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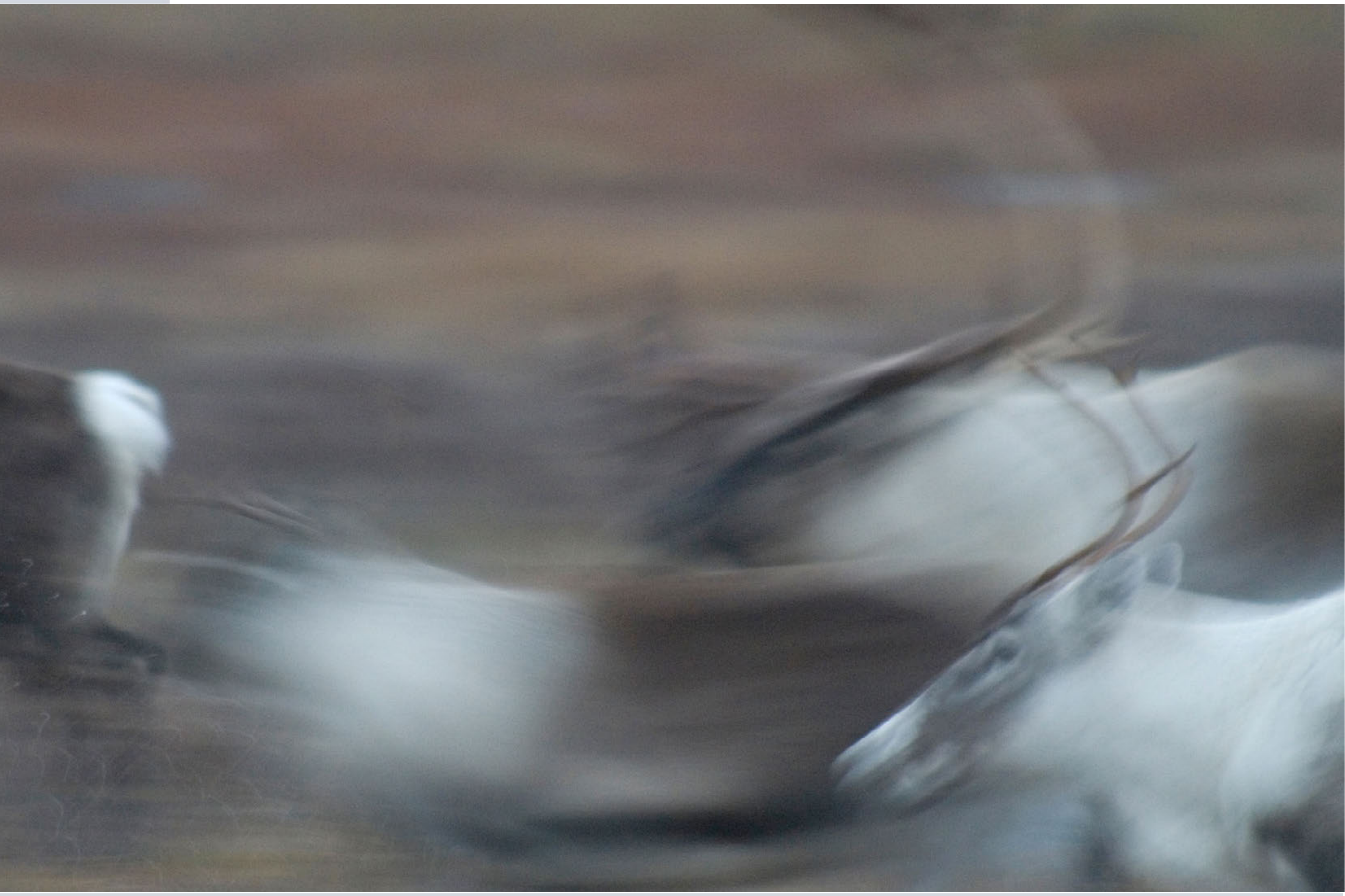
Habitat use of wild Reindeer (*Rangifer t. tarandus*) in Hardangervidda, Norway

Tobias Falldorf



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Habitat use of wild Reindeer (*Rangifer t. tarandus*) in Hardangervidda, Norway

Tobias Falldorf

Dissertation submitted to the University of Hamburg

Dissertation with the aim of achieving a doctoral degree
at the Faculty of Mathematics, Informatics and Natural Sciences,
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submitted by Tobias Falldorf
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Preface

This dissertation is submitted to the Faculty of Mathematics, Informatics and Natural Sciences (MIN) of the University of Hamburg for the degree of Doctorate in Natural Sciences (Dr. rer. nat.). The research leading to this thesis has been carried out at the Norwegian Institute for Nature Research (NINA), Trondheim, Norway, and the doctorate study was affiliated to the Department of Earth Sciences, Institute of Geography, at the University of Hamburg. My work was embedded in the broader research project *Effekter av tekniske inngrep og forstyrrelser i tilknytning til Rv7 over Hardangervidda* (Effects of technical interferences and disturbance associated with Highway 7 (Hw7) over Hardangervidda), financed by the Norwegian Public Roads Administration (NPRA) in cooperation with the Research Council of Norway (RCN), the Norwegian Directorate for Nature Management (DN) and the Norwegian Institute for Nature Research (NINA). The main goal of the project was to study the impact of Hw7 on wild reindeer, both spatially and over time.

This thesis has been supervised by Jürgen Oßenbrügge (Department of Earth Sciences, University of Hamburg), whom I sincerely thank for all his help, encouragement, patience and trust during my study period. Within NINA I am in great debt to Olav Strand, without whose bright ideas, creativity and great knowledge of wild reindeer and their biology this work would not have been possible. I could not have hoped for a more inspiring and enthusiastic advisor to support me and it has been a pleasure to work with him throughout - be it in front of computers or on the back of snowmobiles.

During my time in Norway, I have been lucky enough to meet and work together with many nice and knowledgeable people, who lifted this work significantly and whom I would like to express my gratitude to. While I cannot name everyone, I would like to thank some in particular. Erling Solberg for all his kindness and support, for giving me profound insights in biology and nature (and for making me sweat on skis and chase roe deer in all kinds of weather). Hans Tømmervik for all his valuable help on alpine vegetation and remote sensing. Jiska van Dijk and Roel May as fellow PhD-students for greatly enhancing my learning curve. Manuela Panzacchi, Bram Van Morter and Erlend Nilsen have to be thanked for their ideas and for their comments on the manuscript.

Sincere thanks have to go to Rune Engeseth from the Norwegian Water Resources and Energy Directorate (NVE) for providing snow data, Torfinn Evensen from the Norwegian Trekking Association (DNT) for sharing data on the touristic use of Hardangervidda and the Norwegian Meteorological Institute (met.no) for making weather data accessible for modeling.

I am also grateful to Kjetil Bevanger, Eldar Gaare, John Linnell and Sigbjørn Stokke from NINA and Bjørn Iuell from NPRA for their ideas and support. Inga Bruteig and Norunn Myklebust from NINA have to be acknowledged for putting their trust in me. Frank Hansen, Dag Vegard Gullbrekken and Stein Hoem are thanked for their help with IT and GIS. Bjørn Haugen and Statens naturoppsyn (SNO) have made fieldwork pleasant and shared their deep knowledge of reindeer and Hardangervidda with me.

Finally, I would like to thank Jutta Meiforth for all her support, irreplaceable practical and theoretical help on plants and vegetation communities and for measuring lichen mats together in the field with me for so many days.

I dedicate this thesis to my parents. Thank you for supporting me no matter what I do.

Hamburg, May 2012

Tobias Falldorf

Abstract

As a migratory species living in the (sub-)arctic reindeer are highly sensitive to the effects of habitat fragmentation, cumulated human disturbance and climate change. In a rapidly changing environment a better understanding of their habitat use is therefore crucial for the long-term conservation of wild reindeer and in order to improve management plans. In this thesis I present research on the habitat selection of wild reindeer (*Rangifer t. tarandus*) in Hardangervidda, Norway, focusing on (A) how seasonal differences in distribution and movement patterns of wild reindeer can be described and quantified (chapter 2), (B) how the land cover of the alpine study area can be classified accurately using selected parametric and non-parametric classifiers on satellite imagery with and without ancillary data (chapter 3), (C) how the current status of lichen pastures can be mapped and quantified (chapter 4) and (D) how reindeer habitat selection can be modeled at different temporal and spatial scales (chapter 5).

To answer question (A), 28 wild, female reindeer in Hardangervidda were equipped with global positioning system collars (GPS). Based on the recorded tracking data, a method is presented to detect and define annual seasons empirically (floating cut-off points within correlated random walks (CRW) models). Reindeer are shown to perform seasonal migrations within the study area and the underlying movement patterns are described and quantified using multiple parameters (directionality and regularity of movement, activity level and size/stability of seasonal home range). Significant seasonal differences in movement patterns are detected and related to (potential) underlying factors (climate, differences in spatial distribution of resources between seasons, human disturbance and social behaviour of reindeer).

Answering question (B), a method for land cover classification within a mountainous area is proposed based on Landsat imagery and ancillary data (DEM and derivates, images from different seasons). Relevant land cover classes for resource selection of wild reindeer are defined and the study area is classified accordingly. The kNN classifier demonstrates superior results as compared to maximum likelihood and decision tree classifiers. It is shown, that the use of ancillary data can significantly improve the overall classification accuracies for all tested classifiers and the class accuracies of the vast majority of classes.

Question (C) is addressed proposing a new Lichen Volume Estimator (LVE) to predict lichen volume from a two-dimensional Gaussian regression model using the Normalized Difference Lichen Index (NDLI) and the Normalized Difference Moisture Index (NDMI). The model is parameterized using ground measurements equally distributed across a gradient ranging from 0 to 80 liters of lichen/m^2 and is validated with a 10-fold cross validation procedure, indicating a high parameter stability. Using the LVE, the current status of lichen biomass in Hardangervidda and its spatial distribution is estimated and related to the spatial distribution of reindeer.

To answer question (D), the habitat selection of reindeer is modeled for three core seasons (summer, winter, calving) and at two spatial scales (large-/small-scale) using resource selection functions (RSF). Depending on scale, RSF are build as logistic regression models (LR, large-scale) and discrete choice models (DCM, small-scale). Model results make possible to describe reindeer habitat selection as specific functional responses towards six significant factor groups (land cover, lichen volume, terrain, disturbance, snow depth and wind direction) and to quantify the relative importance of the single factors. The model results are discussed in relation to reindeer biology. Based on the estimated factor coefficients of the large-scale models, habitat preference maps are calculated for the selected seasons. On the basis of these maps I discuss which/why resources/areas are used and which/why potential resources/areas are unused. Simulation models for altered levels of human disturbance and snow depth are used to illustrate the effect of these factors. A profound influence of human disturbance (summer) and snow conditions (winter) on reindeer's seasonal habitat selection can be shown. I discuss the management and conservation implications of the model results and give future prospects.

Zusammenfassung

Als wandernde, (sub-)arktische Art reagieren Rentiere besonders empfindlich auf zunehmende Habitatfragmentierung, kumulierte menschliche Störeinflüsse und klimatische Veränderungen. Für die langfristige Erhaltung der wildlebenden Rentiere ist daher ein verbessertes Wissen über ihre Habitatnutzung entscheidend, auch im Hinblick auf die Anpassung von Managementplänen. In der vorliegenden Arbeit stelle ich Forschungsergebnisse über die Habitatselektion wildlebender Rentiere (*Rangifer t. tarandus*) in der Hardangervidda, Norwegen, vor, mit Fokus darauf, (A) wie saisonale Unterschiede in der Verteilung und den Bewegungsmustern von Rentieren beschrieben und quantifiziert werden können (Kapitel 2), (B) wie die Landbedeckung des alpinen Untersuchungsgebietes mittels parametrischer und nicht-parametrischer Klassifikatoren jeweils mit und ohne Zusatzdaten klassifiziert werden kann (Kapitel 3), (C) wie der gegenwärtige Status der von Flechten dominierten Weidegebiete kartographiert und quantifiziert werden kann (Kapitel 4) und (D) wie die Habitatselektion von Rentieren zu unterschiedlichen Jahreszeiten und unter Verwendung verschiedener räumlicher Maßstäbe modelliert werden kann (Kapitel 5).

Um Frage (A) beantworten zu können, wurden 28 wildlebende, weibliche Rentiere mit GPS-Halsbändern ausgestattet. Auf Basis der aufgezeichneten Tracking-Daten wird eine Methode vorgestellt, um Jahreszeiten empirisch zu bestimmen (gleitende cut-off Punkte innerhalb von correlated random walk (CRW) Modellen). Die Ergebnisse zeigen, dass Rentiere im Untersuchungsgebiet saisonale Wanderungsbewegungen vollziehen. Die zugrunde liegenden Bewegungsmuster werden unter Verwendung multipler Parameter beschrieben und quantifiziert (Gerichtetheit und Regelmäßigkeit der Bewegung, Aktivitätslevel und Größe/Stabilität der saisonalen Reviere). Dabei zeigen sich signifikante saisonale Unterschiede in den Bewegungsmustern, die dann mit ihren möglichen Ursachen in Beziehung gesetzt werden (Klima, Unterschiede in der räumlichen Verteilung von Ressourcen zwischen den Jahreszeiten, menschliche Störeinflüsse, Sozialverhalten der Rentiere).

Zur Klärung von Frage (B) wird ein Verfahren zur Klassifizierung der Bodenbedeckung in einem alpinen Gebiet entwickelt, das auf der Nutzung von Landsat-Bildern und Zusatzdaten basiert (DEM und dessen Derivate, Satellitenbilder aus verschiedenen Jahreszeiten). Mit Hilfe dieses Verfahrens werden die zuvor für die Ressourcenauswahl von wilden Rentieren als relevant definierten Bodenbedeckungsklassen erkannt, und das Untersuchungsgebiet wird klassifiziert. Der kNN Klassifikator erzielt dabei eine signifikant höhere Genauigkeit als die alternativ getesteten Maximum Likelihood- und Entscheidungsbaum-Methode. Zudem wird gezeigt, dass die Verwendung von Zusatzdaten die Klassifizierungsgenauigkeit weiter verbessern kann, sowohl im Hinblick auf die Gesamtgenauigkeit aller getesteten Klassifikatoren als auch auf die Klassengenauigkeit der großen Mehrheit der Klassen.

Um Frage (C) zu beantworten, wird ein neu entwickelter Lichen Volume Estimator (LVE) vorgeschlagen, der es ermöglicht, das Flechtenvolumen durch Anwendung eines zweidimensional gaußförmigen Regressionsmodells zu schätzen, das auf dem Normalized Difference Lichen Index (NDLI) und dem Normalized Difference Moisture Index (NDMI) beruht. Das Modell wird mit Hilfe von Messpunkten aus dem Untersuchungsgebiet parametrisiert, die gleichmäßig über einen Gradienten von 0 bis 80 Liter Flechten/m2 verteilt sind. Die Modellüberprüfung mittels einer 10-fachen Kreuzvalidierung ergibt eine hohe Parameterstabilität. Mit Hilfe des LVE wird die aktuelle Flechtenbiomasse in der Hardangervidda sowie deren räumliche Verteilung geschätzt und die Ergebnisse anschließend mit der räumlichen Verteilung der Rentiere verglichen.

Zur Beantwortung von Frage (D) wird die Habitatnutzung der Rentiere für drei Kern-Jahreszeiten (Sommer, Winter, Abkalben) und in zwei räumlichen Maßstäben (groß- und kleinräumig) mit Hilfe von Ressource Selection Functions (RSF) modelliert. In Abhängigkeit der Maßstäbe werden die RSF als logistische Regressionsmodelle (LR, kleinräumig) oder Discrete-Choice-Modelle (DCM, großräumig) aufgebaut. Die Modellergebnisse ermöglichen es, die Habitatauswahl der Rentiere als spezifische funktionelle Reaktionen auf sechs signifikante Faktorgruppen zu beschreiben (Bodenbedeckung, Flechtenvolumen, Gelände, menschliche Störeinflüsse, Schneehöhe und Windrichtung) und die relative Bedeutung der einzelnen Faktoren zu quantifizieren. Beides wird mit Blick auf die biologischen Verhaltensweisen von Rentieren analysiert. Zusätzlich werden die geschätzten Faktorkoeffizienten der großräumigen Modelle dazu verwendet, für die ausgewählten Jahreszeiten Karten zu errechnen, die den Habitatwert der Gebiete der Hardangervidda unter den gegebenen Bedingungen widerspiegeln. Ausgehend von diesen Karten, erörtere ich, welche Ressourcen/Gebiete derzeit genutzt/nicht genutzt werden und warum. Anhand von Simulationsmodellen kann gezeigt werden, dass menschliche Störungen (Sommer) und Schneeverhältnisse (Winter) einen entscheidenden Einfluss auf die saisonale Habitatauswahl der Rentiere haben. Abschließend diskutiere ich die Auswirkungen der Modellergebnisse für das Management und den Schutz von Rentieren und benenne weiteren Forschungsbedarf.

