was intensively studied from the beginning of 1970s (Kuusela and Poso 1975; Jaakkola et al. 1988), and several projects analysed the usability of different types of satellite images as well as algorithms to classify images (Häme 1984ab; Jaakkola et al. 1988). The resolution, in terms of both spectral and spatial resolution, of the first satellite images was rather low, allowing only coarse classification of forest resources. However, an overall conclusion of the studies was that satellite images can be used to monitor changes in forests, to classify land use and cover as a part of forest inventory, as a part of stratified forest inventory and in estimating the area of different types of forests (Jaakkola et al. 1988).

In Finland, the satellite image-based forest inventory that aimed to cover the whole country was operationalized as part of National Forest Inventory (NFI) in the end of 1980s, and the first so-called Multi-Source National Forest Inventory (MS-NFI) was accomplished in the beginning of 1990s (Tomppo 1991, Tomppo et al. 2008). In addition to satellite images, MS-NFI utilizes NFI field plots and digital maps of fields, peatlands, roads, buildings and inhabited areas to separate forests from non-forest land (Tomppo et al. 2008). The estimation of forest parameters is based in k-nn algorithm and the method can in principle produce estimates of all the variables that have been measured in field plots. As a result, estimates of, e.g., volume by tree species, forest age, development class and site type are produced for every pixel corresponding 25×25 m on the ground (Tomppo et al. 2008).

From 1980s, the development of GIS enabled the handling of spatial data covering large areas (Johnson 1990). There are many definitions of GIS, but, in general, GIS consist of computer software and hardware that can be used to store, handle, combine, analyse and produce outputs of geographically located data (Longley et al. 2001). An important feature of GIS is that it allows for combining data from different sources and the production of new attributes for landscape elements on the basis of multiple criteria. The resulting landscape patterns can then be analysed from the point of view of the study in question. Different types of proximity analysis in GIS also allow for flexible scaling according to study questions. Together, these features make GIS an efficient tool for ecological studies.

In the mid-1980s, a higher resolution was obtained with new sensors in Landsat TM and Spot XS, allowing the surface of the earth to be recorded with the spatial resolution of 10-30 m (Campbell 2002). Along with the increased resolution, an applicability of satellite images to ecological study types other than forest inventory were also studied together with GIS and, as an example, by the mid-1990s, hundreds of habitat models had been developed in northern America (Gray et al. 1996). Satellite images were also found feasible also for producing vegetation maps (Kalliola and Syrjänen 1991). In Finland, GIS and remote sensing data were utilized in wildlife habitat studies from the beginning of 1990s, when the habitat requirements of game species were studied with the aid of located wildlife triangle data (Lindén et al. 1996) and satellite image-based forest data (Helle and Nikula 1995,

Helle and Nikula 1996; Kurki 1997). The first results indicated that GIS and remote sensing data can be used to quantitatively analyse the effects of landscape structure on the habitat selection of animals in boreal forest environments (Helle and Nikula 1996). At the same time, GIS-based analysis was also extended to study other forest-dwelling animals than game species (Virtanen et al. 1996; Mönkkönen et al. 1997; Virtanen et al. 1998).

1.3. Moose as a study animal

1.3.1. History and population development of moose in Fennoscandia

According to archaeological findings, the moose (*Alces alces*, L.) has been part of Fennoscandian nature soon after the retreat of the ice cover, 8000-9000 years BP (Ukkonen 1993). The importance of moose to human populations has been great as a valuable game animal, but also because of its cultural value. The number of moose has varied greatly during times, but overall, moose population has been estimated to be rather low, probably some few thousands until the mid-1900s (Nygrén 1987). After WWII, the moose population started to grow in Finland, but by the end of 1960s, the population was estimated to be too low to be hunted, so hunting was prohibited in 1969-1971 (Nygrén 1987).

The rapid growth of the moose population in all Fennoscandian countries occurred in the beginning of 1970s (Cederlund and Markgren 1987; Nygrén 1987; Østgård 1987) and the population has been relatively high since then. In Finland, moose population increased from the beginning of 1970s, when the moose winter population after hunting was estimated to be about 20,000, to an overwintering population of about 110,000 in the year 1983 (Nygrén 1987). Due to a high number of damage to forestry and agriculture and an increased number of moose-vehicle collisions, moose population was actively reduced until the mid-1990s (Nygrén 2009). After then, the population started to grow again, the highest number of moose so far, more than 140,000, was estimated to exist in the year 2001. From the year 2001 onward, the moose population has gradually decreased to about 70,000-80,000 moose after hunting (source <http://www.rktl.fi/riista/hirvielaimet/hirvi/>). Also, in Sweden the moose population started to grow substantially in 1970s, and in the beginning of 1980s, overwintering population was estimated to be about 300,000 moose (Cederlund and Markgren 1987). A similar development was seen in Norway, where the overwintering population was estimated to be 80,000-90,000 moose in the beginning of 1980s (Østgård 1987).

The reasons behind the population increase have been attributed to several types of changes in land use, like forestry, raising livestock and agriculture (Ahlén 1975). Changes caused by forestry and adopted hunting practices in particular have been attributed as the main reasons behind the growth of moose population (Cederlund and Markgren 1987; Lav Sund 1987; Cederlund and Bergström 1996). Clear-cutting and regeneration using coniferous trees, mostly Scots pine (*Pinus sylvestris* L.), became the prevailing methods in forestry since the end of the 1940s. From the point of view of forestry, an optimal age-class distribution of forests has a large proportion of young successional stages, i.e. plantations. These have been hypothesized to provide, in practice, unlimited amount of food for moose, especially in winter (Cederlund and Bergström 1996). Also, adult and calf moose hunting quotas were defined since mid-1970s, and it was recommended that the unproductive parts of the population, like the young and males, should be hunted more than the others. This

again increased the productivity of the moose population (Nygrén 1987; Nygrén and Pesonen 1993).

1.3.2. Moose damage as a consequence of population growth

Although the moose population was rather small until 1970s, damage caused by moose to forests was discussed by foresters and hunters already in the late 1800s (Ehrström 1888; Kangas 1949). In the mid-1930s, moose damage was also discussed in Finnish parliament, and it was suggested that moose damage should be compensated to land owners (Hirvivaikokomitean mietintö 1960). Because there was no information on the importance of moose damage to forestry, Metsähallitus conducted a survey about damage in the late 1930s. According to the results, most foresters regarded moose damage as a minor problem, and there was no need for compensation to forest owners (Hirvivaikokomitean mietintö 1960). One of the recommendations was also that moose damage should be studied on a more scientific basis. As a consequence, the first scientific study was funded by the state and a report about the occurrence and types of damage was published in 1949 (Kangas 1949).

By the mid-1950s, the moose population had increased in Finland, and damage was discussed in parliament again. It was suggested that the moose population should be reduced and legislative actions to reduce damage should be taken. Due to the lack of reliable information on moose damage, a special committee was established in 1956 to "carry out an investigation <...> to cover only damage caused to forests by the increased moose population and the measures for the prevention of the damage." (Hirvivaikokomitean mietintö 1960). According to the survey conducted by the committee, moose damage was a problem in pine-dominated young stands especially, but damage was also found in other tree species-dominated young stands. The proportion of forest holdings having damage was 5.6%, and thus, damage was judged to be fairly low. However, the committee stated that in individual cases, moose damage could be significant for forest owners and recommended reforestation to be compensated by the state. The compensation system came into force in the year 1963 (Löyttyniemi and Lääperi 1988). The committee also recommended that long-term plots should be established in forest plantations to gather information about the development of browsed trees (Hirvivaikokomitean mietintö 1960). In Sweden, early discussions on moose damage happened in tandem with Finland, and the first report covering the description of damage and the results of moose damage inventory was published in 1958 (Westman 1958).

The first systematic inventory of moose damage that covered the entirety of Finland was made in connection with the 3rd National Forest Inventory in 1951-1953 (Löyttyniemi 1982). Moose browsing was recorded in about 150,000 ha of pine-dominated plantations, of which about 13,000 ha were classified as actual moose damage. Next time, detailed information of moose damage was recorded in the 8th NFI in the years 1986-1994 (Tomppo and Joensuu 2003). Moose damage was recorded on about 2.3% of forest land, which corresponded to about 446,000 ha (Tomppo et al. 2001). According to the 9th NFI (1996-2003), moose damage was recorded in 653,000 ha which corresponds to 3.2% forest land. The 10th NFI (2004-2008) showed that moose damage had again increased, and damage was recorded in about 741,000 ha, corresponding to about 19% of all plantations (Korhonen et al. 2010). In pine-dominated plantations, moose damage was recorded in 24% of plantations, out of which three per cent were classified as severe or having led to the total destruction of the plantation. In Sweden, moose damage was found in 12-15% of pine

plantations in 2004-2013, and the damage was classified as severe in 3% of the plantations (Swedish Statistical Yearbook... 2013).

1.3.3. *Moose food items*

The moose has traditionally been regarded as a generalist browser that can utilise a diverse set of food plants (Belovsky 1981b). On the basis of moose diet, Shipley (2010) defined the moose to be on the continuum between the facultative specialist and facultative generalist because the moose diet consists mainly of one species, e.g., during winter time, but which can expand to cover several species according to the availability of plants. In summer, moose utilise tens of species of plants, but in winter, a moose's diet consists mainly of woody species (Cederlund et al. 1980). Dwarf shrubs, blueberry (*Vaccinium myrtillus* L.) and lingonberry (*Vaccinium vitis-idaea* L.) make a substantial proportion of moose autumn diet before the snow cover becomes too thick (Cederlund et al. 1980). A shift from ground layer plant species to woody species starts when the depth of snow is about 6-30 cm, and moose consume only woody species when the depth of snow exceeds 30 cm (Cederlund et al. 1980). In winter, a moose's diet consists mostly of Scots pine (*Pinus sylvestris* L.), but also birches (*Betula pendula* L and *B. pubescens* L.), willows (*Salix* spp.), aspen (*Populus tremula* L.), juniper (*Juniperus communis*, L.) and rowan (*Sorbus aucuparia* L.) are regularly consumed.

Although, in terms of quantity, moose consume mostly Scots pine in winter, pine is only of median species in the preference list of moose (Månsson et al. 2007). When the availability of different species is accounted for, the most preferred species are in the order of preference: rowan, aspen and willows, after which come birches, Scots pine, juniper and Norway spruce (Månsson et al. 2007). However, in Fennoscandia moose consume only a small amount of Norway spruce (Faber and Pehrson 2000). Although, deciduous species are more preferred than Scots pine, due to the high amount of pines consumed in winter, browsing damage is the most severe for pine (Bergström and Hjeljord 1987).

1.3.4. *Moose damage pattern in forest plantations*

Moose cause damage to trees by breaking leader shoots and the main stem, by browsing lateral shoots and by stripping bark (Bergqvist et al. 2001). Most of the damage occurs in winter, but summer time damage can also be substantial (Bergqvist et al. 2013). The same trees often become browsed in subsequent years, which indicates that moose favour some individual trees over others (Löyttyniemi 1985; Bergqvist et al. 2003). As a consequence of browsing, smaller plants especially can die, but browsing for the most part causes defects in the tree stem and reduces growth or impairs the technical quality of saw wood (Siipilehto and Heikkilä 2005; Wallgren et al. 2014).

1.3.5. *Effects of snow on moose*

In boreal regions snow covers the ground and part of the vegetation for a substantial time of the year, which has several implications for moose. Snow cover impedes movement, and thus, causes extra energy consumption compared with no-snow conditions (Coady 1974). With high legs and a chest height of 80-105 cm, the moose is well-adapted to moving in snow, and movements are only severely restricted when snow depth exceeds 70-90 cm (Kelsall 1969). In deep snow cover periods, moose tend to aggregate and follow the same

tracks probably to lower energy costs (Peek et al. 1974). In addition to snow depth, the quality of snow in terms of density and hardness can also affect the trail-following behaviour of moose (Lundmark and Ball 2008).

Snow cover also affects the timing of migrations between seasonal ranges (LeResche 1974). In Fennoscandia, moose start migration from summer-fall ranges to winter ranges when the snow depth is 42 cm on the average and about one month after the first snow (Sandegren et al. 1985). In spring, the migration to the summer ranges starts when the snow depth is 6 cm on the average, but the timing in relation to snow melt varies between years (Sandegren et al. 1985). Snow cover also causes a shift in moose diet from ground layer vegetation to a woody plant diet when snow depth exceeds about 30 cm (Cederlund et al. 1980). In addition to causing a shift in seasonal ranges, snow has also been shown to affect moose within home range habitat use (Ball et al. 2001).

1.3.6. Moose home ranges

The concept of the home range was first defined by Burt (1943), who defined it as an '... area traversed by the individual in its normal activities of food gathering, mating, and caring for young.' Home ranges can shift during the life time of an individual and migratory animals quite regularly shift from summer home ranges to winter home ranges and back. It is also typical that the size of the home range can vary due to several reasons, like sex and season (Burt 1943), but also due to the varying availability and the depletion of resources (van Beest et al. 2011).

First telemetry studies of moose were conducted in Northern America in the beginning of the 1970s (Van Ballenberghe and Peek 1971). The studies gave more insight to the home range behaviour, movements and habitat use of moose. In Fennoscandia, the first results of moose telemetry studies were published in the 1980s (Sandegren et al. 1985; Cederlund et al. 1987; Cederlund and Okarma 1988; Sweanor and Sandegren 1988). Moose often have separate seasonal home ranges with winter and summer ranges being the most distinct from each other. The distance between summer and winter ranges varies from some few kilometres up to some tens of kilometres (Sandegren et al. 1982; Sweanor and Sandegren 1988). However, for some moose, summer and winter ranges overlap at least partly or are adjacent (Cederlund and Okarma 1988; Sweanor and Sandegren 1988; Lundmark and Ball 2008; Ball et al. 2001), which means that part of the population does not have seasonal migrations (Dingle and Drake 2007).

According to telemetry studies, the size of the female home ranges is 500-740 ha (Cederlund et al. 1987; Cederlund and Okarma 1988; Cederlund and Sand 1994), and for males – 750-1800 ha (Cederlund and Sand 1994; Olsson et al. 2011). Cederlund and Okarma (1988) reported that moose summer ranges are larger than winter ranges, but no all studies have found difference in home range size between seasons (Cederlund and Sand 1994; Olsson et al. 2011). Also, the results of the difference between males and females in the size of the home range vary: Cederlund and Sand (1994) and van Beest et al. (2011), reported that male home ranges are larger in both summer and winter, but Sweanor and Sandegren (1989) did not find difference between the sexes in winter. Extrinsic factors, like climate and snow depth (Sweanor and Sandegren 1989; van Beest et al. 2011), but also intrinsic factors, like the reproductive status, have been shown to affect home range size (van Beest et al 2011), which might explain discrepancies among studies. Also, the method that is used for calculating the size of the home range strongly influences the results

(Lawson and Rodgers 1997). However, telemetry studies indicate that the size of the home ranges varies from some few hundreds of hectares up to some thousands of hectares.

Moose home range selection, i.e., how moose select their home ranges (Johnson's second order selection) has only been studied in a few studies in Fennoscandia (Cederlund and Okarma 1988; Ball et al. 2001; Van Beest et al. 2010; Olsson et al. 2011) and most of the studies have been based on within-home-range habitat selection or compared moose habitat use to overall landscapes. Ball et al. (2001) did not find significant differences between the home range habitat composition and overall landscape, but according to Cederlund and Okarma (1988) and Olsson et al. (2011), home ranges included more coniferous forests, peatlands and clear-cuts than what could be expected. Within home ranges, moose have been found to favour regeneration areas, young successional stages and old forests and to use less than expected agricultural fields and waters (Cederlund and Okarma 1988; Ball et al. 2001; Olsson et al. 2011). Overall, moose respond to variation in food quantity, quality and depletion in home range selection as well as in within-home-range habitat selection (Van Beest et al. 2010).

1.3.7. Factors affecting damage at the plantation level

Most moose damage studies have been based on the effects of plantation level factors on damage, probably because silvicultural actions have been seen as a potential way to reduce damage. At the level of a plantation, at least tree species mixture (Heikkilä 1990; Heikkilä 1991; Heikkilä and Härkönen 1996; Härkönen 1998; Härkönen et al. 1998; Kullberg and Bergström 2001; Härkönen et al. 2008; Milligan and Koricheva 2013) and the density of trees (Lundberg et al. 1990; Heikkilä 1991; Lyly and Saksala 1992; Ball and Dahlgren 2002) have been found to partly explain damage. Other factors at the plantation level that have been associated with damage are the fertility of the site (Niemelä and Danell 1988; Danell et al. 1991; Ball and Dahlgren 2002; Bergqvist et al. 2014) and fertilization (Löyttyniemi 1981; Edenius 1993; Ball et al. 2000). Also, the height of trees, as well as the spatial arrangement of trees has been linked to damage (Heikkilä 1990; Härkönen 1998; Jalkanen 2001; Härkönen et al. 2008).

1.3.8. Moose damage factors at local and regional levels

The effect of local and regional factors on moose browsing have indicated that moose consumption of forage is proportional to the occurrence of different plant species and varies accordingly from one region to another (Hörnberg 2001a). At the regional level, the amount of moose damage has been shown to vary according to variations in moose population, but the amount of damage is not directly linked to population size (Hörnberg 2001b; Månsson 2009). The vicinity of roads and inhabited areas reportedly decreased damage (Repo and Löyttyniemi 1985; Heikkilä 1991), although Ball and Dahlgren (2002) found that moose damage can also accumulate close to highways due to their barrier effect on moose migration.

2. THE AIM OF THE STUDY

A plethora of studies indicates that there are several factors that affect the resource selection of moose as well as damage caused thereof. Resource selection occurs at several scales and the factors that affect selection might vary between scales. Understanding these factors and the scales that they are linked to is one prerequisite for moose management. Furthermore, because moose browsing causes damage in forest tree plantations, understanding the factors behind resource selection can also be of help in integrated moose damage management. In this thesis, I studied these factors, starting from the plot level, representing individual trees and groups of trees up to plantations, the home ranges of moose and, finally, up to levels of landscapes and regions. This thesis consists of four studies numbered **I-IV** in roman numerals.

In study **I**, moose damage risk was modelled with factors that were measured at the levels of plot and forest stand. Tree-species composition and other stand parameters routinely recorded in forestry were used in the modelling. Regional variables, like temperature sum and moose density, were calculated for each plantation and used as stand-level variables. Finally, by using the combination of variables that had the best explanatory power, model predictions of the most powerful variables were calculated and illustrated for different levels of model variables. The questions specifically asked in **I** were:

- 1) What factors explain and predict the browsing of Scots pines at
 - a) The plot level?
 - b) The stand level?
- 2) What are the quantitative predictions of moose browsing probability as a function of the main variables in models?

In study **II**, located data from radio collared moose were analysed with satellite image-based forest and land cover data and compositional analysis. The habitat composition of home ranges was first compared with overall landscape, and in the second phase, habitat compositions around locations were compared with the habitat composition of home ranges. All the analyses were made for all sex (female, male) and season (winter, summer) combinations. Finally, habitat compositions of home ranges, as well as locations, were compared between sexes and seasons. The questions specifically asked in **II** were:

1. Are there differences in habitat selection between sexes within seasons at:
 - a) The home range level?
 - b) Within-home range level?
 - c) The level of locations?
2. Are there differences in habitat selection within sexes between seasons at:
 - d) The home range level?
 - e) Within-home range level?
 - f) The level of locations?