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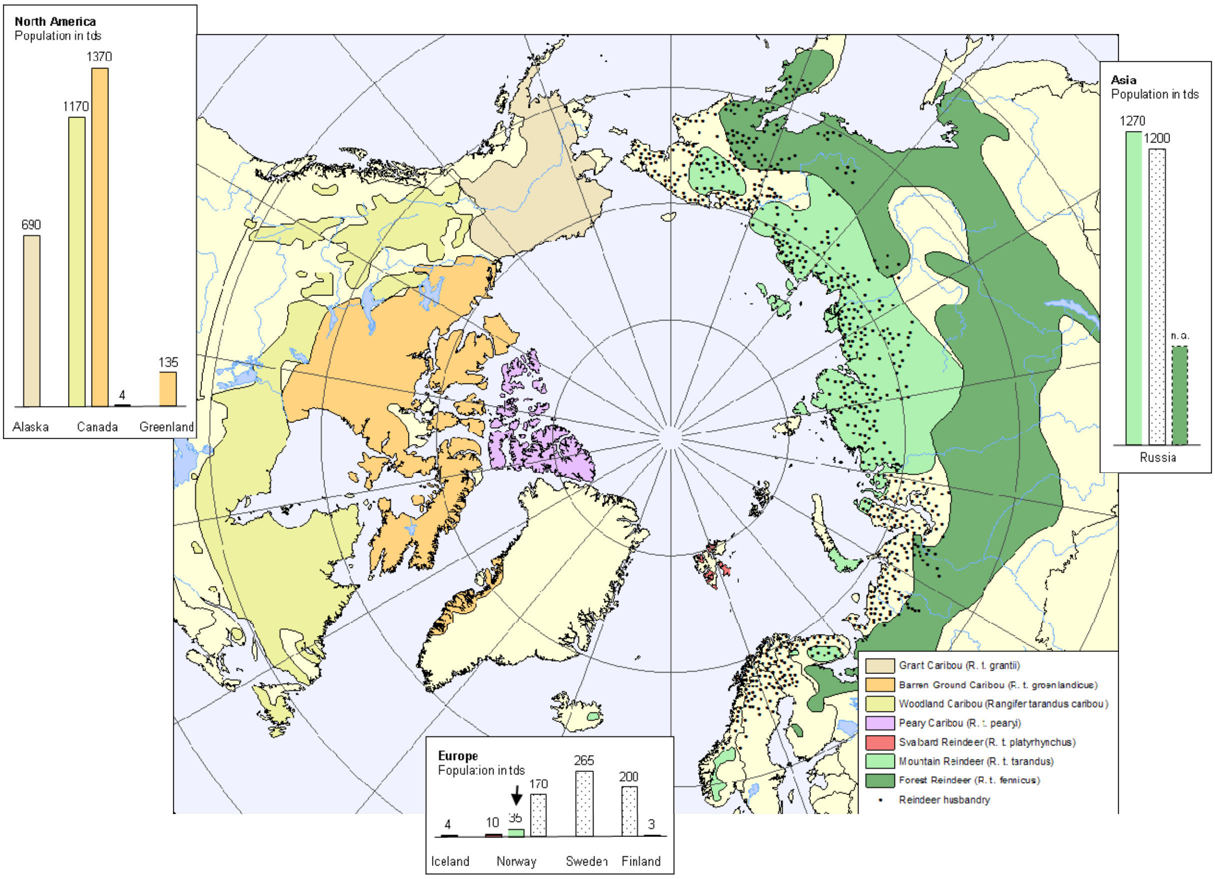
1 General introduction

1.1 Background

Status and conservation challenges for wild reindeer in Norway and Scandinavia

Reindeer and caribou (*Rangifer tarandus*) are one of the great migratory species on earth – with respect to herd sizes, total distribution ranges and length of annual migrations (Skogland 1994b; Berger 2004). Seven subspecies show a circumpolar distribution with three to four million caribou in North America and Greenland and a reindeer population between three to five million animals inhabiting Siberia, Fennoscandia, Iceland and Svalbard (see Map 1-1).



Map 1-1: Global distribution, population estimates and subspecies of *Rangifer tarandus*[1]

While caribou in North America never have been tamed, semi-domesticated reindeer in Europe and Asia constitute app. half of the total population size within these regions. With about 600 thousand animals reindeer husbandry plays an important role for the native population in northern Fennoscandia, both, culturally and economically[2] (Skogland 1994b; Bevanger & Jordhøy 2004). Besides two smaller populations of forest reindeer in Finland and Karelia, the

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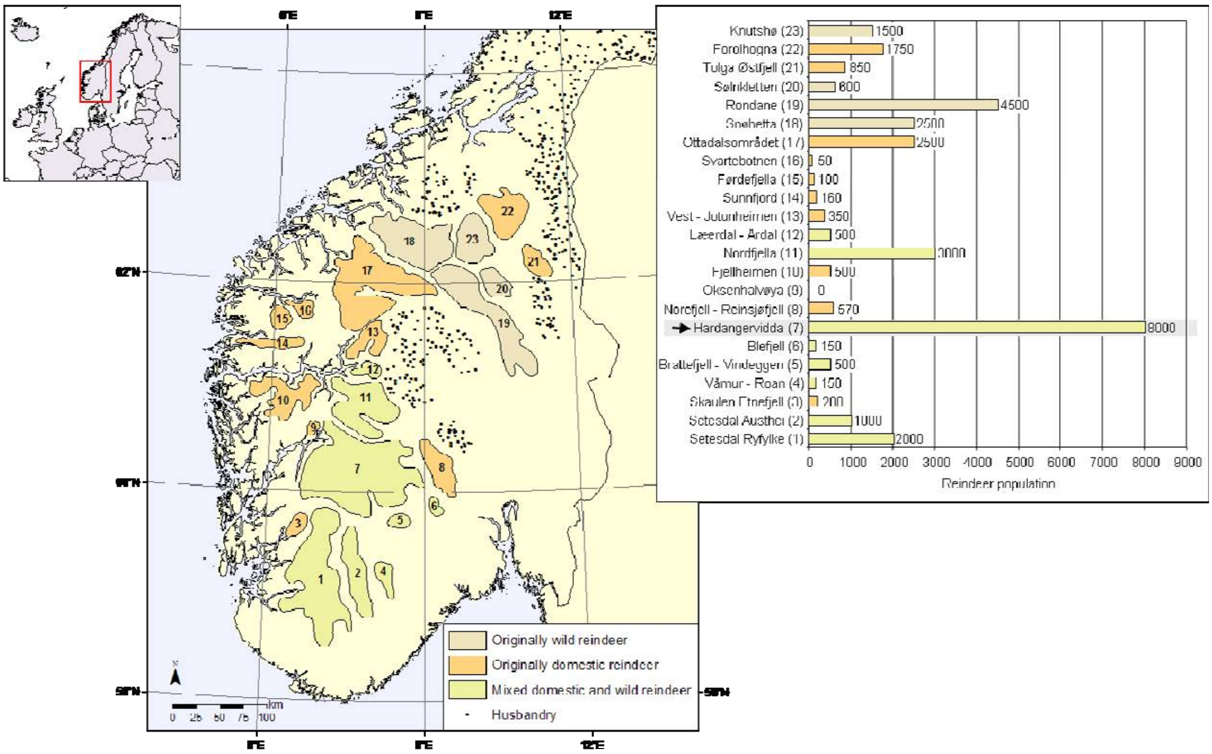
[1] Based on Bevanger & Jordhøy (2004); Skogland (1994b); CARMA (2010).

[2] For the role of reindeer husbandry in southern Norway see e.g. Helland & Stokstad (2005).

only significant population of wild reindeer left in Fennoscandia is located in the mountain areas of southern Norway with a total size of app. 35,000 animals (Skogland 1994b; Bevanger & Jordhøy 2004). This number at present is divided into 23 more or less isolated populations with local estimates ranging from 50 animals in Svartbotnen to 8,000 animals in Hardangervidda (see Map 1-2).



Map 1-2: Distribution, population estimates and genetic origin of reindeer herds in southern Norway[3]

Former migration corridors between the current reindeer areas have been suggested based on studies of pitfall systems and other archeological sites (Wildhagen 1954; Vaa 2002; Jordhøy, Binns & Hoem 2005; Jordhøy 2007, 2008). These studies indicate that prior to industrial development the current reindeer areas were connected and inhabited by two to three larger populations, moving across longer distances between adjacent mountain systems.

Reindeer and caribou are migratory species in general (Berger 2004), but some of the populations show sedentary, nomadic or semi-migratory behaviors (Bergman, Schaefer & Luttich 2000)[4]. Annual migrations have been described as a strategy for optimizing access to changing temporal resources (forage, shelter, etc.) within space while minimizing the risk of mor-

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[3] Based on Skogland (1994b); Bevanger & Jordhøy (2004) and DN (2010a).

[4] Note that spatial behavior of animals rather follows a continuum and exact categorization can therefore be difficult. Just recently, Bunnefeld *et al.* (2011) proposed a model-driven approach to distinguish between migratory, semi-migratory, nomadic and sedentary behaviour.

tality factors like predation or extreme weather events (Skogland 1994b; Fryxell, Greever & Sinclair 1988). In southern Norway reindeer habitats are mainly shaped by two natural environmental gradients: First, a strong altitudinal gradient separates the rugged mountainous terrain above the tree line from its neighboring valleys, which are dominated by forests (Fremstad 1997). Second, a prominent east-west-gradient leads to a more continental climate in the eastern parts of Norway while the western parts are influenced by a more oceanic climate (e.g. Bakkestuen, Erikstad & Økland 2008; Moe 1995). In consequence reindeer migration in Norway has been believed to naturally follow an annual cycle from less snow covered, lichen-rich winter pastures in the east to more graminoid-rich, insect-free summer habitats in the west and that this behavior would still be visible to a larger extent, if habitat availability was not constrained by anthropogenic factors (Skogland 1989b).

Since reindeer generally show a migratory or nomadic lifestyle, they are especially vulnerable to habitat fragmentation because human land use activities can prevent access to valuable forage resources and block important migration corridors (Berger 2004; Berger, Cain & Berger 2006; Sawyer *et al.* 2009)[5]. Since the beginning of the 20th century Norway has suffered a dramatic loss of wilderness areas due to an increase in human land use through traffic systems, human settlements, agricultural use, tourist infrastructure and installations for hydroelectric power production (see Map 1-3).

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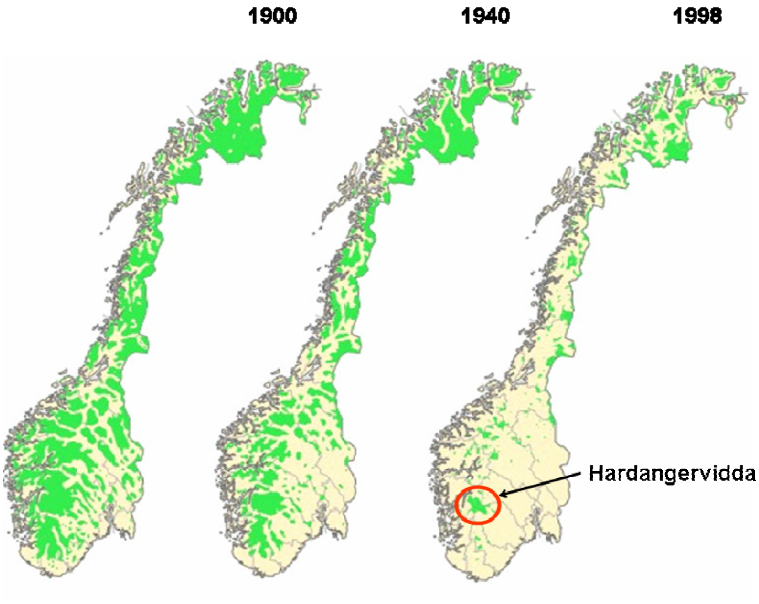
[5] It is well known that reindeer react very sensitive to human infrastructure (e.g. mountain roads and/or cabins) (see e.g. Thompson 1972; Skogland & Grövan 1988; Skogland 1994a; Jordhøy *et al.* 2000; Iuell & Strand 2005 or Iuell, Bevanger & Strand 2005) and possible consequences of new build infrastructure therefore have to be monitored closely (see. e.g. Taugbøl *et al.* 2001; Klein 1971, 1980; Jordhøy & Strand 2004; Jordhøy *et al.* 2002a/b/c or Jordhøy 1987). For a more general discussion on the relative effects of habitat loss and fragmentation on population extinction see also Fahrig (1997, 2003).



Map 1-3: Loss of wilderness in Norway: areas more than 5 km away from human disturbance[6]

As a result of this ongoing fragmentation of habitats through human activities (see e.g. Aanes *et al.* 1996; Bevanger & Henriksen 1996 or Damarad & Bekker 2003)[7] reindeer populations have become increasingly more isolated from one another. While a high focus has been put on small populations and endangered species in this respect[8], far less attention has been paid to larger populations, especially of migratory or nomadic species.

Since migrations, in evolutionary terms, can be explained as adoptions to environmental gradients and avoidance of predators (Berger 2004; Berger, Cain & Berger 2006; Sawyer *et al.* 2009), it is possible to suggest that fragmentation and the inability to undertake migrations might have serious effects on such populations: E.g. a suboptimal distribution and/or a possible disconnection between summer and winter pastures within smaller entities could potentially lead to a decreased carrying capacity of habitats (Vistnes & Nellemann 2008; Jordhøy *et al.* 1996). Likewise, the inability to minimize the stochastic risks of extreme weather events (e.g. severe icing conditions in winter, high snow depth, avalanches) through migration could increase mortality of species like reindeer in such events (Chan *et al.* 2005; Weladji & Holand 2006), even more so, since recent studies indicate that climate change is likely to amplify the above risks as both, precipitation and surface icing, are likely to increase (see e.g. Turunen *et al.* 2009; Stien *et al.* 2010; Aanes *et al.* 2002; Weladji & Holand 2006; Weladji *et al.* 2002; Arctic Climate Impact Assessment 2004; Roald *et al.* 2003; Hansen, Aanes & Sæther 2010)[9].

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[6] Based on Skjeggedal *et al.* (2005); DN (2010b).

[7] See e.g. Bergerud (1974a) or Bergerud, Jakimchuk & Carruthers (1984) for a North American perspective.

[8] E.g. by emphasizing the increased extinction risk through a reduction in genetic diversity (Frankham, Ballou & Briscoe 2010).

[9] For a more general perspective on ecological effects of climate fluctuations see e.g. Stenseth *et al.* (2002).

In consequence, cratering during winter could become more difficult for reindeer (Skogland 1978; Fancy & White 1985; Collins & Smith 1991).

An increased pressure on reindeer habitats and a loss of important grazing areas due to human developments (Wolfe, Griffith & Wolfe 2000; Vistnes & Nellemann 2008) make modern reindeer management[10] into a complicated task, including land use restrictions, rural development plans and human land use in general. In this context, a better understanding of reindeer habitat use is crucial in order to improve management plans and to secure the long-term conservation of wild reindeer.

Cumulated human disturbance and its effects on habitat use

The effects of human disturbance on wild animals have traditionally been studied through modifications of single stimuli such as roads, power lines, cabins or others on behavior or physiological parameters (see e.g. Wolfe, Griffith & Wolfe 2000; Reimers 2001; Strand *et al.* 1997; Vistnes *et al.* 2004; Mahoney & Schaefer 2002; Berntsen *et al.* 1996; Bleich *et al.* 1990; Colman, Jacobsen & Reimers 2001; May *et al.* 2006; Rowland *et al.* 2000 or Côté 1996)[11]. Following this approach, a range of studies has assessed direct impacts of such stimuli on physiological reactions (heartbeat, blood pressure, etc.) or changes in behavior (feeding time, flight distances, etc.) at an individual level (e.g. Jacobsen, Colman & Reimers 1995 or Reimers *et al.* 1994, 2000). Some efforts have also been made in order to extrapolate from such results to effects at the population level (e.g. Aastrup 2000; Klein 1971).

More recent studies have tried to analyze wildlife-human interactions by studying the cumulative effects of disturbance on wildlife (see Wolfe, Griffith & Wolfe 2000 for a review on *Rangifer*). Cumulative effects are defined as the alteration of growth, reproduction, survival or behavior triggered by the sum of external factors that act upon a population (Nellemann *et al.* 2001c; Vistnes & Nellemann 2008). Examples of such effects can be alterations in density, the level of competition, changes in mortality rates, body condition and reproduction as well

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[10] The management system of wild reindeer resembles a theoretical system of threshold harvesting (Lande, Sæther & Engen 1997) where a variable number of animals are removed annually in order to maintain the population at a constant size (termed the escapement population size). The development and application of such harvest strategies are strongly linked to density dependent population processes and the concept of sustainable yield. The theoretical and empirical relationship between ungulate populations, their forage resources, and the effects of high density on reproduction, survival and body size was largely developed during the 1980's. Albeit its acceptance and popularity amongst managers, the empirical tests of these relationships and the long-term effects on habitats by high-density populations still remain largely untested, however (Sinclair 1997).

[11] For the impact assessment of petroleum exploration in North America see e.g. Shideler (1986) and references therein. A number of studies have also analyzed the reaction of reindeer and caribou to aircraft disturbance and military noise (see Larkin 1994 and references therein).

as spatial impacts on vegetation. The strength of this approach is that the effects of disturbance are studied at the same scale where management operates – the population or landscape level. In addition, effects triggered by cumulative disturbance are often visible over large spatial and temporal scales (Walther 1969; Dill & Houtmann 1989; Bonenfant & Kramer 1996; Frid & Dill 2002). This type of studies also bridges studies of human disturbance with density dependent population processes (e.g. Gill, Norris & Sutherland 2001; Frid & Dill 2002). At its beginning the study of density dependence was limited to effects of population dynamics and reductions of vital rates in high-density populations (Bonenfant *et al.* 2008; Sinclair 1997). More recently, density dependence has also been recognized as a theoretically important concept in order to understand behavioral decisions of wild animals facing human disturbance or anthropogenic developments (see e.g. Gill & Sutherland 2000; Gill, Norris & Sutherland 2001; Frid & Dill 2002).

In wild reindeer research the impact of human factors such as traffic, tourism, hunting and human infrastructure has been emphasized for the long-term sustainability of populations due to higher grazing pressure in undisturbed habitats and avoidance of potential habitats under the influence of human activities (Nellemann *et al.* 2001a/b, Vistnes & Nellemann 2008; Andersen & Hustad 2004). As a consequence a reduction in the overall carrying capacity of an area has been assumed due to a reduced net primary production of lichen biomass both, in over- and under-grazed areas (see Figure 1-1).