In study **III**, the number and occurrence of moose damage was modelled as a function of habitat composition, road length and man-made land use and cover types for 1 km², 25 km² and 100 km² landscapes. The sizes of the landscapes refer to the within-home range, home range and landscape-level habitat selection, respectively. Separate models for the occurrence of damage and for the number of damage were developed for two study areas and for all landscape sizes. Marginal effects of model variables were studied by calculating

the predicted number of damage as a function of different proportions of habitats that were significant predictors in models. The questions specifically asked in **III** were:

1. What habitat types and man-made features explain a) the number and b) the occurrence of moose damage at 1 km², 25 km² and 100 km² landscape sizes?
2. Are there differences between Ostrobothnia and Lapland in variables that were significant in models?
3. How do different levels of co-variables in models affect the predicted number of damage at each scale studied?

In study **IV**, the occurrence of moose damage in relation to site type, soil characteristics, bedrock and topography were analysed. Compensated moose damage data for private forest owners was used as a response and undamaged stands in National Forest Inventories from years 1986-2008 served as control data. Bedrock and soil data were derived from Digital databases of the Geological Survey of Finland and topography data were derived from National Land Survey (NSL) data base. The questions specifically asked in **IV** were:

1. Does the bedrock composition affect the number of moose damage?
2. Do site types affect the number of moose damage?
3. How do different bedrock-site type combinations affect the number of damage?
4. How do different soil types affect the number of damage?
5. Does topography affect the number of damage?
6. How are damage located in relation to the location of formerly sub-aquatic and supra aquatic areas during the ancient phases of the Baltic Sea and northern ice lakes after the last deglaciation?

3. MATERIAL AND METHODS

3.1. Study areas

In both studies **I** and **IV**, the study area covered the southern and central parts of Finnish Lapland (**I**, Fig. 1; **IV**, Fig. 1). Also, in study **III** (**III**, Fig. 1), the northern study area consisted of the southern and central parts of Lapland. Part of the south-western Lapland belongs to mid-boreal vegetation zone but Lapland mostly belongs to the northern boreal vegetation zone (Ahti et al. 1968). The main tree species are Scots pine and Norway spruce, which are dominant in about 72% and 20% of the forest land (Finnish Statistical Yearbook... 2011). The rest of the forests are deciduous or mixed. The shrub layer comprises different willows and juniper. About 44% of the forestry land are peatlands of which 24% have been drained. About 36% of forest land is privately owned (Finnish Statistical Yearbook... 2011). Inhabited areas are concentrated mostly alongside the Kemi and Tornio rivers and their arteries. The climate of Lapland varies from subarctic in the north to continental in the east. Variation in altitude also causes large variation in climatic factors. The average annual temperature in the study area varied from +1 °C to -2 °C and the annual precipitation from 500 to 700 mm in years 1981–2010. The period with a permanent snow cover lasts from October to May, and the maximum snow depth ranges from about 60 cm in the south-west to about 90 cm in the northern most part of the area (Pirinen et al. 2012). The altitude in the area ranges from that of sea level in the south-west to 540 m a.s.l. at the top of highest fells in the north.

The whole study area in **II** and the modelling area Ostrobothnia in **III** are located in the western part of the Ostrobothnia province (**II**, Fig. 1; **III**, Fig. 1). In the east, the area restricts to topographic border formed by the highest shoreline after the last glacial period (Ojala et al. 2013), and the area is restricted to the Gulf of Bothnia in the west. The study area belongs to the mid-boreal region (Ahti et al. 1968). The main tree species are Scots pine, Norway spruce, birches, aspen, rowan and alder. Out of these, Scots pine is the main tree species in about 65% and Norway spruce in 11% of the forest land. The rest of the forests are either deciduous or mixed. A typical feature for the area is that about half of the forestry land comprises peatlands, of which about 60% have been drained (Finnish Statistical Yearbook... 2011). The average annual temperature in the area varied from +1.9 °C to +2.6 °C and the precipitation from 470 to 620 mm per year during 1980-2010. Permanent snow cover lasts from October to April and the maximum depth of snow ranges from some few centimetres in the west up to about 56 cm in the east (Pirinen et al. 2012). Terrain is rather flat and the altitude varies from sea level in the west to about 200 m a.s.l. in the east.

3.2. Moose habitat use and damage data

Moose damage data for study **I** came from an inventory of originally 208 randomly selected plantations that had been regenerated for Scots pine, and which were inventoried for regeneration success (Hallikainen et al. 2004). Because only stands with Scots pine as the dominant tree species and with at least one living pine in sample plots were used in modelling, a total of 197 stands fulfilled these criteria. Furthermore, due to the possible autocorrelation problem, stands were not allowed to be closer than 5.7 km to each other, which corresponds to the approximate diameter of moose home range in winter. In addition, because 74 stands were used for test data, a total of 123 stands were used in modelling. The rest of the stands did not fulfil the criteria, either being non-pine-dominated or having no living pines in plots.

In study **I**, plantations were inventoried by using systematic line cruising and sample plots of 20 m². On each plot, all trees taller than or equal to 10 cm were measured by tree species. Moose damage was recorded for artificially regenerated Scots pines, whose leader shoot had been browsed. Explanatory measured variables were divided into stand-level variables and plot-level variables (**I**, Table 1). Stand-level variables either did not have significant variation at the plot level or they could not be assessed in more detail. These included moose density, temperature sum, elevation, site type, soil scarification and some soil element concentrations. At the plot level, the number of all tree species, as well as the height of trees, was recorded. For deciduous trees, the number of trees taller than Scots pine were also recorded. Soil paludification and soil type were also recorded at the plot level.

For study **II**, a total of 73 moose (37 males and 36 females) were located from helicopter, immobilized and equipped with VHF radio collar in Ostrobothnia (Heikkinen 2000). After release, moose were located by triangulation mostly once a week, but in the times of intense movements in spring and autumn, two or three locations per week were assessed. By the end of 1996, the data consisted of 4544 locations. The timing of the seasons, i.e. winter, summer and autumn, were made for each moose individually (Heikkinen 2000). In spring, there was an abrupt increase in the distance of successive locations; the time when moose moved to summer pastures, and the time when moose finally left their winter ranges was used as the end of winter period. In autumn, moose

started to have bouts outside their summer ranges and gradually moved farther away from their summer pastures. The end of summer period was defined as the time point when locations dispersed over a much larger area than the cluster of summer locations. The start of the winter period was defined as a time when distances between locations decreased again, and moose settled in their winter ranges (Heikkinen 2000).

After dividing locations into summer, autumn and winter locations, home range boundaries for each moose and season were determined with harmonic mean method (Dixon and Chapman 1980). A minimum of 20 locations were required for each sex and season. The locations indicated that moose have infrequent bouts of movements causing some of the locations to be clearly outside the main cluster(s) of locations. Therefore, instead of using 100% isopleths, centres of activity were determined by examining the possible points of inflections in utilisation distribution plots (Harris et al. 1990). In most cases, slope discontinuity was found in about 80% of the utilization area, and therefore, 80% isopleths were used in the final home range analyses. After removing overlapping home ranges for the same individual moose in consecutive seasons, there were 33 summer (10 males and 23 females) and 21 winter home ranges (6 males and 15 females) for the analysis.

For studies **III** and **IV**, the data base of compensated moose damage plantations in private forests was utilized. The data were originally collected from Metsäkeskus (Finnish Forest Centre) files of compensated moose damage data. In Finland, the state pays compensation for moose damage to private forest owners for growth and quality losses and for possible regeneration costs. The area of damage must be >0.1 ha and the calculated value of damage has to exceed 170 euros. Compensation for the same plantation cannot be paid until three years have passed since the payment of earlier compensation (Finlex 2014). During the evaluation of the damaged plantation, the exact location of the damaged stand, main tree species, the number of other tree species, site type and numerous other variables are recorded. In study **III**, the locations of 2663 plantations in Ostrobothnia and 1287 plantations in Lapland that had been compensated in years 2002-2008 were used in the study. In study **IV**, data from 5362 compensated plantations from the years 1997-2010 were used. In study **IV**, information from 4551 field plots of National Forest Inventories without moose damage from NFI8 (1989–1994), NFI9 (1996–2003) and NFI10 (2004–2008) was used as control data. NFI plots with moose damage (279 plots) were used as reference data for the compensated damage stands to check whether there were possible differences in the treatments due to different sampling methods and damage criteria (NFI vs compensated moose damage data).

3.3. Land use and forest data

As land use and forest data in **II** and **III**, we used MS-NFI data (Tomppo et al. 2008). MS-NFI data is produced by combining satellite images, field plot data and digital map data of non-forest areas and by producing estimates of forest variables with *k*-nn algorithm. MS-NFI utilizes mostly Landsat TM or ETM+ satellite images, but SPOT HRV XS images have also been used to cover cloudy areas and missing Landsat images. MS-NFI produces separate maps of the estimates of numerous forest variables like tree species, volume by tree species, stand age etc. Estimates are produced for each 25 m × 25 m forest area (Tomppo et al. 2008). The original satellite image in study **II** was recorded in 1991, and in study **III**, MS-NFI data correspond to the year 2005 (source: NFI).

MS-NFI based digital maps of total volume estimates for Scots pine, Norway spruce and deciduous trees, as well as digital maps of agricultural fields, human settlements, roads, water and peatlands (source: National Land Survey), were imported as separate layers into GIS. Estimates of total volume for all tree species were summed by pixel and were further divided to age classes by using the total timber volume as a surrogate for forest age (Tomppo et al. 1998; Tomppo et al. 2012). Non-forest area land use and cover classes were assessed according to digital maps of non-forest areas (source NLS). In **II** and **III**, peatland forests were separated from mineral soil forests by using digital maps of peatlands (source NLS). In **III**, drained peatlands were further separated from non-drained with the aid of digitized ditches. As a result, each pixel could belong to one of 12 land use and cover classes in study **II** (**II**, Table 1) and to one of 15 classes in study **III** (**III**, Table 1).