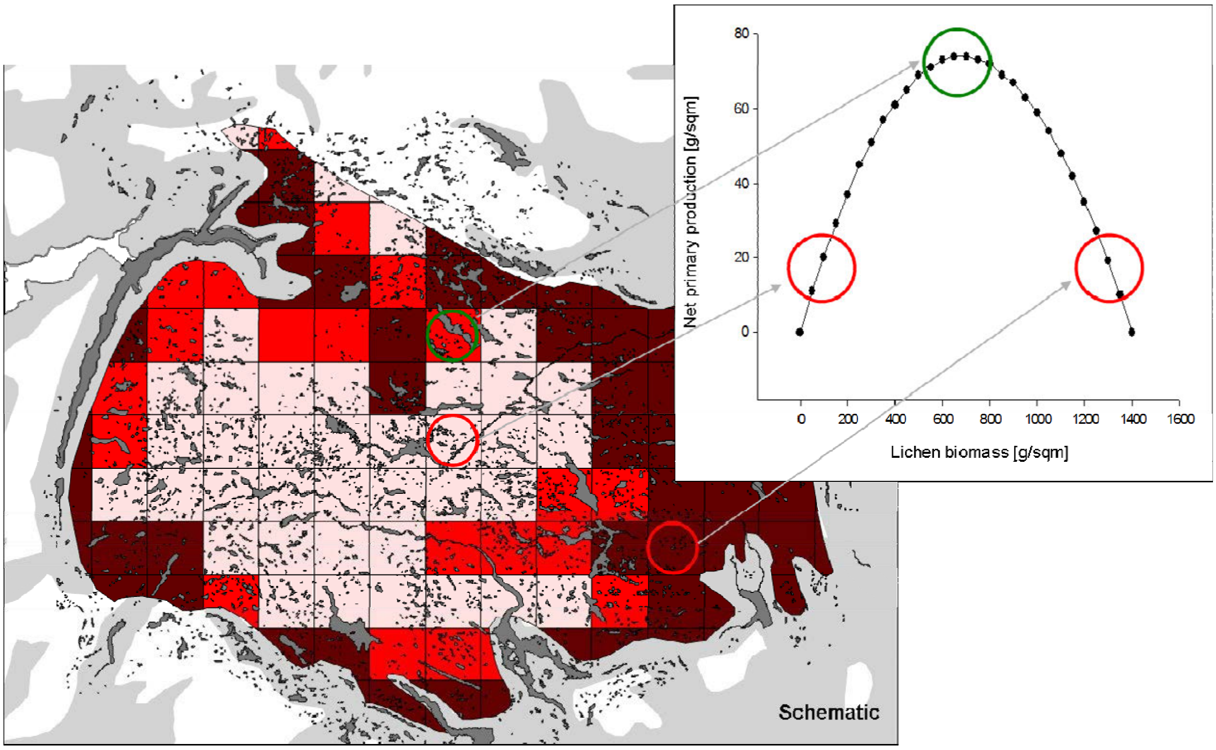

Figure 1-1: Magnitude of cumulated human disturbance and its effect on net primary production of lichen biomass in Hardangervidda – schematic[12]

A growing number of publications with clear indications of such and other density related effects on reindeer populations has been published (e.g. Nellemann *et al.* 2000; Wolfe, Griffith & Wolfe 2000; Dyer 1999; Dyer *et al.* 2001; Vistnes & Nellemann 2001a/b; Vistnes *et al.* 2001; Nellemann *et al.* 2003).

Improved availability of digital data and new modeling approaches available

Within ecological research remote sensing, GPS collars, the improved availability of digital data (topography, elevation models, land use, etc.) and the use of Geographic Information Systems (GIS) have recently provided researchers with (technically) new and improved opportunities for analyzing the impact of cumulated human disturbance on spatial behavior of animals.

Simultaneously new quantitative modeling approaches provide more robust and detailed methods to describe and explain animal movements and habitat use patterns:

Correlated random walk models (CRW) have been successfully used as null hypothesis for analyzing animal movement patterns (see e.g. Berg 1993; Farnsworth & Beecham 1999;

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[12] Based on Strand, Jordhøy & Solberg (2001)

Bergman, Schaefer & Luttich 2000; Mårell, Ball & Hofgaard 2002; Byers 2001; Fortin *et al.* 2003).

Resource selection functions (RSF) have become one of the most common methodologies to assess the impact and importance of potential factors (such as topography, weather, vegetation, human disturbance, etc.) for animal habitat selection (see e.g. Manly *et al.* 2002; Johnson *et al.* 2004; Alldrege & Griswold 2006; Boyce *et al.* 2002; Boyce & McDonald 1999; May 2007). As a special form of RSF, discrete choice models (DCM) have been applied more recently as a means to predict the habitat selection of animals using a "bottom-up approach" and thereby avoiding problems of autocorrelation and scale (e.g. Mysterud, Lian & Hermann 1999).

1.2 Aims of the thesis

Against the above background the principal objective of this study is to improve the knowledge on the habitat use of the last remaining wild reindeer populations in Scandinavia as a basis for their conservation and sustainable management. More specific, the thesis aims to investigate the habitat selection of wild reindeer in Hardangervidda, Norway, at two spatial scales (landscape level and regional level) during three temporal scales (summer, winter and calving). This aim is addressed by focusing on the following research questions:

i. How can the spatial patterns of the current distribution of wild reindeer in the study area be described? To which extent are reindeer performing large and/or small-scale migrations? How can the underlying movement patterns be described and possibly quantified?

ii. How important are seasons? What is their impact on distributions and movement patterns and how do these differ spatially? How can seasonality be detected empirically from the data?

iii. How do reindeer select among available habitats? Which resources are used? Which are unused and why? What can be learned using different measurement scales?

iv. What is the effect of (cumulative) human disturbance on reindeer habitat use? How does disturbance influence the local grazing pressure within the actual and potential reindeer habitats? What are the implications and possible recommendations for reindeer and land use management?

v. To what extent can the applied empirical models help to describe and explain the habitat use of wild reindeer? How robust are they? What are their strengths and weaknesses? Under which circumstances can they deliver relevant information to wildlife management and conservation? What can be derived for other reindeer areas and species?

The availability of forage clearly is a viable resource for every animal and can hence be seen as one of the most important single factors for habitat selection of animals (Manly *et al.* 2002). Information on land cover and lichen biomass is therefore essential for a full model definition of reindeer habitat selection. No such data was available for the study area. Hence, a reliable land cover map had to be compiled, sufficient both, in spatial resolution and accuracy, and covering the entire study area. In addition, a lichen biomass map was needed as a basis for modeling reindeer habitat selection and to detect possible differences in grazing pressure. In consequence, two sets of research questions were added:

vi. What are the relevant land cover classes for resource selection of wild reindeer in Hardangervidda? How do they distribute spatially? Which classifiers work best for vegetation classification within a mountainous area in northern Europe? Can the classification accuracy be improved by using ancillary data?

vii. What is the current status of lichen biomass in Hardangervidda and how does it translate spatially? How does this current distribution of lichen biomass coincide with the spatial distribution of reindeer? Which impact does lichen biomass have on reindeer (winter) habitat selection?

1.3 Methodological approach

The wild European mountain reindeer (Rangifer t. tarandus)

The wild European mountain reindeer (*Rangifer t. tarandus*) is part of the family of deer, suborder of ruminants and order of even-toed ungulates (Banfield 1961; Cronin, MacNeil & Patton 2006). Bucks (females) have a lifespan of up to 10 (14) years and can reach a body weight of app. 60 kg (35 kg) (Reimers 1997; Skogland 1985b)[13]. The physiognomy of the reindeer is extremely well adapted to arctic climates: Their thick, hollow fur in camouflaging colors – ranging from grayish-white (winter) to grayish-brown (summer) – consists of both,

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[13] Note that the size of (wild) reindeer is influenced by (density dependent) resource limitation (e.g. Skogland 1983a, 1988b)

guard hairs and under fur, insolating them up to minus 30 – 40^0 C (Skogland 1990b, 1994b). Reindeer have facial hair down to the muzzle and mucous membrane segments of bone and cartilage within the nose cavity to preheat and moisten the breathed-in air. Big, cup-shaped hooves enable them for efficient locomotion on snow as well as cratering for food during winter. Their ruminant micro flora is adapted to lichens (Thomas & Kroeger 1980, 1981), which reindeer are able to detect up to a snow depth of 60 cm or more due to their sensitive olfactory organs (Telfer & Kelsall 1984; Brown & Theberge 1990). Both sexes carry antlers, which represent their status within the herd (males from July till October, females keep their antlers till after calving, probably in order to increase their social status and thereby maximize their energy intake during winter) (Skogland 1989b).

Reindeer live in herds with sizes believed to result from a trade-off between lower predation risk and forage competition (Skogland 1984a)[14]. The behavior of wild reindeer in southern Norway can be characterized from sedentary to (semi-) migratory[15], depending on populations, and generally follows an annual cycle with seasonal movements between grazing areas (Skogland 1993). Calving takes place within traditional calving grounds during the second part of May with the herd usually widely spread within high, rugged terrain close to relatively rich pastures. The female pregnancy rate is normally high (> 80 %); calf mortality can be substantially (10 – 25%), depending on population density and forage quality (Skogland 1985a, 1990a). Thus the calf to cow and yearling ratio in June and July is normally 45 – 60% within southern Norway (Skogland 1986a; Strand & Solberg 2006). During the short alpine summers (June to August) reindeer maximize their energy intake through intensive grazing following the green-up wave of protein rich herbs and graminoids within large flocks of up to 4,000 animals (Klein 1970, 1990; Skogland 1980, 1984a, 1994b; Bevanger & Jordhøy 2004). Higher, more wind exposed areas are frequently visited for insect relief during warm weather (Coleman *et al.* 2001, 2003; Weladji *et al.* 2003). The rutting season takes place between mid September to mid October. Sexual maturity is reached at one and a half to two and a half years for females while bucks usually do not mate before an age of three years or older. With Harem sizes between 5 to 20 females and highly competitive behavior amongst males, bucks loose a significant amount of body weight during the rut (Skogland 1989b). During winter smaller flocks between 5 to 150 animals are cratering for lichen within less snow covered

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[14] For a more general discussion of behavioral decisions made under the risk of predation see e.g. Lima & Dill (1990) or Lima (2002). See also Ripple & Beschta (2004) on how predation risk can structure an ecosystem.

[15] For a model-driven approach to distinguish between migratory, semi-migratory, nomadic and sedentary behaviour see Bunnefeld *et al.* (2011).

terrain (ridges). Migration between summer and winter pastures takes place in autumn and spring and can be described as a strategy to utilize scare resources (Skogland 1989b).

Mountain reindeer occur predominantly in alpine terrain above the conifer tree line with little competition by other grazers (Skogland 1980, 1984a)[16]. Habitat selection is believed to be driven mainly by forage requirements with significant differences between seasons[17]. During summer reindeer is a concentrate selector for nutritive, protein rich forage (herbs, graminoids) and has been described to follow the green-up wave creating high quality pastures (snowbed vegetation) with high digestibility (app. 70% of intake) (Klein 1970, 1990; Skogland 1980, 1984a). Winter diet consists mainly of lichens (app. 80% of food intake) and evergreen plants with good accessibility (ridge vegetation) but poor digestibility and low protein and nitrogen content (Klein 1990). Habitat selection is further affected by insect harassment (Mörschel & Klein 1997; Anderson & Nilssen 1998), predation (Ferguson, Bergerud & Ferguson 1988; Bergerud & Page 1987; Bergerud 1985; Bergerud, Butler & Miller 1984; Pedersen *et al.* 1999; Seip 1991, 1992) and human disturbance[18] (Wolfe, Griffith & Wolfe 2000; Vistnes & Nellemann 2008).

As for other ungulates, the population dynamics of reindeer are mainly driven by (a) recruitment rates (calves per female) and (b) mortality of calves and yearlings (Skogland 1985b; Sæther 1997; Gaillard *et al.* 2000; Bonenfant *et al.* 2008).

(a) Recruitment rates are mainly influenced by female body conditions, the sex ratio and age structure of the population (Skogland 1984c, 1985a, 1986a, 1990a). The body condition itself is in general determined by three different factors: (i) Forage limitation, which is mainly dependent on population density (increased competition in high densities, reduced forage availability due to former overgrazing), snow depth and snow surface condition during winter as well as the distribution and quality of summer and winter pastures (Skogland 1986b, 1989a; Adams 2005; Barboza & Parker 2009; Reimers 1997; Gerhart *et al.* 1997; Pettorelli *et al.* 2005). (ii) Diseases and parasites can deteriorate reindeer body condition, especially insect harassment through warble flies (*Hypoderma tarandi*) and nose botflies (*Cephenemyia trompe*) (Colman *et al.* 2003; Downs, Theberge & Smith 1986; Skarin *et al.* 2004; Albon *et al.* 2002; Anderson, Nilssen & Folstad 1994; Anderson, Nilssen & Hemingsen 2001;

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[16] Even though competition for preferred plant species and reindeer's avoidance of areas heavily grazed by sheep has been suggested (Colman *et al.* 2003).

[17] For a more detailed discussion of nutrient dynamics of reindeer forage species see e.g. Mårell, Hofgaard & Danell (2005).

[18] Frid & Dill (2002) argue that human-caused disturbance stimuli can also be seen as a form of predation risk.

Arneberg, Folstad & Karter 1996; Bye 1987; Espmark 1967). (iii) Cumulated human disturbance effects can also lower the energy intake-/expenditure-ratio through less time available for foraging (behavioral alterations), fragmentation (barrier effect between habitats) and avoidance of important foraging areas (within habitats) (Wolfe, Griffith & Wolfe 2000; Vistnes & Nellemann 2008).

(b) The mortality of reindeer is mainly determined by three factors: (i) predation, (ii) harvest and (iii) exhaustion. (i) Although predation by wolverine (*Gulo gulo*), golden eagles (*Aquila Chrysaetos*), lynx (*Lynx lynx*) and arctic/red fox (*Alopex lagopus*/*Vulpes Vulpes*) is known to happen occasionally in southern Norway (see e.g. Pedersen *et al.* 1999; May 2007), especially for neonates, the magnitude and thus the impact of these predators on reindeer population dynamics is believed to be neglectable (Skogland 1985a, 1990a)[19]. (ii) In the absence of wolves and other effective predators, populations are managed through harvest[20], which is by far the most significant mortality factor with app. 25 % annual harvest rates. (iii) Finally, exhaustion (starvation[21], hypothermia) during winter, as a result of poor body condition and severe weather conditions, also contributes to reindeer mortality, especially in populations at high densities (Skogland 1985a, 1990a; Solberg *et al.* 2001; Kohler & Aanes 2004).

Study area

This study was performed at the Hardangervidda mountain plateau within southern Norway (app. 59-60^0 N 7-9^0 E). With a current estimate of app. 8,000 animals during summer (2010, based on minimum counts), Hardangervidda is the largest remaining wild reindeer population in Scandinavia (Skogland 1994b; Bevanger & Jordhøy 2004). The population has fluctuated at large during the last 50 years (see. e.g. Skogland 1990a; Fagerhaug 1976 and Loison & Strand 2005), and its number has changed from app. 25,000 to app. 4,500 heads during summer (see Figure 1-2)[22].

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[19] Note that the removal of top carnivores within an ecosystem can have serious consequences for plant biodiversity and productivity (Schmitz, Beckerman & Obrien 1997; Schmitz, Hambaeck & Beckerman 2000; Schmitz 2003).

[20] For reindeer management and the cultural importance of reindeer/hunting in southern Norway/Hardangervidda see also Skogland (1994b, 1988b); Bevanger & Jordhøy (2004); Bråtå (2005, 2008); Bjerketvedt (2000); Blehr (1973) and Blehr *et al.* (1973).

[21] See Skogland (1988a) for the importance of tooth wear by food limitation and its life history consequences in wild reindeer.

[22] Note that Skogland (1990a) concluded up to 35,000 reindeer in Hardangervidda during the 1960ties.

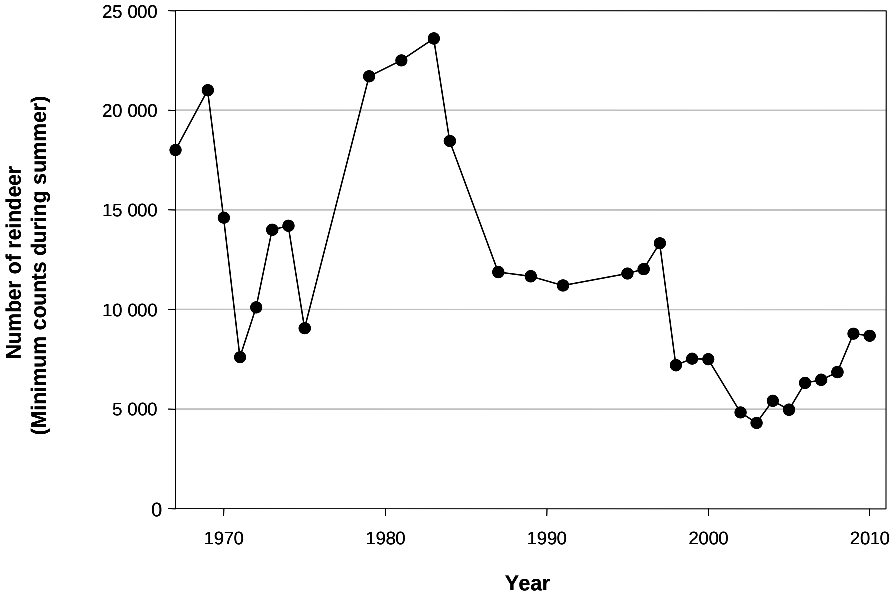

Figure 1-2: Reindeer population development in Hardangervidda 1967-2010[23]

These fluctuations have partially been caused by the management regime[24,25] due to insufficient data (population estimates, high variation in recruitment rates between years, condition of pastures) and also by a lack of knowledge regarding reindeer habitat use and its driving factors[26]. Management has aimed to reduce the long lasting effects of overgrazing[27] and is presently aiming to stabilize the population at app. 10,000 animals (Skogland 1993; Strand *et al.* 2004). The herd's physical condition has been low due to lasting effects of food limitation during winter (Skogland 1985a/c, 1993). Recent studies, however, do indicate that the reduction of the population size has resulted in relaxed density dependence and improved body condition and the reproductive performance among females (Skogland 1990a; Loison & Strand 2005).