3.4. Bedrock, soil, ancient shoreline and topographic data

For study **IV**, digital maps of bedrock and soil were obtained from the Hakku-service of the Geological Survey of Finland (hakku.gtk.fi). The Bedrock of Finland data set (Bedrock of Finland 2014 – DigiKP, Geological Survey of Finland (GSF), version 1.0.) was used as bedrock data. In bedrock data, lithological and stratigraphic information is presented as polygons, and the data are at 1:200000 scale. The data consists of 20 rock classes originally which have been further divided into 173 lithological units (http://tupa.gtk.fi/metaviite/kalliopera_bedrock_200k_legenda_legend.pdf). For our analysis, we classified data into six larger groups, according to their origin and features (Koljonen 1992a; Koljonen 1992b): 1) Carbonate rocks (limestone, dolomitic carbonate rock, carbonatite, calcsilicate-rock and skarn), 2) Mafic and ultramafic rocks (e.g., gabbro class rocks, mafic tuff, tholeiitic basalt, peridotite komatiite, peridotite), 3) Schist and phyllite-class rocks (graphite, graphite sulphide and biotite paraschist, black schist, phyllite, semipelite), 4) Felsic and intermediate rocks (e.g. granite, dacite, diorite, granophyre, tonalite, felsic tuff), 5) Gneiss class rocks (e.g. migmatitic paragneiss, tonalitic migmatite, garnet-cordierite gneiss, quartz feldspar paragneiss, arkose gneiss) and 6) Quartzite class rocks (arkose quartzite, orthoquartzite, sericite quartzite). Gneisses and migmatites were grouped in the same class, independent of their origin (Koljonen 1992b). The first three classes can be considered as “fertile” rock types, and the three last ones are known as “non-fertile” rock types, according to their effects on the fertility of the growth sites (Kalliola 1973).

For study **IV**, soil data were derived from the Superficial deposit map of Finland (Superficial deposits of Finland 2013 – DigiMP, GSF, version 1.0). The data are at 1:200000 scale and consists of 12 soil types (Hyvönen et al. 2007). For the analyses, the surface and subsoil types were classified into five classes: 1) Fine-grained stratified soil (mainly silt), 2) Coarse-grained stratified soil (from fine sand to gravel), 3) Rocky soil (bedrock openings, block fields, cobbles and boulders, 4) Non-stratified soil (till) and 5) Peat (thin and thick peat formations).

In **IV**, the location of moose damage stands and NFI stands were also studied in relation to ancient shorelines and elevation. Information on shorelines was derived from the Ancient Shoreline Database© (ASD; GSF, version 6.1). The database shows the maximum extension for the Litorina Sea and for the highest shoreline of the Baltic Sea basin in Finland as well as known local ice lakes and ice-dammed lakes in Northern Finland (Ojala

et al. 2013). The elevation of each stand was measured by using the Topographic database© of the National Land Survey of Finland.

3.5. Statistical analysis and modelling

In study **I**, the browsing rate proportions on plots were skewed and included an excessive number of zeros, i.e., non-browsed plots. Therefore, the response was defined as binary, browsing or non-browsing. Because the variables that were used in modelling represented two hierarchical levels, plot and stand, a logistic regression with a random factor was selected as the modelling technique (McCullagh and Nelder 1989). A binomial assumption of the distribution of the error term and logit link function were used. The random variable, the stand effect, was assumed as normally distributed. The models were constructed with SAS (ver. 9.1.3) MIXED procedure and GLIMMIX macro with a restricted pseudo-likelihood estimation method (Allison 1999). The comparison of the models and the selection of the best model was made by first checking Pearson's residuals against the modified predicted probabilities and then by comparing ROC (Receiving Operating Characteristic), specificity and sensitivity values (McCullagh and Nelder 1989). Model predictions were calculated with the best model for deciles of risk for both predicted and observed probabilities (Steinberg and Colla 2004).

In addition to hierarchical logistic models, five stand-level general linear models (GLM) were constructed to test whether the degree of browsing can be predicted with the same accuracy using averaged variable values from plots without the within-stand variability in variable values. The response value was the average proportion of browsed pines in a stand that was square-root and arccos-sin transformed to meet the distribution requirements of the GLM.

In study **II**, a compositional analysis (Aebischer et al. 1993) was used to analyse differences in the proportions of habitat classes between home ranges and overall landscapes and between the proportions of habitats used within home ranges and those available at home ranges. Analyses were made separately to compare both sexes and seasons and at both levels of selection. The rationale behind compositional analysis is that because there is a unit-sum constraint, i.e., the sum of proportions is 1, the proportions of habitat types are non-independent (Aitchison 1982). By transforming all habitat proportions to log-ratios using one of the habitat classes as a denominator renders log-ratios linearly independent (Aebischer et al. 1993). The habitat class 'Other' (**II**, Table 1) was used as a denominator. Zero proportions were replaced with an order of a magnitude smaller value (0.001) than what was found in the real data (Aebischer et al. 1993).

The proportion of each habitat was calculated for every combination of sex×season home range and for randomly placed home ranges. The original home ranges were randomly placed into the study area to represent overall landscapes and were restricted to have at a maximum of 19.13% class 'Other', 11.75% human settlements and 36.32% agricultural land. Those were the maximum values found in home range data. Because the locational accuracy of triangulated location data varies with distance, topography and vegetation cover, a 200 m buffer was formed around each location, and habitat proportions were calculated from this area for home-range to within-home range comparisons as well as for the comparisons between locations. There were 217 locations for males in the summer, 73 locations for males in the winter, 628 locations for females in the summer and 186 locations for females in the winter.

Due to a small amount of home ranges for some sex×season combinations, we used randomization (Manly 1997) in all the comparisons. A total of 5000 randomizations were used for HR vs overall landscape comparisons as well as for comparisons between locations. In home range vs location comparisons, 10000 randomizations were used. Before proceeding to univariate comparisons of habitat types, a multivariate comparison of mean differences among groups for a combination of all habitat classes was made by using Wilk's lambda, sum of log(F) and sum of squares (E-statistics) (Manly 1997).

In study **III**, three grids with the size of 1×1 km, 5×5 km and 10×10 km (later referred to as 1 km^2 , 25 km^2 and 100 km^2 cells and landscapes, respectively) were superimposed on both study areas of Ostrobothnia and Lapland. Only grid cells that fulfilled the following criteria were used for modelling: 1) privately owned forest land had to be $>50\%$ of the area, 2) there had to exist >0.5 ha privately owned plantations in the cell, and 3) after removing cells that did not fulfil previous criteria, the remaining cells still had to have a minimum of two adjacent cells. The number of moose damage was calculated for every cell and used as a response variable. Due to the possible autocorrelation, the average number of damage in neighbouring cells (2-8 cells) was also calculated and forced into every model (Dormann et al. 2007). A total of 15 land use and cover classes (**III**, Table 1a) were formed from MS-NFI data and the National Survey of Land digital map data and used as explanatory variables. In addition, ten sums of different original variable combinations (**III**, Table 1b) as well as the length of the roads of five different road classes (Digiroad database of the Finnish Transport Agency, FTA) were calculated for every cell and used as explanatory variables (**III**, Table 1a).

The number of non-damage cells was excessive in 1 km^2 and 25 km^2 cell sizes indicating zero inflated data (McCullagh and Nelder 1989). The mean number of damage was smaller than variance in all cell sizes, which possibly makes the data overdispersed (McCullagh and Nelder 1989). Therefore, we assumed the data to be zero-inflated negative binomially distributed (ZINB) (Zuur et al. 2009). In 100 km^2 cells, the number of moose damage cells was higher than non-damage cells in both study areas, but to preserve the comparability of the models among cell sizes, we used a ZINB-based modelling procedure for 100 km^2 cells as well.

As a modelling technique, we used zero inflated count models that are two-component mixture models, in which zeros can originate from two stochastic processes, the binomial process and the count process (Zuur et al. 2009). The data in **III** can contain zero (non-damage) cells for at least two reasons. First, so-called false zeros (Martin et al. 2005) might occur because a land owner had not applied for compensation, even though moose damage had occurred in a cell. Second, zero cells can also be so-called true zeros when there is no moose damage in a cell, even though it contains plantations susceptible to damage. In ZINB regression, the response variable Y_i ($i = 1, \dots, n$) has a probability mass function given by

$$P_r(Y_i = y_i) = \begin{cases} p_i + (1 - p_i) \left(\frac{\theta}{\mu_i + \theta} \right)^\theta, & y_i = 0, \\ (1 - p_i) \frac{\Gamma(\theta + y_i)}{\Gamma(y_i + 1)\Gamma(\theta)} \left(\frac{\mu_i}{\mu_i + \theta} \right)^{y_i} \left(\frac{\theta}{\mu_i + \theta} \right)^\theta, & y_i = 1, 2, \dots \end{cases} \quad (1)$$

Where $0 \leq p_i \leq 1$, $\mu_i \geq 0$, θ is the dispersion parameter with $\theta > 0$ and $\Gamma(\cdot)$ is the gamma function.

Zero inflated models use binomial general linear models (GLM) to model the probabilities of measuring zeros, and the count process is modelled by a Poisson, or as in study **III**, negative binomial distribution (Zuur et al., 2009). In ZINB modeling zero-part of the model is estimated with binary model, and conditional to that, estimates for the count part of the model are calculated. As a result, two models are produced. The first gives the best combination of variables for predicting zero-cases, i.e., non-damage cells in our data. The second model gives variables that best predict the number of damage.