With an area of over 8,100 sqkm and an average elevation of app. 1,200 m a.s.l. ranging from 900 – 1,800 m Hardangervidda is the largest mountain plateau in Northern Europe (see e.g.

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[23] Based on Skogland (1990a) and Loison & Strand (2005).

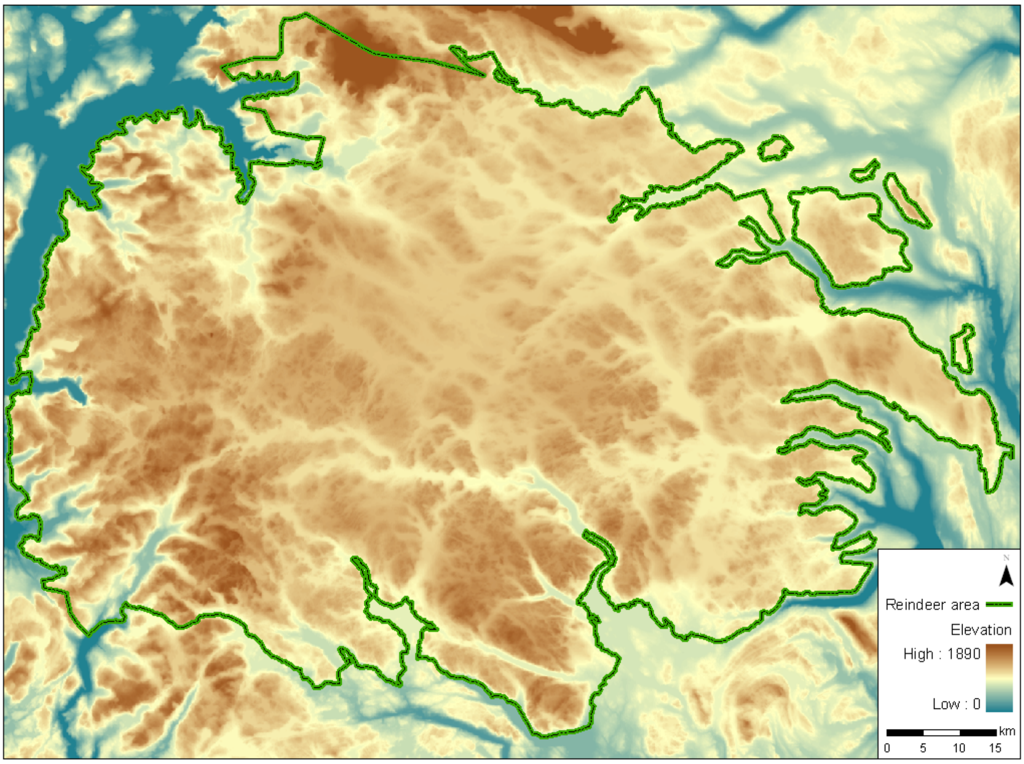
[24] For the management of reindeer in Hardangervidda and adjacent areas see Landbruksdepartmentet (1911); Krafft *et al.* (1978, 1979a/b); Krafft, Gaare & Reimers (1970); Holthe (1977); Gaare & Skogland (1979); Skogland (1988b, 1983b, 1984b); Solberg *et al.* (2010); Strand *et al.* (2001b, 2004, 2005); Jordhøy *et al.* (1996) and Bråtå (2005, 2008).

[25] Note that fluctuations of reindeer and caribou can also to a certain extent be seen as a natural phenomenon (see e.g. Morneau & Payette 2000).

[26] Some description on reindeer habitat use in Hardangervidda can be found in Skogland (1985c, 1989c, 1993); Gaare (1976); Gaare, Thomson & Kjos-Hanssen (1975); Pedersen (2001) and Smukkestad (2000).

[27] For a more detailed description of reindeer-pasture interactions in Hardangervidda and adjacent reindeer areas see Gaare & Hansson (1989, 1990); Gaare & Skogland (1980); Gaare, Tømmervik & Wilmann (2001); Gaare (1971, 1985, 1986); Tveitnes (1980) or (Ihse & Allard 1995). For a general perspective on the differential effects of reindeer on high arctic lichens see e.g. Van der Waal *et al.* (2001).

Østbye 1975). Its spatial extent can be approximated by the 900 m contour interval given by the conifer tree line (see Map 1-4).



Map 1-4: Hardangervidda elevation [28]

Hardangervidda's plateau-character is particularly prominent in the central areas. Lakes and rivers cover app. 10% of the terrain; app. 1% is covered by glaciers (with Hardangerjøkull extending over 120 sqkm). Hardangervidda's climate is characterized by alpine and partially sub-arctic conditions with an average temperature of -1^0 C, ranging from -30^0 C (winter) to 10^0 C (summer). Precipitation falls between 700 to >2,000 mm. The open landscape experiences high average wind speeds (app. 3 m/s) with predominant wind directions from SW and SE. Hardangervidda is influenced by a pronounced east-west-gradient; with the western part experiencing an increasing oceanic influence to climate with higher precipitation (rain/snowfall) and a higher, more rugged and inaccessible terrain (Wielgolaski 1975; Bakkestuen, Erikstad & Økland 2008). Hardangervidda national park (3,460 sqkm) is the largest in Norway.

Hardangervidda is characterized predominantly by low to middle alpine vegetation (Wielgolaski 2000; Tveitnes 1980). Its core is entirely above the tree line, although some birch forest occurs in deeper valleys (see Map 1-5).

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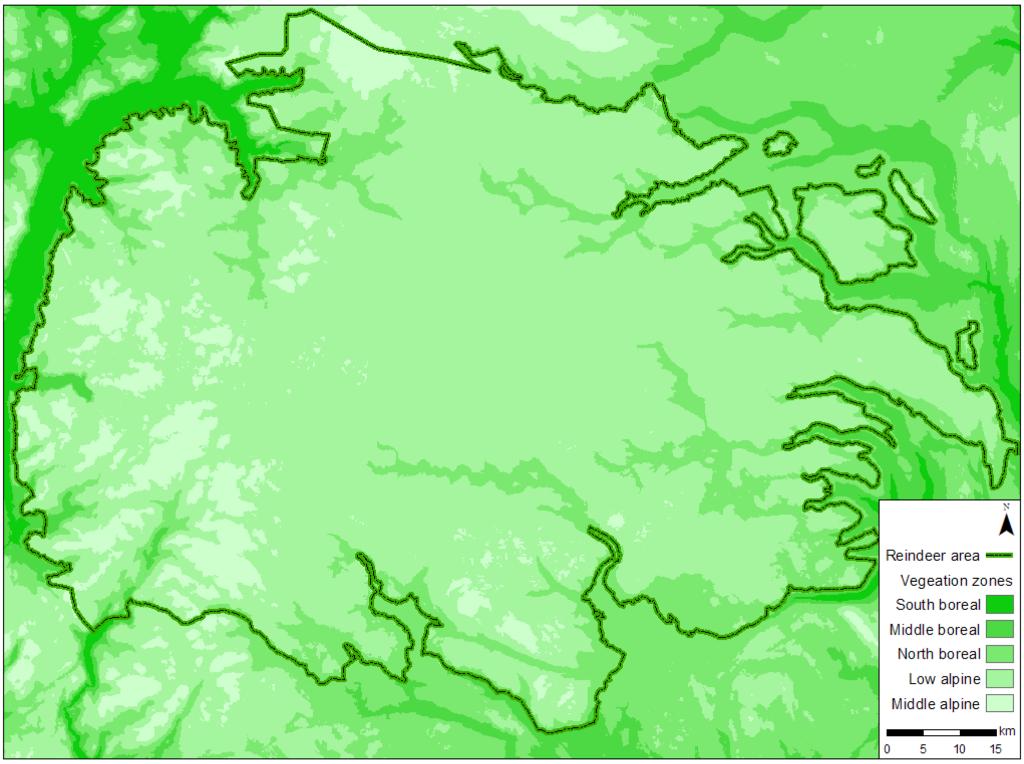
[28] Based on Statens Kartverk (2006)



Map 1-5: Hardangervidda vegetation zones [29]

The east-west-gradient and regional differences in geology and soil produce pronounced differences in vegetation communities between areas (Hesjedal 1975a/b): The western and south-central parts of Hardangervidda are characterized by abundant patches of snowbed vegetation, willow thickets and bogs as well as by a considerable proportion of rocky terrain and unproductive areas. On the other hand, the more eastern areas are dominated by lichen-heath communities (ridge and leeside vegetation). Lichen pastures have been severely affected by periods of overgrazing during the 1960's and early 1980's with 90% of the lichen communities characterized by strong or intermediate damage from grazing (Gaare & Hansson 1989; Tveitnes 1980; Skogland 1990a, 1993). In earlier studies only 15% of Hardangervidda's total habitat has been classified as winter pastures, which is considerable less as compared to other Norwegian reindeer areas (e.g. Rondane, Forollhogna) (Skogland 1984a/b, 1985c; Jordhøy *et al.* 1996). Winter pastures have therefore by some authors been considered to be the limiting factor for the reindeer carrying capacity of Hardangervidda (Skogland 1990a, 1993)[30].

The reindeer population in Hardangervidda is believed to have been more or less isolated from neighboring populations for the last decades (Strand, Bevanger & Falldorf 2006). This is

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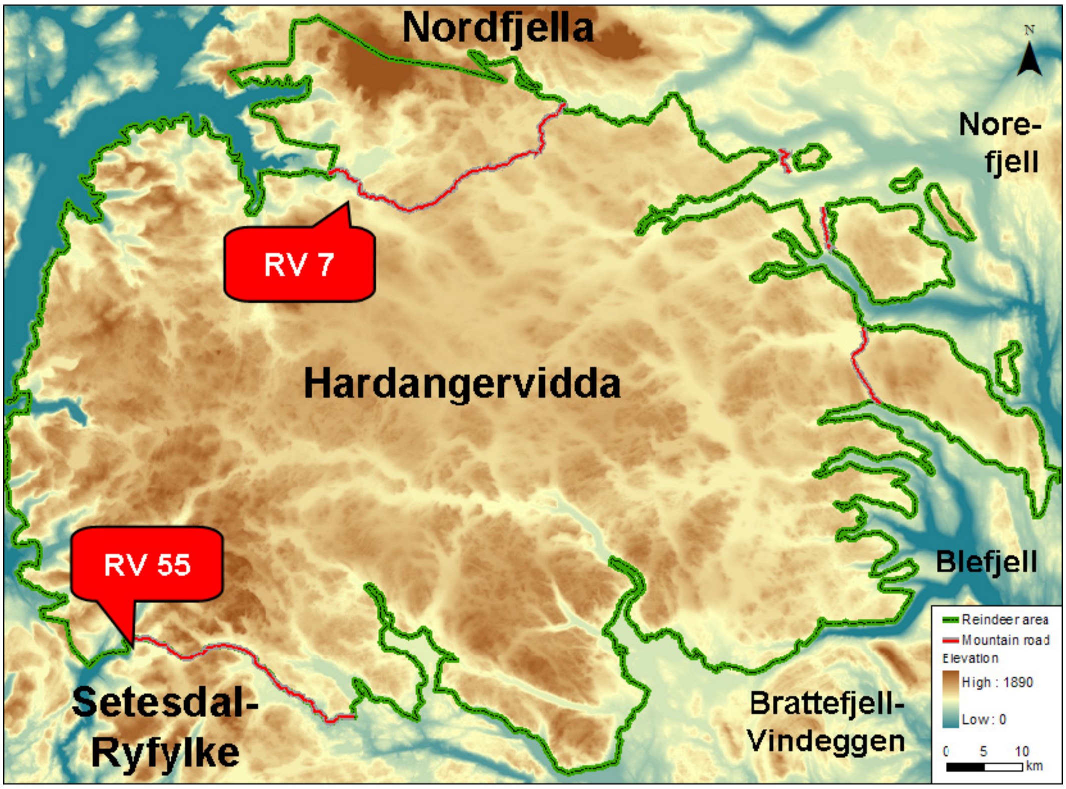
[29] Based on Moen (1998), Moen & Odland (2002) and Lieng (2002).

[30] Note that other authors have rejected this view and emphasized the importance of protein rich summer pastures, instead (see e.g. Reimers 1997).

most probably the result of an ongoing process of fragmentation caused by the piecemeal building of human infrastructure concentrating on the outskirts of the area. Examples of such barrier effects are the two mountain road stretches Rv7 and Rv55, which are assumed to be responsible for reduced reindeer migrations to Nordfjella in the north and Setesdal-Ryfylke in the south[31,32] (see Map 1-6).



Map 1-6: Habitat fragmentation in Hardangervidda through natural and human barriers[33]

In addition to the anthropogenic changes it is believed that the reduction in population size by management has reduced reindeer's dependency to search for grazing areas outside of Hardangervidda.

Strand, Jordhøy & Solberg (2001) suggest four historical periods regarding reindeer habitat use of Hardangervidda and its adjacent areas based on recent observations, spatial differences in grazing pressure and historic pit-fall systems (see Map 1-7):

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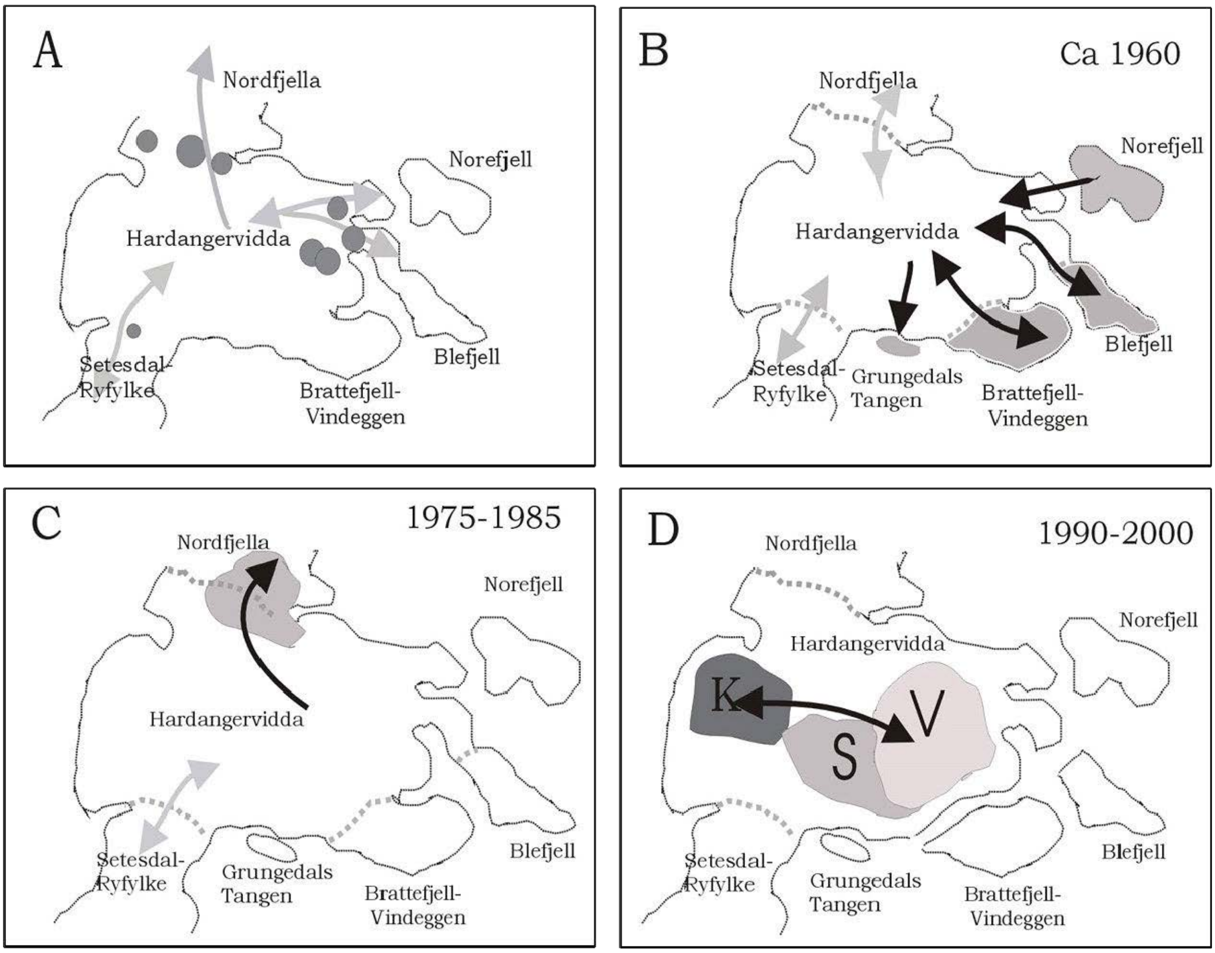
[31] For a more detailed description of Rv7 and its effect on the Hardangervidda reindeer population see also Strand, Bevanger & Falldorf (2006); Strand, Jordhøy & Solberg (2001); Strand *et al.* (2001a); Vegdirektoratet (2001); Dervo & Stenseth (1997) and Wathne *et al.* (2000). An assessment on the ecological effects of roads in general can e.g. be found in Seiler (2001) and Yanes, Velaso & Suarez (1995) or Iuell (2005) for a Norwegian perspective; for an overview see also Spellerberg (1998).

[32] Mountain road stretches like Rv7 are considered barriers for reindeer migration especially during winter both due to disturbance caused by prominent noise levels of heavy machinery used for snow clearing and high snow walls as a result of it (see e.g. Bjørkheim 2004). For more details on hearing in reindeer see e.g. Flydal *et al.* (2001). A more general review on the effects of noise on wildlife is e.g. given by Dufour (1980).

[33] Based on Statens Kartverk (2006)



Map 1-7: Historic changes of reindeer habitat use in Hardangervidda – schematic[34]

A. Historic evidence (pit-fall systems) indicates large-scale reindeer migration corridors between Hardangervidda and neighboring mountain areas: Setesdal (south), Nordfjella (north), Norefjell, Blefjell and Brattefjell-Vindeggen (east).

B. Hardangervidda is more and more isolated from its neighboring areas from 1960. Some observations of (winter) habitat use of Norefjell, Blefjell and Brattefjell-Vindeggen during the peak of the Hardangervidda population in the 1960ties are made.

C. Animals of the Hardangervidda population are frequently observed in the Nordfjella area during some severe winters of the second population peak between 1975 and 1985. Strong grazing pressure on the winter pastures and winters with harsh snow conditions are believed to be the reason.

D. The reindeer population is more or less constrained to the Hardangervidda core area. Calving areas are located in the western area of Hardangervidda, the south central

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[34] Based on Strand, Jordhøy & Solberg (2001).

area is used as summer range while the eastern parts are used as winter pastures. Very few observations of reindeer are made in the north of Rv7.

Habitat fragmentation and cumulative human disturbance have been suggested as the main causes for this change in habitat use and therefore described as possible threats for the long-term conservation of wild reindeer. In this context, increased knowledge about the combined effects of habitat fragmentation and cumulative human disturbance in density dependent populations is needed to disentangle some of the mechanisms and possible long-term effects upon such systems. Such knowledge will also improve management, which will have to balance the needs of reindeer habitat conservation and human development in rural areas.

Structure and study design

The above aims of this thesis translate into four different chapters:

a. In chapter 2 GPS movement data of reindeer in Hardangervidda is analyzed using fractal dimensions and correlated random walk models in order to describe and quantify reindeer's seasonal differences in distribution and movement patterns.

b. In chapter 3 selected parametric and non-parametric classifiers using satellite imagery and ancillary data are compared in order to accurately classify the land cover in the alpine region of Hardangervidda.

c. Based on this land cover map a new method for quantifying lichen biomass from satellite imagery is proposed in chapter 4. The current status of lichen pastures within Hardangervidda is quantified and mapped.

d. In chapter 5 reindeer habitat selection in Hardangervidda is modeled in a series of RSF models, including a seasonal comparison at different spatial scales.

Each of the applied methods above will in detail be presented and discussed in the method sections of the individual chapters. Nevertheless, upon studying the habitat use of animals some general crucial methodological decisions have to be made, concerning (i) modeling techniques, (ii) survey methods and (iii) spatial and temporal scales. As these are relevant for all of the chapters and in order to make the chosen alternatives within the study design more transparent, the relevant and most fundamental concepts within each of the three sets above are described in overview below:

(i) Predictions of habitat use and distribution of animals through models are fundamental for conservation and management in ecology (Elith *et al.* 2006). Even though models can never fully capture real world processes (Levins 1966), they can provide valuable information about the ecology of a species and their requirements for survival (Manly *et al.* 2002). The most common technique used to evaluate resource selection by animals is to compare used with available resources (areas) (Thomas & Taylor 2006). Technically, this is often done with resource selection functions (RSF) built as logistic regression models (LR). In principal, these models compare telemetry or GPS positions (used entities) with a random sample of available positions (available entities) and try to explain the variance of the resulting binary response variable through the spatial qualities of the used/available entities (Aebischer, Robertson & Kenward 1993). Within these models the concept of availability is crucial (Keating & Cherry 2004; McClean *et al.* 1998) and more recently discrete choice models (DCM) as a particular form of RSF have tried to solve the problem of spatial and temporal autocorrelation[35] of the collected data through comparing selected and available locations individually for each sampled position (Legendre 1993; De Solla, Bonduriansky & Brooks 1999; Nielsen *et al.* 2002).

In this thesis logistic regression models (LR) and discrete choice models (DCM) are used as RSF in order to assess reindeer habitat selection (chapter 5) as these quantitative methods offer unprecedented possibilities to test for the significance and relative contribution of multiple individual factors influencing reindeer's selection behavior. They are also able to deal with large amounts of data on the individual-level and can be utilized for different temporal and spatial scales (see below). Finally, it is possible to get direct estimates on reindeer's functional response to individual factors and thereby derive valuable information for management. A more detailed description will be given in chapters 2.2 and 5.2.

(ii) Choosing the right survey method is a critical factor for assessing resource selection of animals. Several techniques (direct and indirect) have been employed successfully over time: Faecal pellet-group and animal track counts are the most frequently used indirect survey methods. They have been used by researchers to indirectly capture the total abundance of animals over a certain period and at the same time link it to various habitat attributes like vegetation type or topography (e.g. Marques *et al.* 2001; Campbell, Swanson & Sales 2004; Hemami & Dolman 2005; Harkonen & Heikkila 1999)[36]. Focal sampling, aerial surveys and

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[35] See also Otis & White (1999) for the autocorrelation of location estimates and the analysis of radio tracking data.

[36] For a comparison of telemetry data and pellet-group counts for determining habitat selection see e.g. Guillet *et al.* (1995).

the use of radio telemetry or GPS collars – on the other hand – are examples for direct observation methods. In this group, focal sampling is the classic method for studying the behavior and activity pattern of animals through direct observations of a random animal within a group or herd at defined intervals during the observation period (Neff 1968; Altmann 1974). Aerial surveys are most commonly used for population estimates in management (Buckland *et al.* 2001). While radio telemetry has been used in habitat selection studies since 1959 (see e.g. Harris *et al.* 1990), the introduction of the Global Positioning System (GPS) has provided researchers with excellent opportunities for sampling high quality and frequent location data, irrespective of accessibility, time of day or weather conditions (Millspaugh & Marzluff 2001). Examples of such are e.g. James (1999); Welch (2000) and Fortin *et al.* (2005), among others[37].

LR and DCM models require a considerable amount of data. In this thesis analysis of seasonal movement patterns and habitat selection models were therefore based on radio-tracking data of 28 individual female reindeer equipped with GPS sensors in Hardangervidda. Data was collected between 2001 and 2006 (n = 91,701 positions). For more details see chapters 2.2 and 5.2.

(iii) The importance of scale for resource selection of animals has been recognized for at least three decades (Johnson 1980; Peterson & Parker 1998; Wiens 1989; Boyce *et al.* 2003; Boyce 2006). In order to address the hierarchy in habitat selection, it has therefore been common to perform resource selection studies at different scales (e.g. Apps *et al.* 2004; Johnson *et al.* 2004; Johnson *et al.* 2002a; Schaefer, Bergman & Luttich 2000; Johnson, Parker & Heard 2001; Johnson, Seip & Boyce 2004; Chamberlain *et al.* 2003; Krawchuk & Taylor 2003; Fortin *et al.* 2003 or Roslin 2000)[38]. Senft *et al.* (1987) developed a concept of hierarchical foraging decisions in grazing ecology, based on herbivore foraging response patterns at three different levels (regional, landscape and patch level)[39]: At the regional scale, the animals' movement decisions deal with migration between seasonal areas or home ranges, determined by forage, geomorphology, regional climate, density of predators, etc. (Senft *et al.* 1987; Rettie & Messier 2000; Dussault *et al.* 2005; Bergerud & Page 1987; Bergerud 1985; Bergerud, Butler & Miller 1984; Bergerud, Ferguson & Butler 1990; Brown 1999; Brown, Laundre & Gurung 1999; Brown 2001). At this scale migrations between summer and winter pastures

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[37] See also Strand, Solberg & Tømmervik (2001) on experiences with GPS senders on reindeer.

[38] See also Meyer & Thuiller (2006) for a discussion of the accuracy of resource selection functions across spatial scales.

[39] See e.g. Stephens & Krebs (1986); Pyke (1984) and Fauchald (1999) for foraging theory.

ranging from 50 km to over 3,000 km are described for reindeer (Berger 2004). At the landscape level, herbivores select feeding sites, patches or plant communities that are attractive, with site selection further influenced by topography, weather, water locations or predators (Bailey *et al.* 1996; Senft *et al.* 1987). Distances moved from day to day vary among species. Sedentary reindeer/caribou usually do not move more than 2 km a day (Johnson *et al.* 2002b; Rettie & Messier 2001), while migratory caribou are shown to move an average of 7 – 8 km a day (Bergman, Schaefer & Luttich 2000). At the patch level, feeding stations, plants and plant parts are selected (Senft *et al.* 1987). For reindeer the spatial extant of these small-scale feeding site optimization patterns usually is limited to a couple of meters[40]. Spatial and temporal scales are naturally linked (Wiens 1989), with temporal scale describing both, the individuals' allocation of time in certain habitats (Mysterud & Ims 1998) and the dependency of the animals' selection process on time (e.g. season and daytime) (Allen & Hoekstra 1992).

Within this thesis, modeling will be done on two spatial scales: the regional and the landscape level, following the concept of Senft *et al.* (1987) (see chapter 5.2). Patch scale will not be addressed since both, the sampling intervals (3h) and spatial resolution of input layers for modeling (e.g. snow depth, land cover and lichen biomass maps, terrain) (30 m to 1 km), do not yield the necessary detail for valid analysis and interpretation. To make interpretation easier, in the following, the regional level will be referred to as "large-scale" and the landscape level as "small-scale" (compare chapter 5.2).

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[40] In this context note that Mårell, Ball & Hofgaard (2002) suggest that during summer reindeer select for certain plant species rather than for patches.

2 Seasonal distributions and movement patterns

2.1 Introduction

Uneven distribution of animals within habitats

Animals are unevenly distributed within their habitats (e.g. Manly *et al.* 2002; Vuilleumier & Metzger 2005; Ager *et al.* 2003). Six possible drivers for these observational differences are commonly discussed in literature:

(i) Spatial differences in resource distribution (e.g. Brown 2001; Bergerud 1974b; MacArthur & Pianka 1966), (ii) predation risk (e.g. Bergerud & Page 1987; Bergerud 1985; Bergerud, Butler & Miller 1984; Brown 1999; Brown, Laundre & Gurung 1999; Ferguson, Bergerud & Ferguson 1988; Grand & Dill 1999; Mao *et al.* 2005; Peacor & Werner 2000; Wolff & Van Horn 2003 or White, Feller & Bayley 2003), (iii) likelihood of disturbance/competition by/with other species and/or humans (e.g. Yost & Wright 2001; Hebbelwhite, Merrill & McDonald 2005; Hebbelwhite & Merrill 2009), (iv) social behavior (rut, calving, foraging, etc.) favoring social organization in herds (e.g. Christman & Lewis 2005; Bergerud, Ferguson & Butler 1990; Gunn & Miller 1986; Romey 1995), (v) spatial differences in environmental conditions (current situation and perception of long-term stochastic risks e.g. of factors like surface icing or snow depth) (e.g. Skogland 1978; 1985a, 1990a; Kohler & Aanes 2004; Chan *et al.* 2005; Hansen, Aanes & Sæther 2010; Stien *et al.* 2010) as well as (vi) random components (e.g. Cain 1985). Static distributions of animals can thus be seen as the result of dynamic movement decisions of individuals (e.g. Russel, Swihart & Feng 2003), and a better understanding of observed differences in static distributions of animals therefore requires knowledge about their movement dynamics.

Two different concepts of movement

Movement enables animals to optimize for spatially differing habitat qualities within a dynamic environment (e.g. Bell 1990; Turchin 1998; Kernohan, Gitzen & Millspaugh 2001). Depending on an animal’s knowledge/awareness of its environment, there are two different concepts of movement:

First, movement can be seen as a strategy to cover the distance between locations of interest while optimizing for shortest distance, lowest energy expenditure, shortest traveling time, or some other fitness gaining measure (e.g. Zollner & Lima 1999). In a small-scale perspective, locations of interest can e.g. be feeding sites, resting places, access to water, protection from predation, etc. In a large-scale perspective they can be seasonal habitats, triggering seasonal migrations. This kind of movement requires a certain degree of knowledge/awareness (location, environment and terrain)[41] from the animal, either direct (visibility, smell, etc.) or indirect (memory[42], communication, herd behavior, etc.) (e.g. Zollner & Lima 1999).

Second, movement can be regarded as searching behavior within an unknown environment (e.g. Bartumeus, F. 2007; Fortin 2003; Zollner & Lima 1999). In this case, movement can be interpreted as a strategy to optimize habitat use within an unknown environment through a geometrical pattern, allowing for an enlarged stochastic probability to encounter locations (resources) of interest (e.g. feeding sites). Again, movement patterns can also be influenced by factors like energy expenditure, wind direction or other (e.g. Zollner & Lima 1999; Fortin 2003).

Movement patterns dependent on scale

As noted above, movement patterns of animals follow different spatial and temporal scales (compare chapter 1.3). Within the concept of hierarchical foraging decisions in grazing ecology developed by Senft *et al.* (1987) the assessment of reindeer movement patterns within this chapter focuses on the regional and landscape level, that is both, large-scale migrations between seasonal habitats and small-scale movements between feeding sites are being analyzed. Optimization patterns within feeding sites (patch level) are not in focus as such studies are dependent on high resolution data on both, animal movements (temporal resolution) and environment (spatial resolution), and are thus beyond the scope of this thesis.

Methods for detecting movement patterns often with compromises

Methodologically movement patterns have traditionally been described by field observations using protocols (e.g. Altmann 1974; Skogland 1978; Hagemoen & Reimers 2002) or single numerical parameters, such as movement direction, average step length or turning angle between consecutive steps, calculated from telemetry data (Ferguson & Elkie 2004; Amstrup *et al.* 2000; Brown *et al.* 1986) and more recently also from GPS data (e.g. Schaefer & Luttich 1998). The relatively simple analytical models used during the 1970’s and 1980’s have developed significantly and more recently quantitative models such as correlated random walks (CRW) (e.g. Berg 1993; Bergman, Schaefer & Luttich 2000; Fortin *et al.* 2003), fractal di-

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[41] See also Olden *et al.* (2004) for context dependent perceptual ranges and their relevance to animal movement.

[42] See e.g. Haefner & Crist (1994) for the role of memory within a spatial model of movement and foraging in harvester ants.

mensions[43] (e.g. Ferguson, Rettie & Messier 1998; Nams 2005 or Nams & Bourgeois 2004) and lévy flights[44] (e.g. Mårell, Ball & Hofgaard 2002; Edwards *et al.* 2007) have been applied in studies of animal movement patterns[45].

Using these methods four compromises are most frequently described: (i) First, observational data often suffers from small sample size and/or biases during recording and sometimes has been described as subjective. (ii) Second, telemetry based studies deliver more objective data, but, until recently, were also limited to small sample sizes, yielding significant spatial errors (especially VHF/UHF, ARGOS) and few or limited possibilities to include behavioral data (e.g. Leban *et al.* 2001). (iii) Third, data is normally divided into seasons or sub-seasons to account for temporal scales. Seasonality within these studies (e.g. summer, winter, rutting seasons, etc.), however, is often defined on theoretical assumptions or from an anthropogenic perspective (e.g. Bergman, Schaefer & Luttich 2000; Rettie & Messier 1998; Dyer *et al.* 2001; Poole, Heard & Mowat, 2000) and seldom based on empirical data allowing for a biologically more meaningful classification of data into suitable time periods (e.g. Ferguson & Elkie 2004). (iv) Finally, within research one-dimensional concepts of movement patterns still prevail. Until now no integrated systematic for the detection and description of movement patterns has been commonly accepted.

Systematic information on spatial distribution of reindeer in Hardangervidda is scarce: Snapshots on spatial distribution are available through aerial surveys conducted within the last 30 years for population estimates (Solberg *et al.* 2010). Furthermore, killed animals during hunting can be allocated spatially on community level (Solberg *et al.* 2010) and indications on traditional migration corridors have been described from archaeological sites such as pitfall systems (see chapter 1.3). However, no spatially explicit, continuous distribution data for reindeer within the study area exists. Even less information is available on reindeer's movement patterns within the study area. While some fragmented observations from fieldwork do exists (e.g. Skogland 1974, 1994b, Thomson 1971, 1973), no comprehensive model of seasonal distribution and movement patterns for reindeer in Hardangervidda has been developed.

Objectives

Against this background three main objectives are in focus within this chapter:

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[43] See Mandelbrot (1977).

[44] See Viswanathan *et al.* 1999; Shlesinger, Yaslavsky & Frisch (1995)

[45] See also Turchin (1998) and Walton *et al*. (2001) for the quantitative analysis of movement.

i. The first aim is to empirically detect and define relevant seasons within the annual cycle from a reindeer perspective based on movement and habitat use patterns. Relevant questions are: How important are seasons? What is their impact on reindeer distribution and movement patterns and how do they translate spatially? How can seasons be detected empirically?

ii. The second objective is to comprehensively describe the distributions of reindeer with respect to the detected seasons. Or: How can the distribution of wild reindeer in Hardangervidda be described? Can spatial distribution patterns be detected with respect to season (and if so how can they be described)?

iii. The final objective is to quantify seasonal differences in reindeer's movement patterns and to discuss the possible ecological drivers (also as a basis for modeling reindeer habitat selection in chapter 5). It is asked: How do reindeer move? To what extent are they performing large or small-scale migrations? And last: How can those movement patterns be described and possibly quantified?