Due to a large number of variables and numerous combinations that these variables can have, it was not feasible to test all parameter combinations. Furthermore, all parameter combinations are not necessarily meaningful, and therefore, ten hypotheses of the effects of different habitat types, as well as the length of roads, on moose damage were formed and tested (**III**, Table 2). All ten models (Model#1-Model#10) were built separately for all landscape sizes and both study areas. Each model was run as many times as needed to have only significant predictors, if any, in both the count and zero models. After producing all the models for all ten parameter combinations and landscape sizes, the final model candidate for each landscape size was formed by adding all the significant variables from models #1-#10 to the model and by recalculating models as many times as needed to only have significant predictors left in both the count and zero models. To account for the possible autocorrelation among adjacent cells, the average number of damage in neighbouring cells was forced on all models (Dormann et al. 2007). The comparisons of the models in each model step and final models were made with Akaike's Information Criteria, AIC. Models with $\Delta AIC > 2$ were considered to be significantly different from each other (Burnham and Anderson 2002).

Models were built by using R and package `pscl` for zero inflated negative binomial and binomial modelling (Zeileis et al. 2008). We used R-package `MASS` (Venables and Ripley 2002) for calculating 95% confidence interval for predictions. In calculating confidence intervals, we assumed a normal distribution of variables and used 2500 random samples per unit for each estimate. Finally, because we only modelled the main effects, we also calculated the marginal effects of variables and produced the graphs of the predicted number of moose damage for the variables included in the final models by using 25%, 50% and 75% quartile levels for the main covariables in models. Due to highly skewed distributions, 90 or 95% quartile levels were used for some variables. The proportion of plantations was used as the main variable in marginal effect calculations, because moose damage mostly occurs in these. For zero models, only the mean models of each significant variable were presented.

In study **IV**, bedrock class and soil type for compensated damage plantations, as well as NFI-control stands and NFI-damage stands, were assigned by overlaying the locations of plantations and NFI-plots with respective data. Elevation for data points was assigned similarly with the aid of NLS elevation model. The site type for damage plantations was derived from the register of compensated plantations and for control plantations – from NFI-plot data. Statistical differences in the distributions of different rock and soil classes, as well as forest types, between NFI-control stands, NFI-damage stands and compensated damage stands were tested with the `crosstabs` function of SPSS (20.0) by using the Pearson's Chi-square test for overall differences and z-test for column (dependent) proportions. The difference in altitudes between control and compensated damage stands were tested with the t-test for the equality of means (SPSS 20.0).

The frequency of moose damage might depend directly on the amount of plantations in some areas and the differences between areas due to other factors might be obscured. Therefore, in **IV**, we calculated the area of development classes 2–4 for each municipality in the study area by using MS-NFI data (corresponding to year 2005) and analysed the correlation between the number of damage and the proportion of development classes 2–4 with the Spearman’s non-parametric correlation test (SPSS 20.0). According to NFI definitions, development classes 2–4- refer to young seedling stands, advanced seedling stands and young thinning stands, respectively.

4. MAIN RESULTS AND DISCUSSION

4.1. Study I

Six models, including different combinations of variables from both plot, as well as stand level, were produced. As judged with the ROC curve (Receiver Operating Characteristic), specificity and sensitivity, the performance of the models was relatively good. ROC values ranged from 80.2 to 84.1. Sensitivity, i.e., the percentage of correctly predicted moose damage, ranged from 64.4 to 72.3. and for no-damage plots (specificity) from 77.2 to 81.6. Overall, the performance of all the models was fairly good, and the measures used for comparing models indicated that the differences among models were slight. When the probability of damage was calculated by deciles of risk, the models showed slight underestimates in the lowest deciles and overestimates in the highest deciles.

Overall, the probability of finding a damage on a plot increased along with the increasing number of living pines and deciduous trees. However, when the number of pines was divided into two categories, naturally regenerated pines and artificially regenerated pines, only the number of artificially regenerated pines was significant in the same model. Similarly, when the number of deciduous trees was divided into those shorter than pines and taller than pines, only the number of deciduous trees taller than pines was a significant variable in the same model. The number of artificially regenerated pines and deciduous trees taller than pines improved the performance of all models and were included in all the final models 2-4.

The probability of browsing increased along with an increasing number of living pines on plot-level models. Several studies have shown that the number of browsed pines increases when the number of available pines increase (Heikkilä 1991; Heikkilä and Mikkonen 1992; Ball and Dahlgren 2002). However, an increase in browsed biomass and, consequently, leader shoots have been found not to follow the 1:1 rate linearly, and therefore, the number of unbrowsed trees also increases along with density (Heikkilä and Mikkonen 1992; Heikkilä and Härkönen 1996; Ball and Dahlgren 2002). A logical conclusion of this result is that to ensure the adequate number of pines from the silvicultural point of view, the number of regenerated pines should be increased at least in areas with high moose damage risk. The models in **I** do not allow further conclusions about the number of pines required to ensure the silviculturally sustainable number of growable pines, but some earlier studies have suggested that if the number of pines is increased to some 4000-5000, pines it should ensure an adequate number of pines (Lyly and Saksa 1992; Ball and Dahlgren 2002).

However, the probability of browsing was strongly dependent on the soil preparation method (**I**, Fig. 3) indicating that the amount of pines needed to ensure an adequate number of growable trees is also dependent on the other properties of the stand like soil type. According to our model (**I**, Fig. 3), the probability of browsing was >0.5 when the number of pines exceeded about 2000-2800 living pines in plantations with the heaviest soil preparation. Assuming the smaller than 1:1 ratio (Ball and Dahlgren 2002), in the proportion of browsed pines, when the number of pines increases, the result in **I** confirms the recommendations to increase the number of regenerated pines, at least in sites with heavy soil preparation. As stated, however, the models in **I** do not allow for a more detailed assessment of the recommended pines to be given, therefore I only refer to the recommendations of Lyly and Saksala (1992) and Ball and Dahlgren (2002).

The second most important variable, predicting increasing browsing damage, was the number of deciduous trees taller than pines on a plot (**I**, Table 3). Also, the total number of deciduous trees on a plot increased the probability of browsing, but when the number of deciduous trees taller than pines was added to the model, the effect of the total number of deciduous trees was overridden. Overtopping deciduous trees have been detected to increase the browsing of pines in earlier studies as well (Heikkilä 1990; Bergqvist et al. 2014). The mechanism behind this has been attributed to the shading effect of tall deciduous trees on pines which may affect either the structural characteristics of pines, by making the trunk and shoots slender, or shading might change the proportions of chemical compounds in the trees more favourable for moose (Edenius 1993).

The results of the effect of deciduous trees on pine browsing have been variable in earlier studies. In most of the studies, deciduous trees either did not increase the browsing of pines or the increase was slight (Heikkilä 1990; Danell et al. 1991; Edenius 1991; Härkönen et al. 1998; Bergqvist et al. 2012; Bergqvist et al. 2014), while some studies have found a positive effect between most favoured deciduous species and pine browsing (Heikkilä and Härkönen 1996; Milligan and Koricheva 2013). According to the stand level models in **I**, the number of deciduous trees did not predict the proportion of browsed pines to increase when the average number of deciduous trees was used. This indicates that in addition to the height of deciduous trees, the within-stand density variation of deciduous trees might affect browsing probability. Dense deciduous tree groups around pines possibly provide moose with a better chance to maximize both energy and nutritional needs (Shipley 2010). In tree species-rich patches, moose are less selective, due to which, less preferred species are also browsed more than in less species-rich patches (Milligan and Koricheva 2013). From the theoretical point of view this is in accordance with plant association theory (Barbosa et al. 2009), according to which, the associational susceptibility occurs when lower quality plants get more frequently browsed, when there are high quality plants present in the same patch.

However, because of the lack of data of the browsing intensity of species other than pine, I can only conclude that the spatial variation in the distribution of deciduous trees within stands is possibly one factor affecting the selectivity of moose and, consequently, the browsing probability on pines. To conclude, the number of deciduous trees *per se* is probably not a determinative factor explaining browsing on pine. Instead, the effect of deciduous trees should be examined by various structural components like horizontal and vertical distribution of deciduous tree mixture in plantations in relation to pine.

The probability of moose damage was highest in stands with heavy mechanical soil preparation (MSP) (**I**, Fig. 3). Ploughing increased the browsing risk two to six times more as compared with slighter methods. To my knowledge, MSP has not been linked to moose

browsing in earlier studies, but browsing has been found to occur more on fertile sites (Ball and Dahlgren 2002). MSP has been commonly used in sites with a thick humus layer and fine-grained mineral soil to increase the soil temperature as well as to reduce the water content of the soil. Also, the mineralization of the nutrients is enhanced, and the effects of MSP have been shown to continue throughout the time that pines are available for moose browsing (Mäkitalo 1999). Therefore, one possible explanation for the higher browsing probability in heavy MSP sites is the better nutrient composition, higher biomass or the combination of these in trees. However, the higher magnesium in high browsing probability stands also suggests that the differences in soil nutrients among sites might partly explain browsing (see also Study IV).

The predicted probabilities of model 3 did not show abrupt changes as a function of moose density, the number of artificially regenerated living pines or the number of deciduous trees taller than pines and any of the soil treatment methods (I, Fig. 3). The probability of moose browsing was >0.5 only when the soil treatment was ploughing and the height of pines >75 cm. Because site type was not a significant predictor, the results further support the idea that MSP has an independent effect on the palatability of trees, at least in heavy MSP sites.

The stand-level models with averaged variable values indicated that it was possible to predict the number of browsed pines with about the same combinations of variables than what explained the probability of browsing on a plot level. The R^2 of the models varied from 0.35 to 0.39. However, the number of deciduous trees taller than pines and paludification were not significant variables in any of the final stand level models, indicating a loss of important parameters of within-stand variation.