2.2 Methods

A three-step approach was chosen to detect and describe the seasonal distributions and movement patterns of reindeer in Hardangervidda:

a. A total of 40 female reindeer was equipped with GPS collars within the study area and locations were recorded between 2001 and 2006. Data from 28 reindeer could successfully be retrieved.

b. GPS location data was used for CRW-analysis in order to detect differences in reindeer movement patterns within the annual cycle. Based on these differences, seasons were defined empirically using cut-off points obtained through regression analysis.

c. Distribution and movement patterns of wild reindeer in Hardangervidda were then compared between these seasons. In order to quantify reindeer movement patterns, a multi dimensional framework based on GPS collar data was developed and applied using fractal analysis, correlated random walks, activity level and size/inter-annual stability of used habitat as descriptors.

Telemetry data

Between 2001 and 2003 30 adult (≥2-years old) female reindeer in Hardangervidda, Norway, were captured using aerial darting from helicopters. Capturing was carried out in winter (February to March): Animals were collared in different herds and the individual females were selected randomly in order to reduce pseudo replication[46] of data (Hurlbert 1984). Captured reindeer were fitted with Televilt Simplex Global Positioning System (GPS) radio collars (Lindesberg, Sweden). Radio collars were programmed for 3-hr fix intervals at 0-, 3-, 6-, 9-, 12-, 15-, 18- and 21-hour GMT. Due to malfunctioning of 10 of the employed collars the decision was made to capture another 10 adult female reindeer in winter 2004 (December) to restore sample size.

Following the retrieval of collars in March 2006, a total of 91,701 locations was recovered from 28 individual reindeer (see Table 2-1).

REIN ID	First fix	Last fix	No. of fixes	Fix rate (%)	Quality (%)		DOP (%)	
					2D	3D	<6	>6
6a	20-Jan-01	13-Sep-02	4487	93.3	36.8	63.2	95.5	4.5
3a	19-Mar-01	24-Mar-02	2776	94.0	25.0	75.0	96.9	3.1
2a	20-Mar-01	14-Nov-02	4302	89.0	43.7	56.3	94.3	5.7
4a	29-Mar-01	20-Feb-03	4983	89.9	43.6	56.4	94.0	6.0
1a	30-Mar-01	07-Dec-02	4833	98.0	37.3	62.7	95.5	4.5
8a	18-Mar-02	16-May-02	475	99.6	16.2	83.8	97.7	2.3
7a	18-Mar-02	24-May-02	536	100.0	11.2	88.8	98.5	1.5
11a	21-Mar-02	21-Sep-02	1475	99.9	19.3	80.7	97.2	2.8
16	21-Mar-02	31-Jul-02	1051	99.9	24.7	75.3	96.7	3.3
15a	22-Mar-02	18-Feb-03	2659	99.8	22.4	77.6	96.8	3.2
7b	18-Mar-03	06-Jan-05	5123	97.0	34.4	65.6	96.1	3.9
15b	18-Mar-03	06-Mar-04	2485	87.9	28.9	71.1	94.9	5.1
8b	18-Mar-03	16-Aug-05	6848	97.0	40.6	59.4	95.9	4.1
11b	18-Mar-03	19-Jul-05	6646	97.3	42.2	57.8	95.3	4.7
4b	18-Mar-03	25-Apr-04	3225	99.8	24.7	75.3	96.8	3.2
17	20-Mar-03	08-Aug-03	1122	99.6	27.6	72.4	97.1	2.9
19	22-Mar-03	30-Apr-03	310	98.7	47.4	52.6	93.2	6.8
18	24-Mar-03	14-May-04	3107	93.1	60.9	39.1	92.3	7.7
24	18-Dec-04	06-Mar-06	3517	99.3	12.6	87.4	99.6	0.4
25	18-Dec-04	19-Feb-06	3377	98.7	13.5	86.5	99.6	0.4
26	18-Dec-04	22-Mar-06	3651	99.4	9.6	90.4	99.8	0.2
23	18-Dec-04	08-Mar-06	3548	99.7	10.5	89.5	99.9	0.1
21	18-Dec-04	07-Mar-06	3540	99.7	10.7	89.3	99.7	0.3
22	18-Dec-04	08-Mar-06	3504	98.5	12.9	87.1	99.7	0.3
27	19-Dec-04	08-Mar-06	3533	99.5	9.5	90.5	99.8	0.2
28	19-Dec-04	10-Mar-06	3534	99.1	12.9	87.1	99.7	0.3
30	20-Dec-04	21-Mar-06	3588	98.4	16.3	83.7	99.5	0.5
29	20-Dec-04	05-Mar-06	3466	98.5	14.3	85.7	99.5	0.5
Total			91701	96.7	27.3	72.7	97.1	2.9

Table 2-1: Telemetry data by reindeer

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[46] See also Maier & White (1998) for time and synchrony of activity in caribou.

While six of the retrieved collars stopped to record data at an earlier stage (operating time of two to six month resulting in 475 to 1475 fixes), the majority of collars continued recording for more than one year (nineteen collars containing between 3,107 to 6,848 fixes equaling operating times of 12 to 29 month). The remaining three collars fell slightly short of recording a full annual cycle (2,485 to 2,776 fixes).

The available quality parameters (fix rate, dilution of precision in meters (DOP), dimensionality of position) indicated a high quality of the retrieved GPS data (see Table 2-1):

Despite the extreme weather conditions in Hardangervidda (temperatures up to below minus 30 degrees C in winter) radio collars showed a high overall fix rate of over 95 percent (96.7) probably due to the open terrain above the tree line. Approximately three quarter of the positions (72.7 percent) were recorded in 3D. Over 95 percent of the fixes showed a DOP smaller than six meters (97.1).

The DOP values provided by the hardware only represent one contributor to the overall GPS accuracy (measure for geometric distribution of satellites) and do not show any clear correlation with the root mean squares of location errors (RMS) (D'Eon *et al.* 2002). As the RMS is not directly observable, and to avoid biasing data (D'Eon & Delparte 2005), the decision was made not to further censor raw data (compare e.g. Turney & Roberts 2004)[47].

Empirical definition of seasons

The correlated random walk model of Kareiva & Shigesada (1983) has been used within animal movement analysis as a null hypothesis to test whether animals move randomly or not. To do that, the observed net squared displacement after n steps, R^2_n (hereafter called the $NSQD_{obs}$), of an individual from a given origin is compared with the expected net squared displacement after n steps, $E(R^2_n)$ (hereafter called the $NSQD_{exp}$). Assuming the turning angles between locations are equally distributed between right and left, the expected net squared displacement ($NSQD_{exp}$) can be calculated using the following equation:

$$E\left(R_n^2\right) = nE\left(l^2\right) + 2E(l)^2 \frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right) \qquad (2\text{-}1)$$

where c is $E(\cos\theta)$ and θ is the turning angle [in radians], and l is length of one step [km]. $E(\cos\theta)$ is estimated by the mean $\cos(\theta)$, $E(l)$ is estimated by the mean step length and $E(l^2)$ is

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[47] For an alternative of satellite telemetry error see Keating (1994).

estimated by the mean (step length)^2. Step length and turning angle, used within the above equation are taken from the actual distribution of the individuals. Since the animal's turning angles between steps usually do not show a uniform distribution, walks are referred to as correlated random walks (and not random walks; see e.g. Holgate 1971).

Results from CRW models are traditionally used to test for site fidelity (over-prediction of $NSQD_{exp}$ as compared to $NSQD_{obs}$) or migratory behavior (under-prediction of $NSQD_{exp}$ as compared to $NSQD_{obs}$) (see e.g. Fortin 2003). Other authors (e.g. Bergman, Schaefer & Luttich 2000) have more recently employed CRW models in order to define seasons empirically by utilizing the relative stability of detected movement patterns within seasons. Following the latter approach, periods with relative homogeneity of site fidelity or migratory behavior, respectively, were identified through cut-off points derived from floating linear regression models. These cut-off points were later used as starting points (new origins) to again determine NSQD. Each cut-off point thereby indicates a significant change in movement patterns.

Within this approach $NSQD_{exp}$ and $NSQD_{obs}$ were calculated by individuals on the basis of 3-hour interval GPS positions using estimated calving dates as starting points. Individual $NSQD_{exp}$ and $NSQD_{obs}$ for single fixes were later averaged over individuals and day of year. Floating linear regression was used to determine cut-off points. Calculations were programmed in R release 2.3.1 (R Development Core Team 2006).

Movement patterns and seasonal distributions

Four different parameters have been chosen in order to characterize and describe seasonal movement patterns:

i) As noted above, CRW can be used to compare $NSQD_{exp}$ with $NSQD_{obs}$ to assess directionality of movement (site fidelity vs. directed movement). Therefore both, $NSQD_{exp}$ and $NSQD_{obs}$, were calculated by sub-season on individual level and single GPS fixes using individual and sub-season specific parameters (number of moves, mean (squared) step length and cosine of turn angels). $NSQD_{exp}$ and $NSQD_{obs}$ were than averaged over individuals and sub-seasons.

ii) The fractal dimension of sub-seasonal movement paths on individual level was used to detect and quantify the regularity of movements within a single value. Fractal dimension has been shown to reflect the sensitivity of contour line length (or movement paths) to the employed measurement interval (see Mandelbrot 1977). More recently this quality has been used within the analysis of movement patterns in order to quantify regular vs. irregular movement by animals (e.g. Ferguson, Rettie & Messier 1998). The fractal dimension D of a movement path is calculated using the following equation (Mandelbrot 1977):

$$D = 1 - s\,, \tag{2-2}$$

where s is the slope of the log/log plot of path length and measurement interval. An illustrative example of this concept is given in Figure 2-1 (irregular movement path of reindeer during calving 2002 with fractal dimension D = 1.43) and Figure 2-2 (directed movement pattern of reindeer during autumn migration 2002 with D = 1.13):

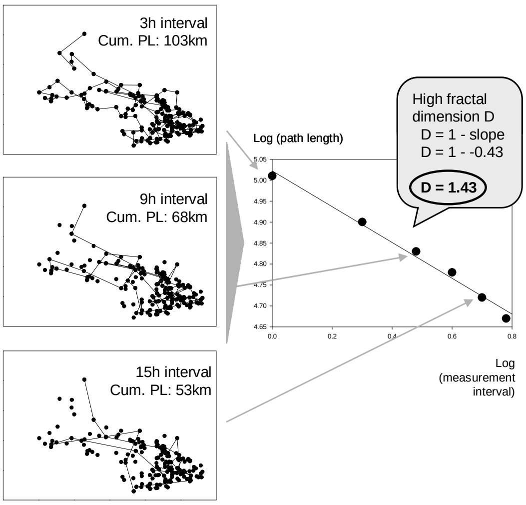

Figure 2-1: Irregular movement path of reindeer during calving 2002 (example) captured by fractal dimension

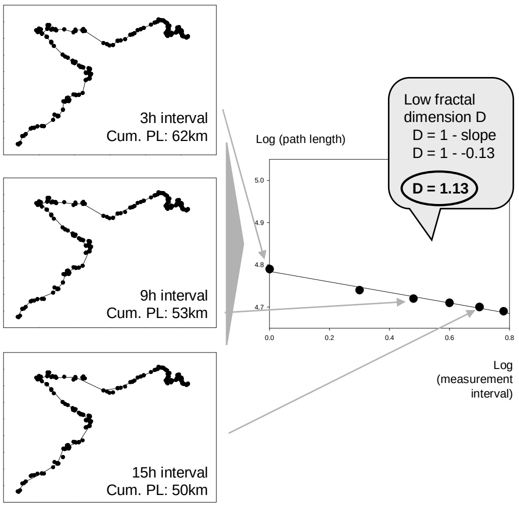

Figure 2-2: Directed movement pattern of reindeer during autumn migration 2002 (example) captured by fractal dimension

The illustrative examples within the above figures show the differences in the cumulated path lengths when the measurement intervals change: While for an irregular movement as in Figure 2-1 the path length is very dependent on GPS fix-rate (3h interval vs. 9h interval vs. 15 hr interval) the path length depicted in Figure 2-2 representing a directed movement is far less sensitive to reductions in fix rates. When combinations of measurement intervals and resulting cumulated path lengths are plotted in log/log graphs a higher directionality in the movement path translates into a flatter slope and hence a lower fractal dimension D (compare Figure 2-1 to Figure 2-2). Following this approach fractal dimensions D were calculated for all identified sub-seasons by individuals. Values were later averaged over individuals and years[48] to allow for comparisons between sub-seasons on population level. Again, calculations were programmed within R release 2.3.1 (R Development Core Team 2006).

iii) Average step length per hour is commonly used within animal movement studies as an indicator for low vs. high activity (see e.g. Pepin *et al.* 2004) and was used to describe reindeer's activity level It was opted against standardized step length calculated from fractal analysis to account for the differing length of the identified sub-annual periods. Step length was calculated from time and distance between two consecutive steps of individuals by sub-season using ArcGIS (ESRI 2005) and Hawth's Analysis Tools for ArcGIS (Beyer 2004). Calculated step length were later averaged by sub-season over individuals and years[48].

iv) Finally, size and inter-year stability of the sub-seasonal home ranges were chosen as additional parameters to complete the movement patterns: Home range size for the identified seasons were estimated using 95 percent home range kernels calculated from GPS point density (compare e.g. Seaman & Powell 1996; Worton 1989). Inter-year stability of seasonal home ranges was calculated as the average spatial overlap in percent of all possible annual combinations within the five-year study period. Calculations for both parameters were carried out using ArcGIS (ESRI 2005).

Estimating a cumulative disturbance map

For a first assessment of the relative importance of cumulative human disturbance a map was calculated using spatial information from the topographical map 1:50.000 (Statens Kartverk 2006) and DNT data (unpublished). Four factor groups were used as potential contributors (roads and railroads, trails, other line-related features and point-related features).

Roads and railroads included European roads, regional roads, county roads, municipal roads, private roads, tractor roads and railroads. Trails were specified by DNT summer trails, other marked summer trails and unmarked summer trails. Other line-related features were given by power-dams, power lines, cableways, ski lifts and illuminated ski trails. Point-related features, finally, included hotels/lodges, tourist cabins, restaurants, camping sites, farms, houses, cabins, shacks, power stations, towers and masts.

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[48] Analysis of both estimated overall path length and fractal dimension by single years (2000 to 2005) showed no significant overall differences between single years (p>0.44 and p>0.74 respectively). It was therefore decided to pool data between years even though some significant differences within sub-seasons were detected for both parameters using one-way ANOVA when seasonal means were considered not to significantly differ between years for p>0.05.

All single information-layers were extrapolated into space using kernel density estimates with 100 m grid size within ArcGIS (ESRI 2005). A constant search radius of 5 km was assumed for all disturbance related factors, as no other valid empirical information was available. The resulting density raster were than overlaid to create a cumulated disturbance map. Weighting of single layers was difficult, as very little empirical data existed for calibration. Summer trails could be weighted by frequency of use based on census data provided by Den Norske Touristforening (DNT) (unpublished). Analogue, single DNT cabins were weighted by their average overnight stays (DNT unpublished). Roads were weighted by their average usage frequencies provided by Statens Vegvesen (unpublished). In absence of other relevant data, equal weights were assumed for all other disturbance related factors.

To further analyze the potential impact of cumulated human disturbance on reindeer (and in order to develop initial hypothesis for habitat selection models later in chapter 5), the cumulated human disturbance map was overlaid with the recorded reindeer tracking-data during the summer seasons.

Creating snow depth maps

Snow conditions are believed to influence movement patterns and the spatial distribution of reindeer during winter significantly. To some extent they can be described by parameters like snow depth and liquid water content (Kohler & Aanes 2004). Various methods have also been suggested in order to combine weather data (e.g. wind speed, number of taw days, etc.) into indices describing snow surface conditions (Kohler & Aanes 2004), whereas few direct measures from remote sensors are available for such analysis at the moment. Note, however, that the formation of ice crusts after rain-on-snow (ROS) events or general surface thawing with subsequent refreezing have more recently been monitored using satellite data. A monitoring scheme for observation at the circumpolar scale based on data from the active microwave sensor SeaWinds on QuikSCAT (Ku-band), which is sensitive to changes on the snow surface, has been presented by Bartsch (2010).

As a first approximation for later analysis and in order to develop initial hypothesis on the impact of snow conditions on reindeer’s spatial distribution for modeling (see chapter 5), the spatial correlation between snow depth (SD) and liquid water content (LWC) provided by

Norges vassdrags- og energidirektoratet (NVE)[49] and reindeer's GPS locations were analyzed for LATE WINTER (see below). Snow parameters were de-averaged by single years within the study period (2001 to 2006) and snapshots of SD- and LWC-values were taken at the mid-dates of LATE WINTER from 2001 to 2006 (see below).

2.3 Results

Empirical sub-seasons and directionality of movements

As to be expected for a migratory species returning to preferred calving grounds, the annual CRW model on population level revealed a clear over prediction (site-fidelity) of $\mathrm{NSQD}_{\mathrm{exp}}$ as compared to $\mathrm{NSQD}_{\mathrm{obs}}$ (see Figure 2-3).