Moose density, temperature sum and altitude m a.s.l. were all significant predictors of browsing. Due to high correlations between these variables, however, they could not be included in the same model. In addition, the replacement of these variables with each other in models affected on the performance of the model only slightly. However, moose density and altitude both had independent explanatory power when included in the same model. Lower elevation, higher temperature sum and high moose densities co-exist with high browsing probability in the south-west part of Lapland. Climatic factors, like snow cover and the length of the growing period, have been found to contribute to the variation in moose damage level (Hörnberg 2001b). Climatic and topographic factors are confounded in our study area and might have ambiguous effects on moose browsing. On the one hand, trees grow faster above the height when they are susceptible for moose browsing in higher temperature sum areas (Hörnberg 2001b), but on the other the overall productivity of the vegetation is also higher in high temperature sum areas, making these probably more favourable for moose.

4.2. Study II

A multivariate comparison of summer and winter home ranges indicated that there was a significant difference in habitat composition between seasons (0.74% of randomizations $<$ original Wilk's Λ), and therefore, seasons were analysed separately. Instead, a multivariate comparison of summer home range habitat compositions between males and females did not show difference and, therefore, sexes were pooled for the analysis.

4.2.1. Summer home ranges

In the multivariate comparison of pooled summer home range compositions with overall landscapes, only Wilk's Λ gave significant difference (0.02% of randomizations < original Wilk's Λ). Of all the habitat classes, only non-pine-dominated thinning forests were more abundant in home ranges than in the overall landscape (**II**, Fig. 2).

The multivariate comparison of habitat compositions in within-home range selection in summer showed a significant difference between sexes with all the statistics used (0.01% of randomizations < original Wilk's Λ , 2.38% for sum of log(F) and 0.01 for E statistics). Within home ranges, females used areas with more non-pine-dominated plantations and all kinds of thinning forests than found on home ranges, whereas pine-dominated plantations on peatlands/shrub land were less frequent around female locations. Around male locations, instead, there were significantly more mature forests and non-pine-dominated young forests than expected. There was also a similar trend towards pine-dominated thinning forests. Overall, although several comparisons of within-home range habitat use by both males and females showed significant differences, the differences in terms of proportions, were quite small, a maximum of only 2-3 percentage units.

Only a few studies have addressed moose summer habitat selection (Cederlund and Okarma 1988; Hjeljord et al. 1990; Bø and Hjeljord 1991; Heikkilä et al. 1996). In general, moose have been suggested to be able to use a variety of habitats in summer, instead of being strictly adapted to certain types of habitats (Hjeljord et al. 1990). Also, the results in **II** support this view because summer home ranges had a habitat composition close to that of the overall landscape. However, non-pine-dominated forests were more abundant in home ranges, and moose also used non-pine-dominated forests more within home ranges than expected (**II**, Fig. 3), which indicates that moose select areas with more fertile habitats in the summer (Bergström and Hjeljord 1987; Hjeljord et al. 1990). Also, mature forests have been suggested to be important habitats during snow-free periods due to important food plants in the dwarf shrub layer (Cederlund et al. 1980) and due to delayed phenological changes in food plants, especially in late summer (Hjeljord et al. 1990). The proportion of mature forests in home ranges was not different from that in the overall landscapes suggesting that mature forests do not direct moose summer range selection. However, within home ranges mature forests were used more than expected indicating these to be important habitats at scales smaller than home ranges.

4.2.2. Winter home ranges

Male and female winter home ranges did not show significant differences in habitat compositions, and therefore, sexes were pooled for the home range level analysis. The multivariate analysis showed a significant difference or a trend between pooled home range habitat compositions and overall landscapes (0.02% of randomizations < original Wilk's Λ , 7.2% for sum of log(F) and 3.22 for E statistics), and therefore, habitat classes were compared separately further on. Moose winter ranges included more pine-dominated, young forests than expected on the basis of the overall landscape habitat composition. In particular, pine-dominated plantations and thinning forests on peatlands were more abundant in moose home ranges than found in the overall landscape. Instead, there were significantly less settlements and agricultural land in moose winter ranges than found in the overall landscape (**II**, Fig. 2).

The multivariate comparison of within-home range habitat use between males and females showed a significant difference (3.12% of randomizations < original Wilk's Λ , 5.62% for sum of $\log(F)$ and 3.41% for E statistics), and therefore, further comparisons were made separately for both sexes. Habitat compositions around female winter locations contained significantly more non-pine-dominated plantations and thinning forests, and there were less settlements and agricultural fields than expected on the basis of home range habitat compositions. For males, the only difference between home range habitat compositions and the habitats around locations was that males used slightly more non-pine-dominated plantations than expected.

In winter snow covers most of the ground and shrub layer vegetation and moose use lower quality food nutritionally than in summer (Cederlund et al. 1980). Moose also spend less time feeding in winter than in summer, and therefore, moose should seek areas with relatively densely distributed feeding habitats to fulfil the energy needs even at the cost of nutritional demands (Cederlund 1989). Because a large proportion of winter range habitats were pine-dominated forests of young successional stages, the results in **II** seem to support the idea that moose respond to food quantity at the home range level (Cederlund 1989; Wallace et al. 1995). Within home ranges, instead, moose favoured areas with non-pine-dominated forests more, which indicates that, in addition to summer (Hjeljord et al. 1990), habitats with a mixture of tree species other than pine are also important in winter.

Pine-dominated peatland forests were the most abundant habitat class in winter home ranges, comprising one third of the range on average. There were also significantly more pine-dominated peatland forests in home ranges than found in the overall landscape. Within home ranges, however, peatland habitats were used in about the same proportions as found in home ranges. More peatlands have been found in areas with higher moose densities (Heikkilä and Härkönen 1993), and peatlands have been suggested to be important for moose all year around (Heikkilä et al. 1996). Heikkilä and Härkönen (1993) hypothesized that the mechanisms behind this might be linked to accelerated nutrient mobilization in drained peatlands, which affects, e.g., secondary metabolite production and/or increase in the growth of trees and other food plants. However, peatland forests are rather excessive in our study area and are more or less bound to be included in the large home ranges of moose. Also, the contradictory finding that peatland forests were used less than expected within home ranges might be due to the fact that peatlands within home ranges are abundant enough for moose to satisfy their needs related to peatland forests with relatively little use of these habitats (Johnson 1980). In conclusion, the results in **II** seem to support the idea of peatland forests being important habitats of moose winter ranges.

4.2.3. *HR habitat composition between sexes*

The comparison between male and female habitat compositions of home ranges did not show significant differences in summer, or in winter. Also, in within-home range habitat use, the differences were slight. Male summer locations tended to have more pine-dominated plantations on mineral soils, whereas there were more pine-dominated thinning forests around female locations. In winter, males were located more in pine-dominated forests with mineral soils than females.

The comparisons of habitat selection between sexes alone do not necessarily reveal the preference for certain habitat types, but the comparisons should also include within-sex habitat selection at both the home range level as well as at within-home range levels. This is because the habitat selection for both sexes is conditional to the habitat composition at the

order of the higher level of selection, not on the other sex. However, when also taking the results of the within-range habitat use of both sexes into account, males and females seem to use slightly different habitats both in summer and in winter. Females and males are spatially segregated during most of the year, and due to differences in body size, their energy and nutritional needs are probably different (Cederlund and Sand 1994). In winter, male moose used more pine-dominated habitats than females, which supports the hypothesis that males seek habitats with good food availability, rather than quality (Cederlund and Sand 1994). Other factors, like the effect of offspring, have also been shown to cause different habitat selection between males and females (van Beest et al. 2011), but the data at hand in **II** did not allow for further analysis of the effect of offspring.

4.2.4. *HR habitat composition between seasons*

In the comparisons of summer and winter home range habitat compositions, there were less only human settlements and agricultural fields in winter ranges than in summer ranges, but the differences between other habitat types were not significant. The negative correlations of other habitat classes and settlements (**II**, Table 2) further suggested that winter ranges are located in areas with less inhabited areas.

Migration distances between summer and home ranges in our study population were quite short, 15-25 km (Heikkinen 2000), which indicates that migration does not reflect any substantial variation in habitat characteristics or, e.g., snow depth. The start of spring migration temporally coincides with snow melt (Sandegren et al. 1985) and the emergence of fresh green vegetation (LeResche 1974), which in our study area, might be the proximate reason for moose to migrate closer to the coast and an earlier emergence of fresh vegetation in there. Thus, the habitat compositions do not necessarily have to show large differences between winter and summer seasons (Ball et al. 2001). However, winter ranges included slightly more pine-dominated habitats and, in particular, moose used more thinning forests within home ranges, which could be related to snow depth or the quality of snow (Ball et al. 2001).

4.3. Study III

Numerous models with significant variables could be constructed both for Ostrobothnia and Lapland and for all landscape sizes. However, when compared with Δ AIC, the differences between models were in most cases tens of AIC units (**III**, Annexes 3 and 4), indicating high variability in probabilities for models to have the best set of variables. For all landscape sizes and for both study areas, the final model had the lowest AIC.

A 'Mature forest' was a significant variable in five out of six final count models and in four zero models. An increase in the proportion of mature forests increased the number of damage and decreased the probability for damage in the landscape. Mature forests have been found to be important determinants of moose habitat selection in earlier studies as well (Bjørneraas et al. 2011; Olsson et al. 2011). In autumn, dwarf-shrubs are an important source of food before snow covers them (Cederlund et al. 1980), but in winter, mature forests do not necessarily provide much food. Instead, they might provide cover, but also lower energy costs due to lower snow depth or the quality of the snow (Ball et al. 2001; Bjørneraas et al. 2011). Regeneration areas in the private forests of Finland are relatively small, 1-2 hectares, and consequently, edge density is high, making food resources

(plantation) and cover (mature forest) adjacencies frequent. From the point of view of moose, forest landscapes might thus appear fine-grained which has been hypothesized to lead to higher browsing as compared with landscapes with coarser grain size (Edenius et al. 2002; Cassing et al. 2006).