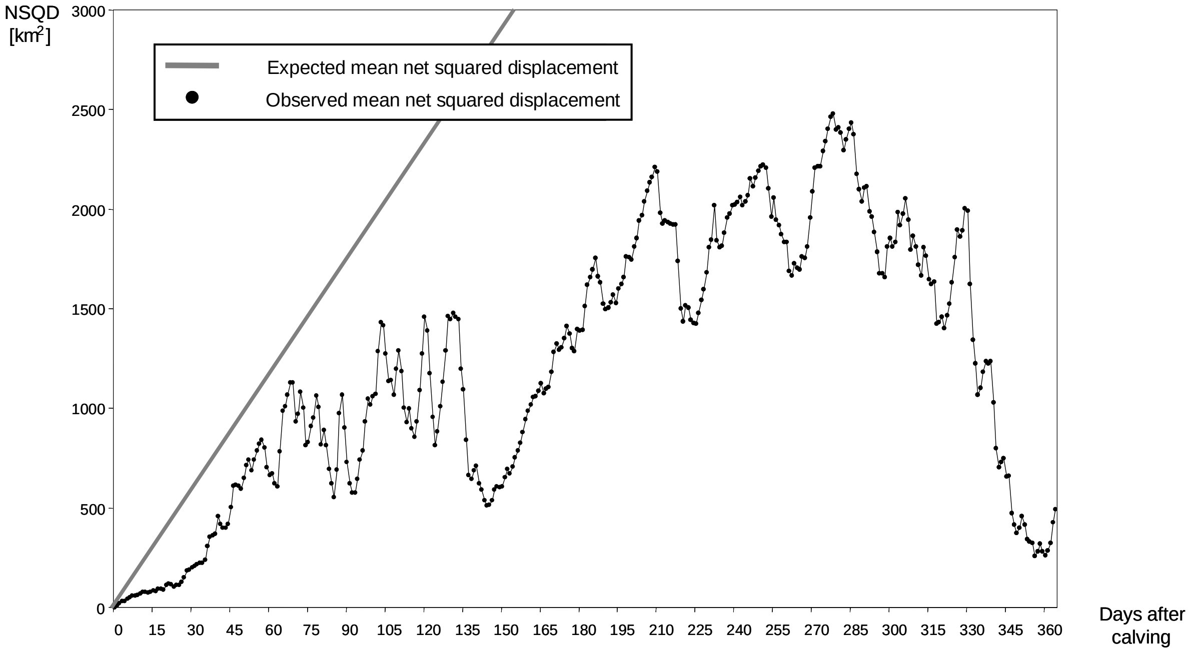

Figure 2-3: Expected vs. observed mean of net squared displacement within annual CRW model

Within the first ~30 days after calving $\mathrm{NSQD}_{\mathrm{obs}}$ depicted an almost linear but minor increase followed by a period of accelerated (linear) withdrawal from calving grounds (app. days 30 to 60). Between app. day 60 and 150 $\mathrm{NSQD}_{\mathrm{obs}}$ demonstrated large fluctuations without reindeer showing a clear tendency for further distancing themselves from calving grounds. In contrast, between app. days 150 to 210 $\mathrm{NSQD}_{\mathrm{obs}}$ from calving grounds increased continuously demonstrating linearity. For app. 60 days after this period a new phase of varying $\mathrm{NSQD}_{\mathrm{obs}}$ was vis-

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[49] Data available online (URL http://www.senorge.no/). For methods and data description see Engeset, Sorteberg & Udnœs (2000) and Stranden (2010). Note that due to the limited number of weather stations within the mountainous terrain of Hardangervidda, grid size for both parameters was rather coarse (1x1 km^2) and standard errors of estimates were above average values for Norway.

ible until app. at day 270 when reindeer reached their furthest distance from the calving grounds. Between app. days 270 to 320 reindeer slowly reproached towards their calving grounds: During this period they still showed larger fluctuations in NSQD$_{obs}$ until app. within the last 40 days of the annual cycle when they displayed a much more directed migration towards their calving grounds.

Results from floating cut-off points within CRW indicated 13 distinct sub-seasons where the GPS data suggest reindeer to demonstrate a (more or less) homogenous behavior regarding site fidelity/migration within and heterogeneous behavior between sub-season (see Figure 2-4):

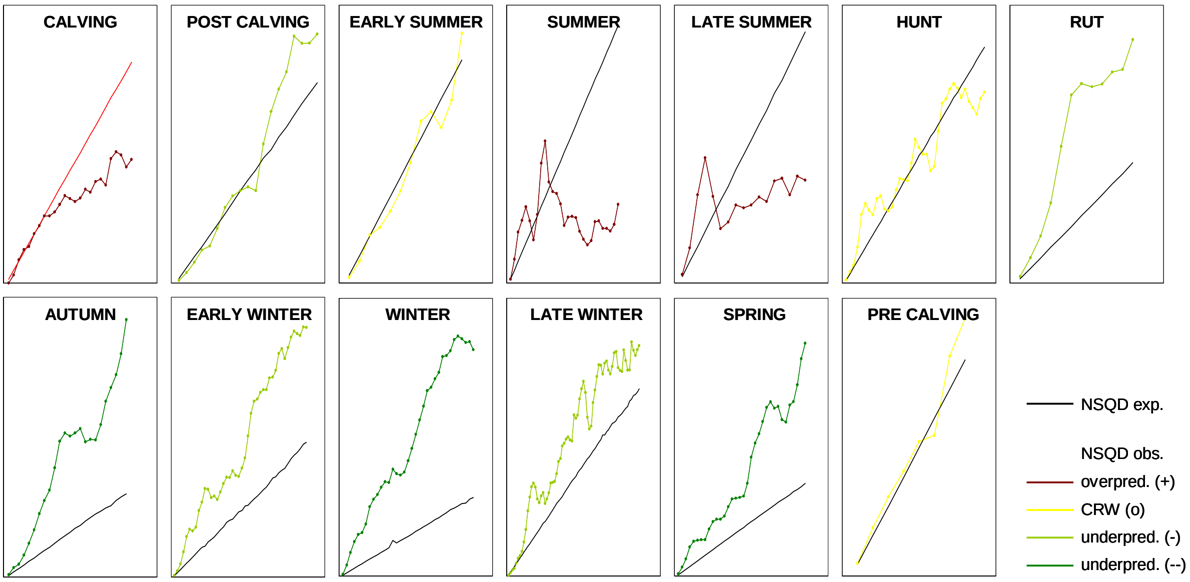

Figure 2-4: Expected vs. observed mean of net squared displacement within sub-season CRW models

NSQD$_{exp}$ during CALVING (May 14th to Jun 7th) calculated from sub-season specific parameters on individual level (mean (squared) step length and mean of the cosine of turn angels) showed significant over-prediction (site fidelity) when compared to NSQD$_{obs}$ derived from GPS positions. During POST CALVING (Jun 8th to Jun 26th) modest under-prediction (directed movement) was discovered, while for EARLY SUMMER (Jun 27th to Jul 8th) NSQD$_{exp}$ was inline with NSQD$_{obs}$ (movement inline with correlated random walk). For both, SUMMER (Jul 9th to Aug 6th) and LATE SUMMER (Aug 7th to Aug 23rd), models indicated significant over-prediction of NSQD$_{exp}$, indicating site fidelity. Large fluctuations were visible within both sub-seasons. During HUNT (Aug 24th to Sep 29th) no clear tendency to either site fidelity or directed movement was visible and NSQD$_{exp}$ values were highly variable. Modest under-prediction (directed movement tendency) was found during RUT (Sep 30th to Oct 11th). The strongest tendencies for directed movements (strong under-prediction) were found during AUTUMN (Oct 12th to Nov 4th), WINTER (Dec 19th to Jan 22nd) and SPRING (Apr 2nd to May 5th), while both for EARLY WINTER (Nov 5th to Dec 18th) and LATE WINTER (Jan 23rd to Apr 1st) under-prediction of $NSQD_{exp}$ was visible, but not as strong as for the three sub-seasons earlier. PRE CALVING (May 6th to May 13th), finally, demonstrated no clear tendency for site fidelity or directed movement.

Regularity of movements

Results from fractal dimension analysis of movement paths on population level revealed significant differences between sub-seasons (see Figure 2-5).

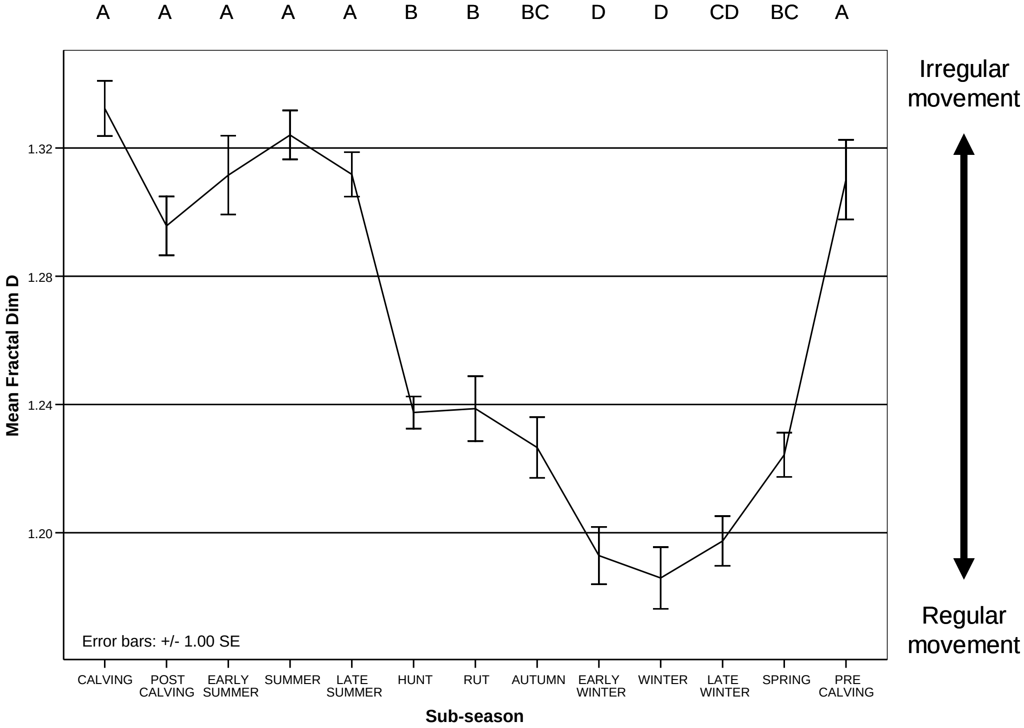

Figure 2-5: Mean fractal dimension by sub-season[50]

Six significantly differing sub-season groups with respect to estimated fractal dimension D have been identified: The group with the highest estimated means of fractal dimension D (app. 1.29 to 1.33) suggests highly irregular movement patterns in all three summer sub-seasons (EARLY SUMMER, SUMMER, LATE SUMMER) and the three calving related sub-seasons (PRE CALVING, CALVING, POST CALVING). CALVING demonstrated

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[50] Capital letters indicate significantly differing means of fractal dimension D based on SNK multiple comparison test ($\alpha=0.05$); means with the same latter do not significantly differ. Error bars depict +/- one standeard error of fractal dimensions estimated from annual values.

highest fractal values (~1.33) while PRE/POST CALVING yielded lowest Ds (app. 1.29 to 1.30). All three summer seasons fell within the 1.31 to 1.32 fractal dimension interval.

Both, HUNT and RUT, demonstrated a fractal dimension D off app. 1.24 and thereby constituted a second group, which is significantly different from other sub-seasons. Movement patterns of these seasons are judged as intermediate between regular and irregular movement trajectories.

Analysis further showed that EARLY WINTER and WINTER differ significantly as compared to other groups as the mean fractal dimensions within these seasons was estimated to fall between app. 1.18 to 1.19. Movement patterns were thereby clearly characterized as regular. LATE WINTER with an estimated D off ~1.20 can also be regarded as belonging to this group even though significance fell slightly short.

Finally, both, AUTUMN and SPRING, yielded comparable fractal dimensions of app. 1.23 (and thereby intermediate values without a clear preference of regular or irregular movement patterns). This group can either be viewed as part of the second group (HUNT, RUT) or constituting its own significantly differing group of sub-seasons.

Activity level

As for the analysis of the fractal dimensions, also the estimates of activity level (mean step length per hour) revealed significant differences between sub-seasons (see Figure 2-6).

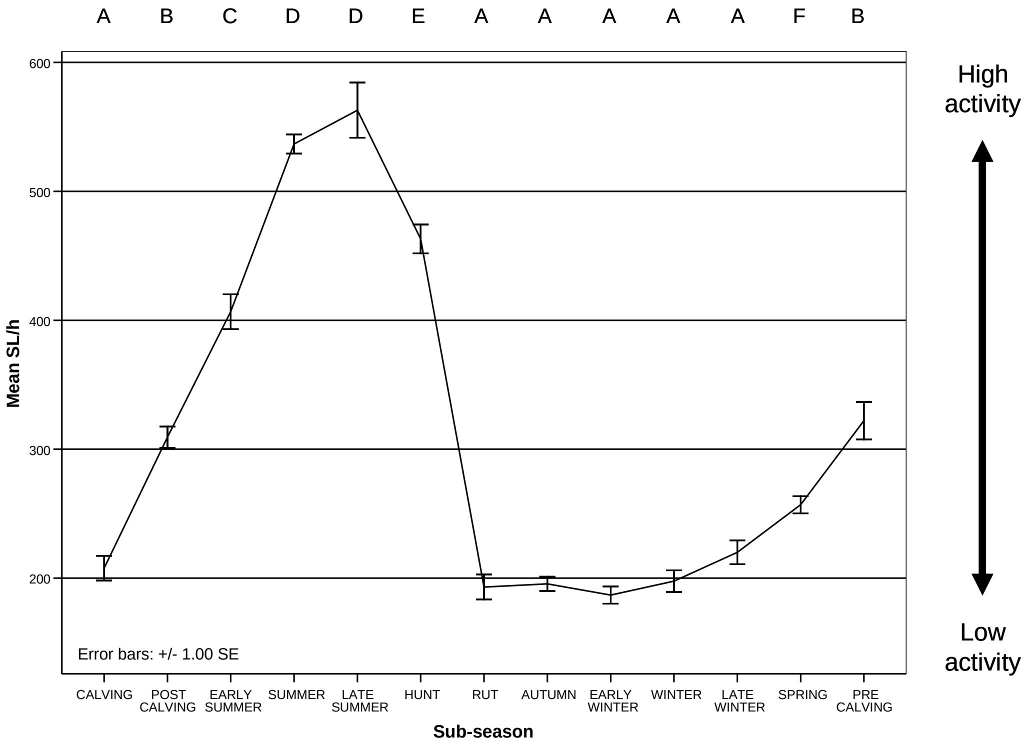

Figure 2-6: Mean average step length by sub-season[51]

CALVING, RUT, AUTUMN, EARLY WINTER, WINTER and LATE WINTER, were identified as the largest group to significantly differ from other sub-seasons. It demonstrated the lowest activity rates (estimated mean of 200 m per hour). Estimated activity rates during SPRING were slightly higher (~260 m per hour) and differed significantly from all other sub-seasons. POST CALVING and PRE CALVING formed a third group (intermediate activity rates of ~310 m per hour), followed by EARLY SUMMER with a mean movement rate of app. 400 m per hour. HUNT as a single sub-season yielded app. 460 m per hour, while SUMMER and LATE SUMMER depicted highest activity rates (estimated mean of app. 550 m per hour).

Size/stability of sub-seasonal home ranges

Both, size and stability of sub-seasonal home ranges as estimated using 95% kernels, showed significant differences during the annual cycle (see Figure 2-7).

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[51] Capital letters indicate significantly differing means of fractal dimension D based on SNK multiple comparison test (α=0.05); means with the same latter do not significantly differ. Error bars depict +/- one standard error of fractal dimensions estimated from annual values.

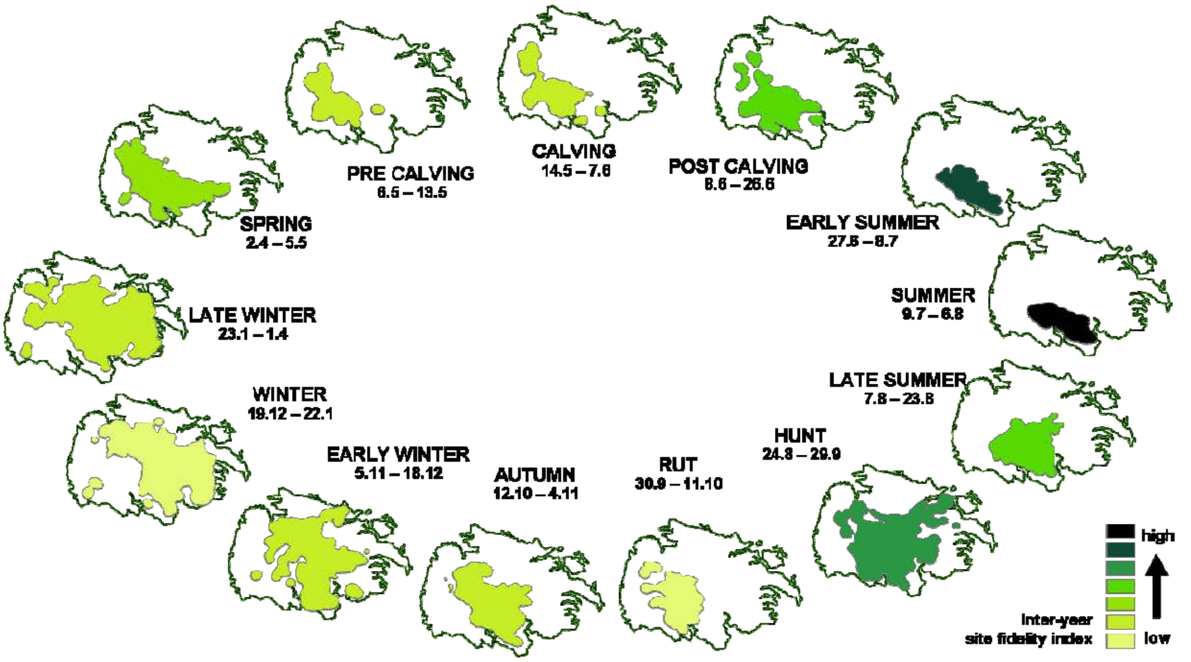

Figure 2-7: 95% home range kernels by sub-season[52]

During PRE CALVING, CALVING and POST CALVING the estimated kernel home ranges were located within the western and south-central areas of the study area. GPS-positions of the reindeer also were more clustered as compared to other sub-seasons and the site fidelity between years was intermediate during the study period (2001 to 2006).