Thinning forests affected the number of damage in various ways, depending on the landscape size and the type of thinning forests. Both in Ostrobothnia and Lapland, an increase in the proportion of thinning forests increased the number of damage. The mechanism for this is probably the same as for mature forests; thinning forests do not provide much food in winter, but they might provide better cover and lower energy costs due to lower snow depth or the structure of the snow (Bjørneraas et al. 2011). In Lapland, however, an increase in pine-dominated thinning forests decreased the number of damage although a posteriori test showed that there was a strong correlation between the proportions of pine-dominated thinning forests and pine-dominated plantations on mineral soil (Spearman's $\rho = 0.68$, $p < 0.001$). One explanation for this might be the legacy of post-WWII forestry that produced large areas of coniferous, mostly pine-dominated forests. Although, deciduous trees are a common mixture in regeneration areas, stands regenerated for pine might develop as more or less monocultures with little deciduous trees, at least in most less-productive sites. Therefore, the combination of pine-dominated thinning forests and pine-dominated plantations probably does not provide a more attractive habitat than habitats with a more diverse tree species composition (see also **II**). This again would cause there to be less damage in areas with a large amount of pine-dominated thinning forests.

The proportion of plantations alone was not a good predictor of the number of damage, and the difference between landscapes with and without damage was low (**III**, Annexes 1a, 1b, 2a and 2b). Instead, as stated above, the number of damage increased when plantations were embedded in a mosaic of mature forests. It has been suggested that modern forestry with relatively small treatment units has homogenized forest landscapes and increased the effective habitat area for moose (Edenius et al. 2002). This, in turn, could make the habitat use of moose relatively even across the favoured habitat types in a home range. Another plausible explanation is that because moose are not territorial, the density of moose can be locally substantial, and, at least in high moose density areas browsing leads to the depletion of food resources. This leads to a shift in habitat use (Van Beest et al. 2010), and as a consequence of several shifts, to a more or less even use of resources within home ranges.

There was less moose damage in plantations close to roads and inhabited areas than in plantations farther apart. In Ostrobothnia, inhabited areas were a significant predictor in models, whereas in Lapland, the length of connecting roads had the same effect as inhabited areas in OB. The negative effects of inhabited areas and roads were significant in 1 km² and 25 km² models, which implies that the disturbance of human activities reduces moose damage at these scales. However, there is a strong correlation between the proportion of inhabited areas and the length of roads and in both Ostrobothnia and Lapland (depending on the landscape size, Spearman's ρ 0.56-0.72, $p < 0.001$). Therefore, these two factors are at least partially intertwined.

Less moose damage has been found close to inhabited areas and roads (Repo and Löyttyniemi 1985; Heikkilä 1990), and moose have been found to move farther from inhabited areas and roads in times of high human activity (Lykkja et al. 2009; Neumann et al. 2013). Thus, the results in **III** together with earlier findings seem to support the hypothesis that human disturbance causes predator avoidance-like behavior of moose (Frid and Dill 2002). As a consequence, moose damage is also lesser in the vicinity of inhabited areas and roads. However, Ball and Dahlgren (2002) found moose damage to aggregate

close to densely trafficked road, probably due to the barrier effect. The results of **III** how there was less damage close to roads, are not necessarily contrary to those of Ball and Dahlgren's, but might be explained with different traffic density and the structure of roads. In Lapland, connecting roads are the most common road type after forest roads, and by the definition, connecting roads are 4-5 m wide with mainly asphalt pavement. Of all road types, moose-vehicle collisions are the most common in connecting roads (Finnish Transport Agency 2014), which confirms that connecting roads do not form barriers to moose. However, the vicinity of roads might not be favoured by moose which, again, is seen as the lower number of damage close to roads.

In study **II**, there were significantly more pine-dominated forests on peatlands in moose home ranges than on the average in the overall landscape, which coincides with the results of Cederlund and Okarma (1988), Heikkilä and Härkönen (1993) and Olsson et al. (2011). However, pine-dominated forests, either on drained or undrained peatlands, did not have any effect on the predicted number of moose damage in study **III**. Pine-dominated forests on mineral soil and pine-dominated forests on peatlands correlate significantly at 1 km² (Spearman's rho = 0.18, p<0.001) and 5 km² (Spearman's rho=0.39) landscapes, but peatland forests were significant variables in only four out of 30 models in Ostrobothnia. This is probably due to the fact that peatlands in the Ostrobothnia study area are quite excessive and peatlands inevitably become included in relatively large home ranges of moose (Olsson et al. 2011). Therefore, the finding in **II** could be explained by the fact that peatlands are more or less unavoidable habitats found in the mosaic of food and cover, although they might not provide much forage in winter. Another possibility is that if peatland forests are an important food resource for moose (Heikkilä and Härkönen 1993), they might reduce the amount of food obtained from plantations on mineral soil, and thus reduce moose damage risk in these. Indeed, peatlands indicated a negative effect on the number and occurrence of damage in 1 km² landscapes, but it should be remembered, however, that peatland forests were not significant variables in final models. However, the role of peatlands in moose ecology and their effect on moose damage still remains to be assessed in future studies of the actual use of peatland habitats by moose.

4.4. Study IV

In Study **IV**, the majority of the damaged stands were located in South-West Lapland and in eastern Lapland (**IV**, Fig. 2). In **IV**, the regional distribution of neither the number of damage nor the proportion of damaged plantations could be explained with the proportion of young forests of development classes 2-4.

When bedrock composition alone was studied, the overall distribution of rock classes was significantly different between compensated damage stands and NFI-control stands (**IV**, Fig. 3). Compensated damage stands were located more on nutrient-rich carbonate rocks, mafic and ultramafic rocks, but less on gneisses and felsic and intermediate rocks. Intriguingly, compensated damage stands were located also on quartzite class rocks more often, although these were classified as nutrient-poor rocks. The finding that compensated damage stands were located more often on nutrient-rich rocks was further confirmed when testing the frequency of compensated damage stands and control-NFI stands in the pooled nutrient-rich class rocks (classes 1-3) and nutrient-poor class rocks (classes 4-6). Pooled nutrient-rich class rocks were also found more frequently in all site types in compensated damage stands as compared with control NFI-stands (**IV**, Fig. 4). The proportion of

nutrient-rich rocks as underlying rock types, however, decreased along with the decreasing fertility of the site type.

Out of all site-types studied, mesic and sub-xeric were the most frequent ones (84-98% of the stands), and consequently, most compensated damage stands, as well as NFI-control stands and NFI-damage stands, were found in these. However, compensated damage stands, as well as damaged NFI-stands were located statistically significantly more often in mesic and sub-xeric sites than control NFI-stands. Instead, the most nutrient-rich as well as nutrient-poor site types were more common in both types of NFI-stands than in compensated damage stands. This seems to be contrary to the fact that moose prefer fertile sites, but one explanation might be that there were more nutrient-poor rocks in NFI-sites than in compensated damage sites (**IV**, Fig. 4), which might be reflected in the composition or amount of nutrients in trees (see also discussion of soil type below).

A large body of studies show that moose prefer more fertile habitats over poorer ones (Niemelä and Danell 1988; Heikkilä 1990; Heikkilä and Härkönen 1993; Ball and Dahlgren 2002; Månsson et al. 2009), but the site type itself seems to not be linked to, e.g., chemical compounds of the trees that affect the food selection of herbivores (Stolter et al. 2010). The consumption of biomass by moose is higher in fertile habitats, which provide better quality and a larger quantity of food, but also a larger collection of alternative food plants (Niemelä and Danell 1988; Heikkilä 1990; Heikkilä and Härkönen 1993; Månsson 2009). The results in **IV** indicated that the site type alone was not a very good predictor of moose damage, but the vulnerability to damage might partly result from underlying bedrock. Nutrient-rich rocks were more frequent in damaged plantations than in undamaged ones, whereas nutrient-poor rocks were more abundant in undamaged stands in all site types. This might at least partly explain why there were more undamaged stands in, e.g., the second most fertile site type, herb-rich heaths. Overall, the results suggest that the assessment of moose damage risk by site type should be done in association with bedrock composition. The results might also partly explain why the site type did not explain moose damage risk in **I**, but the moose damage risk was the highest in sites with heavy mechanical soil preparation.

Non-stratified soil (till) is the most common mineral soil type in Scandinavia (Koljonen and Tanskanen 1992), and consequently, most of the compensated damage stands as well as NFI-stands located on till soil (63.7-81.5% of the stands). Compensated damage stands, however, were located significantly more often on till than control NFI-stands, whereas these were more common on grained soils, peatlands and rocky soils. In Lapland, Scots pine and Norway spruce naturally regenerate on different soils. Norway spruce inhabit areas of fine-grained, Mg- and Ca-rich till, whereas Scots pine typically grows in more coarse-grained, dry, acidic and nutrient-poor soil (Sutinen et al. 2002; Sutinen et al. 2007; Sutinen et al. 2011). The analysis in **IV** did not separate soil types by site-type, but because more than half of the damaged stands were located on moist or sub-xeric heaths with nutrient-rich bedrock, presumably some of the pine plantations were located on former Spruce sites. Former spruce sites have been hypothesized to be sub-optimal growth sites for pine due to higher soil moisture (Sutinen et al. 2007). Heavy mechanical soil preparation have been often used in these sites to improve soil properties for pine, and the effect of soil preparation on the growth of pines has been shown to continue throughout the time that the leader shoots of pine are available for moose (Mäkitalo 1999). However, there is some evidence that the effect of MSP starts to decline after some 12-20 years, partly due to the excess leaching of some minerals like P, Ca and Mg (Sutinen et al. 2007). As a consequence, pines growing on moist, fine-grained soils might suffer from nutrient

imbalance, which together with excessive moisture, might lower pine resistance to herbivores (Phelan et al. 1996).

In SW Lapland, compensated damage stands were found at higher altitudes more often than control NFI-stands, whereas in the east and north, the situation was the opposite (IV, Fig. 6). In general, compensated damage stands were also more often located in areas that were sub-aquatic under the ancient phases of Baltic Sea and Lithorina Sea or under northern ice lakes ca. 7000-11,000 years ago. Because large parts of Lapland were under water by that time, some of the observed pattern might just be an anomaly. However, in some formerly submerged areas, soil formation is a result of the mechanisms caused by water. The finest particles of soil leached away from fell slopes and were deposited at lower altitudes (Lindroos 2003; Sarala and Rossi 2006). As a consequence, the top soil of low-lying areas often contains fine-grained material on the surface of non-stratified fine-grained till making these areas moister than could be deducted from the top soil layer only. As a consequence, these soils have atypically fresh vegetation for a superficially coarse-grained soil (Lindroos 2003), which probably makes them favoured habitats by moose. However, the data in IV did not allow for the direct investigation of this phenomenon, so it remains to be assessed in detail in future studies.

5. MOOSE RESOURCE SELECTION AT MULTIPLE SCALES AND IMPLICATIONS FOR DAMAGE RISK

The results in this thesis largely confirm the assertion that the habitat selection of moose and resources therein are affected by numerous factors, and that the selection takes place at several levels. But by which criteria do moose select their habitats and resources, and what are the implications for moose damage risk?

5.1. Region level

At a regional scale, some environmental conditions, like topography, bedrock and climatic factors, vary naturally. These factors partly affected the variation in the spatial distribution of moose damage. Moose damage was the most frequent in areas with the most nutrient-rich bedrock, Lapland Greenstone Belt in the east and Peräpohja Schist Belt in the SW Lapland. Also, post-glacial processes like soil deposition in submerged areas, have formed anomalies in soil properties that exist in patches, the size of which ranges from some hundreds of meters to some few kilometres. Bedrock and soil together form anomalies that extend to the regional level. Also, climatic factors like snow depth vary at a regional level, which is probably one factor explaining differences in the occurrence of damage in relation to altitude.

Although there are several factors affecting the regional distribution of damage, the effect of moose population density cannot be totally ruled out to be one more factor behind this. Due to the long period of time that both the moose damage data as well as NFI-data covered in IV, the effect of regional differences in moose population on the amount of damage could not be assessed. Population changes of moose and moose damage have been shown to correlate with each other at a regional level, but a direct connection between moose density and the level of damage has not been found (Hörnberg 2001b). It is

probable, that the primary production of vegetation is higher in the areas of nutrient-rich bedrock and soil, and the quality of food is also better than in low-production areas. Although it goes beyond the scope of this thesis, it can be hypothesised that the recruitment of moose population in these areas is more efficient, which calls for careful monitoring of moose population and moose damage.

In addition to factors that vary naturally, the amount and distribution of man-modified landscapes also vary from one region to another, and different factors affect the amount of moose damage in different regions. There was less damage close to inhabited areas in Ostrobothnia, but instead, less damage was found close to the connecting roads in Lapland. The amount of inhabited areas and the length of roads are strongly correlated, and these two factors are thus at least partly intertwined. Indeed, in Ostrobothnia, both of these factors had independent explanatory power in predictive models, but in Lapland, the length of roads was virtually the only factor that reduced the amount of damage. Manmade features in landscapes might play a different role from one region to another, depending on their amount and spatial distribution. The mechanism behind both factors, however, is that manmade landscapes and related disturbance cause trade-offs in the habitat use of moose. From the point of view of moose, the quality of the habitats of otherwise similar characteristics might be lower when close to manmade features than farther apart. This effect was found to extend up to some three kilometres, but because winter ranges of moose are also located farther from inhabited areas, I make a conservative inference, that the predictive effect of manmade features on moose damage might not reach that far.

5.2. Home range level

At the moose home range level, seasonal ranges did not have substantial differences in habitat composition, but in winter, moose selected ranges with abundant food resources. In summer, moose use a more diverse set of habitats due to their capability to use a variety of food plants. In addition to the amount of food, the spatial arrangement of food and cover are also important at the home range level. Landscapes with abundant food-cover adjacencies are favoured over more homogenous landscapes with a more narrow distribution of forest age classes or tree species composition.

In summer, moose are able to use a variety of food plants, perhaps due to which, the role of habitat type is not as important as in winter. However, in summer, moose seem to favour more fertile habitats than in winter. Fertile habitats provide better-quality food in terms of food quantity, but probably due to a more diverse plant species composition as well. In winter, when only a limited composition of plant food species is available, the bulk of food is more important to gain the energy needed. Male and female moose use slightly different types of habitats, which might be related to different energy needs between sexes, also to the effect of offspring.

Within home ranges moose use a more diverse set of habitats than what drives the habitat selection at the home range level. However, some basic criteria, like the amount of food at the home range level, must first be fulfilled.

The number of moose damage did not show any abrupt changes in relation to the habitat composition of landscapes at any scales studied. At least for the two smallest scales that refer to the approximate home range level (25 km²) and within home range level (1 km²), two explanations are plausible. First, it is possible that intensive forestry with relatively small treatment units has homogenized landscapes, and there is no significant variation in

terms of, e.g., patch size at the home range level and at larger scales. Empirical studies from Finnish forest landscapes have shown that the patch size of canopy-cover habitats is strongly skewed towards small patch sizes of 1-2 ha, and the differences in e.g. average patch size start to level off at the radii of 1-2 km (Löfman and Kouki 2003). However, edge density has been found to remain the same independent of the scale studied (Löfman and Kouki 2003). From the point of view of moose, landscapes thus show up fine-grained with abundant food resources in terms of plantations but also in terms of cover. Because the selection criteria regarding food-cover distances are rather similar among plantations, browsing does not concentrate on certain plantations more than others, but is more or less even among plantations.

Another plausible explanation is that because moose are not territorial, the density of moose can be locally substantial, and, at least in high moose density areas, browsing leads to depletion of food resources. Depletion, again, leads to shift in habitat use (Van Beest et al. 2010), and as a consequence of several shifts, to more or less even use of resources within home ranges.

5.3. Plantation and plant level

The results at the smallest level of selection, i.e., plant and plant communities, confirm the findings of earlier studies that moose browsing increases as the amount of food increases. In particular, overtopping deciduous trees in the immediate vicinity of pines increase the risk for pines to become browsed. Because a similar effect was not found for the total amount of deciduous trees at the whole plantation level, the results suggest that cleaning deciduous trees around the immediate surrounding of pines should be an adequate way to reduce browsing risk for single pines.

In general, pine plantations growing over nutrient-rich bedrock and fine-grained soils become browsed more frequently than plantations growing on nutrient-poor bedrocks and on more coarse-grained soils. More damage was also found on sites with heavy mechanical soil preparation. Soil preparation could just be a proxy for soil properties, and not the proximate reason for having more damage in heavy MSP sites. On the other hand the mineralization of nutrients is enhanced by heavy MSP, which might result in better palatability of plants in these sites. Another plausible explanation is that the availability of nutrients changes in the course of time and becomes imbalanced for trees, increasing the palatability. So far, the underlying mechanisms are not well known and remain to be assessed in future studies. From the browsing risk point of view, however, the result appears to be the same.

It is also plausible to consider, but could not be analysed in more detail from the data at hand, that if moose learn that the food gain is not better in surrounding plantations than in the present one, due to depletion of food, the properties of the plantation become less important. Therefore, at least in the most browsed areas, e.g., cleaning the plantation from deciduous trees does not necessarily lower the attractiveness of the plantation, but leads to the browsing of pines because of the lack of browsable resources in surrounding plantations. If this holds true, it is beneficial to leave deciduous trees to plantations or to have a denser plantation in general because the proportion of browsed biomass decreases in relation to increased biomass. As a consequence, relatively more trees will be saved from browsing.

At least in high moose density areas the degree of damage in a single plantation might thus be a result of a process, where it is not profitable for moose to move to surrounding plantations, but, instead, the same food gain is acquired even if the browsable food in the plantation is quantitatively and qualitatively non-optimal. This leads to variation in the damage degree but, also to confusing results about the effect of plantation characteristics to damage risk.

6. FUTURE PROSPECTS

Satellite image-based land use and cover classification is not very accurate at the level of single pixels and small areas (Tokola and Heikkilä 1997). In particular, the precision of the classes, i.e., how detailed the information is that they provide, about the structural characteristics of forests and other habitats, is rather low. Novel remote sensing techniques, like airborne laser scanning (ALS) (Packalén and Maltamo 2007), provide more detailed data of trees and other vegetation than satellite data used in this study (II-III). ALS data have been shown to explain the habitat selection of moose at small spatio-temporal scales (Melin et al. 2013), which gives promise that new data might be valuable for studying some questions that remained correlative in this thesis further. In particular, studies of the effect of different kinds of mosaics comprising plantations and other types of forests and peatlands on the behaviour of moose under varying environmental conditions, like snow depth, would give new insights to, e.g., damage risk. However, accurate moose location data with detailed habitat data should be accompanied by actual resource use data (Owen-Smith et al. 2010), like the use of different food items, to gain more insight into mechanisms underlying moose habitat use and resource selection.

Technologies like Geographic Information Systems, the internet and the availability of the ever-growing and qualitatively more precise environmental data, provide, in principle, tools to link information together from different sources and to combine the data for moose management purposes or damage risk assessment. As an example, bedrock-soil composition is, in practise, permanent property of the stand and serves as a starting point for the damage risk assessment pretty much as such. On the other hand, forested habitat types of different tree species also drive the habitat selection of moose at home range and within-home range levels. This gives promise that by analysing these factors together with the state-of-the-art modelling techniques, it is possible to assess moose damage risk at scales down to the level of plantation. The resulting damage risk models can further be presented in digital maps and be updated along with updated forest data, and utilized in, e.g., forest planning.

Finally, in spite of the technological development and the increasing availability of accurate data, scientifically rigorous research that assesses various questions related to, e.g., resource selection remains as an indispensable starting point to acquire information for also applied purposes.

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