During both, EARLY SUMMER and SUMMER, reindeer were found to be concentrated within a smaller part of south-central Hardangervidda. Inter-year site fidelity was very high for both seasons. During LATE SUMMER these tendencies still held true but estimated kernel home range extended significantly toward the south-east of the study area and site fidelity between years decreased to intermediate values.

During HUNT reindeer appeared to be distributed across the entire study area, but did not cross Rv7 in the north and Rv55 in the south of Hardangervidda. Stability of sub-seasonal home range between years was found to be intermediate to high during this season.

Following HUNT the distribution of reindeer during RUT was again found to be clustered within the western to central parts of Hardangervidda similar to what was found during LATE SUMMER but was to a larger degree shifted to the western parts of the area. Inter-year site fidelity, however, was found to be rather low as compared to the average values of other sub-

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[52] Note that both, the length of the different sub-seasons and number of individuals, differ by sub-season. The size of the 95% home range kernels can therefore not be directly compared. Figure 2-7 should hence only be seen as illustrative for the spatial shifts in home range locations.

seasons. During AUTUMN the estimated kernel home range significantly increased in an easterly direction and inter-year stability of home ranges was slightly higher but still below average as compared to the whole annual cycle.

During EARLY WINTER, WINTER and LATE WINTER reindeer utilized extensive areas in the eastern and central parts of Hardangervidda. From EARLY to LATE WINTER home range sizes increases significantly. For all three seasons large area sizes corresponded with low values for inter-year stability.

During SPRING, finally, the analysis suggests a contraction in home range size and a westwards shift towards the calving areas. Stability of the estimated home range between years yielded intermediate values for SPRING.

Cycle of annual movement patterns

Combining the four parameters described above within an annual cycle of movement patterns, revealed significant differences between seasons (see Figure 2-8):

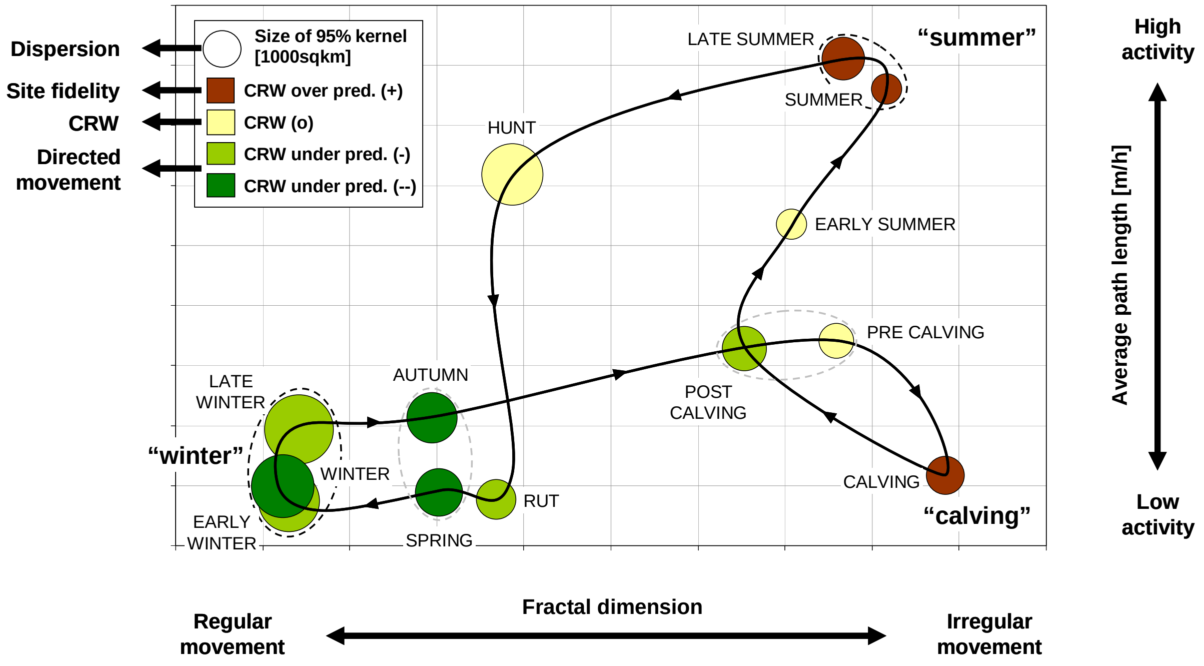

Figure 2-8: Cycle of annual movement patterns[53]

Three distinct sub-seasonal groups define the extremes of this cycle: "calving", "summer" and "winter"):

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[53] Again, as for Figure 2-7, it should be kept in mind, that length and number of individuals differed by sub-season and that therefore the size of the 95% home range kernels should only be seen as illustrative.

Movement patterns during “calving” (CALVING) can be summarized by a low activity levels (~200 m per hour), dominated by irregular movements with high fractal dimensions (~1.33) and site fidelity (over-prediction of $NSQD_{exp}$ compared to $NSQD_{obs}$ within CRW). Estimated kernel home ranges were clustered within western and south-central Hardangervidda, but with some considerable variation between years within the study period (2001 to 2006).

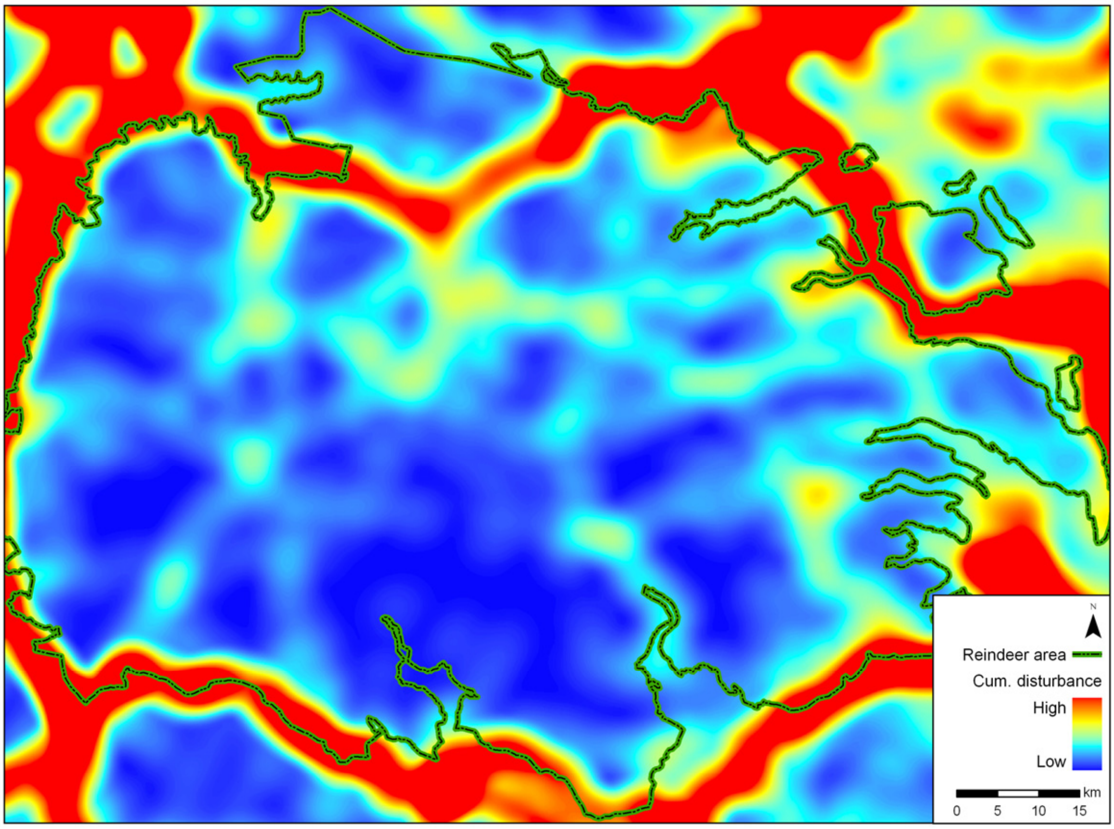
During “summer” (SUMMER, LATE SUMMER) on the other hand, movement patterns were characterized by very high activity levels (app. 550 m per hour), again by irregular movements (~1.32) and high site fidelity (over-prediction of $NSQD_{exp}$ as compared to $NSQD_{obs}$ within CRW), but depicted a high concentration within a very confined area in the south-central parts of the study area also with high inter-year stability of sub-seasonal home ranges.

Movement patterns during the “winter” periods (EARLY WINTER, WINTER, LATE WINTER), the third characteristic sub-season group, yielded very low activity rates (app. 200 m per hour), showed regular (app. 1.18 to 1.20) and directed movements (under-prediction of $NSQD_{exp}$ compared to $NSQD_{obs}$ within CRW) with an extensive home range use covering more or less the entire eastern and central parts of Hardangervidda with high variations between single years of the study period (2001 to 2006).

Five additional sub-seasonal groups can be clustered according to movement pattern parameters, characterized by intermediate values: “migration” (SPRING, AUTUMN), “rut” (RUT), “hunt” (HUNT), “early summer” (EARLY SUMMER) and “pre/post calving” (PRE CALVING, POST CALVING). During “migration” the activity rate is comparable to the “winter” seasons. While movements seemed to be only slightly more irregular, the directionality of movement was even higher as compared to “winter” periods and home ranges were more stable between years. “Rut” shared similar activity rates and directionality of movements with the “winter” seasons, but movements were more irregular and home ranges were significantly more stable between years. During “hunt”, on the other hand, home ranges showed higher inter-year stability as compared to the “winter” seasons and movements were significantly less directed and more irregular, while activity rate was by far greater. “Early summer” depicted similar activity rates and directionality as “hunt” and home ranges were relatively constant between years. In addition, movements were more irregular. During “pre/post-calving”, finally, intermediate values were reached for all parameters (activity level, fractal dimension, size/stability of home range as well as CRW results).

Cumulated human disturbance vs. summer tracking-data

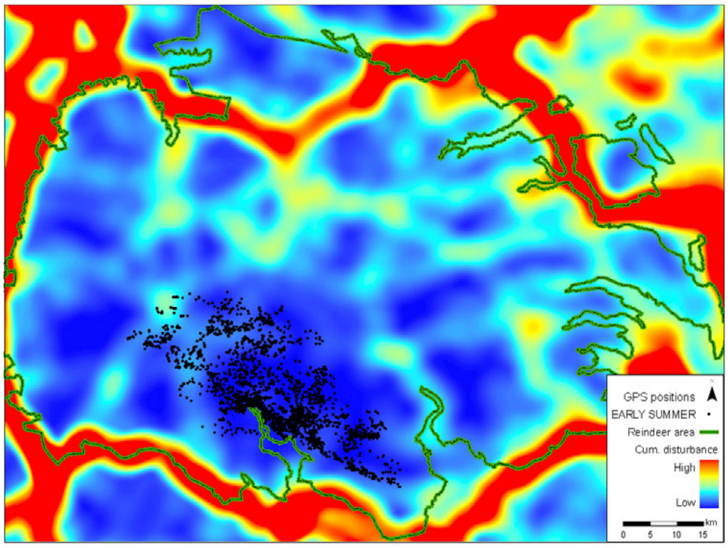
The level of cumulated human disturbance in Hardangervidda as estimated in chapter 2.2 revealed significant spatial differences within the study area (see Map 2-1):



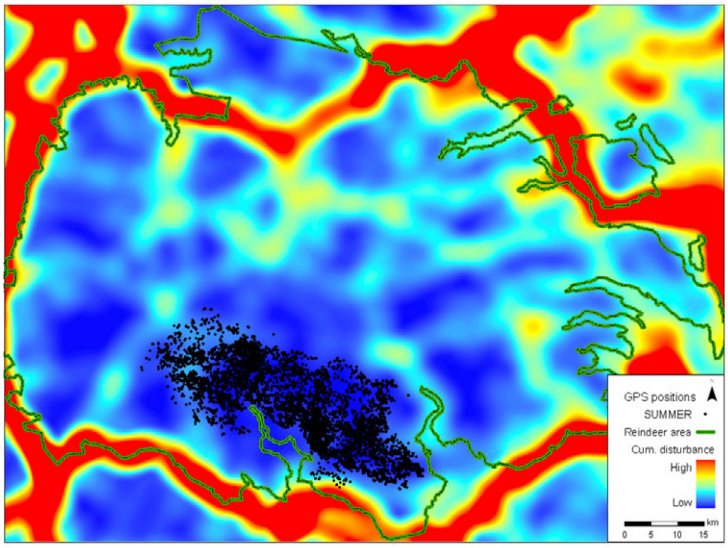
Map 2-1: Cumulative disturbance in Hardangervidda – illustration

As to be expected, the Hardangervidda reindeer area is generally bordered from its neighboring areas by stretches of high cumulated disturbance intensities. A clear impact of Rv7 in the north is visible, separating the Hardangerjökull area from the rest of the study area. In the north-east the adjacent habitat islands are also separated from the main area by clustered human infrastructure. Within the main area of Hardangervidda the (north-) eastern parts seem to be more affected by human disturbance than the (south-) western parts. Especially the south-central part is depicted as little influenced by human disturbance.

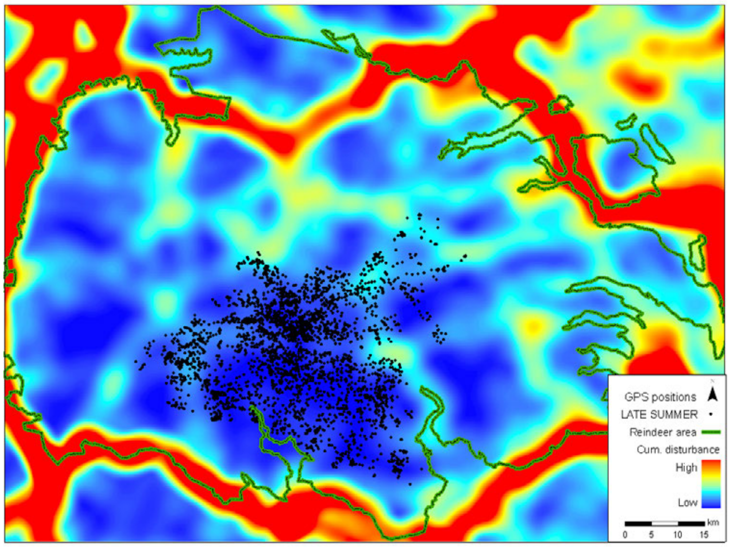
Map 2-2, Map 2-3 and Map 2-4 give the results of the overlay of the above map with the distributions of reindeer during EARLY SUMMER, SUMMER and LATE SUMMER.



Map 2-2: Cumulative disturbance vs. reindeer distribution in EARLY SUMMER – illustration



Map 2-3: Cumulative disturbance vs. reindeer distribution in SUMMER – illustration



Map 2-4: Cumulative disturbance vs. reindeer distribution in LATE SUMMER – illustration

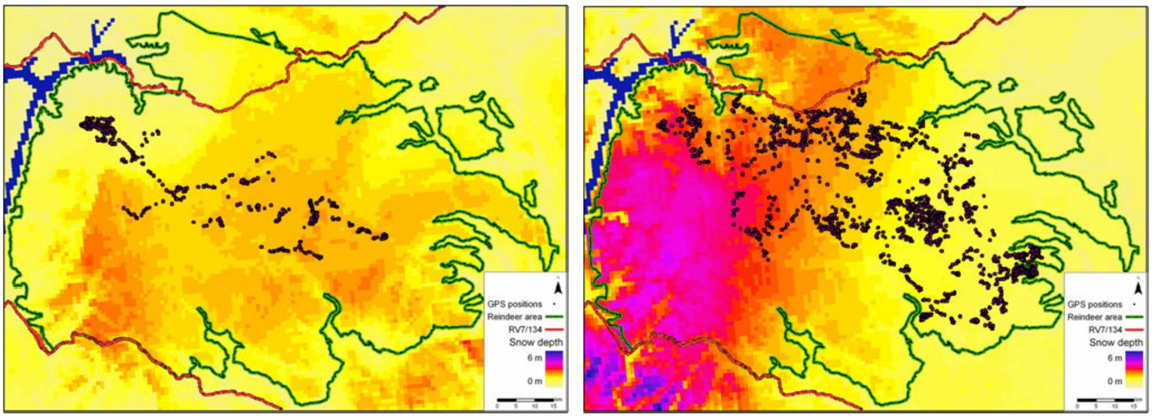
Visual interpretation of these maps indicates a strong and positive correlation of the selected sub-seasonal habitats with low levels of cumulated human disturbance for all three summer seasons. Even though other areas within the study area depict low levels of disturbance (especially within the western parts of Hardangervidda), the selected summer habitat within the south-central part of Hardangervidda is by far the largest continuous area with low levels of cumulated human disturbance.

Snow condition vs. winter tracking-data

Map 2-5 visualizes the spatial relationship between snow depth and reindeer distribution (GPS fixes) in Hardangervidda for LATE WINTER between 2001 and 2006:

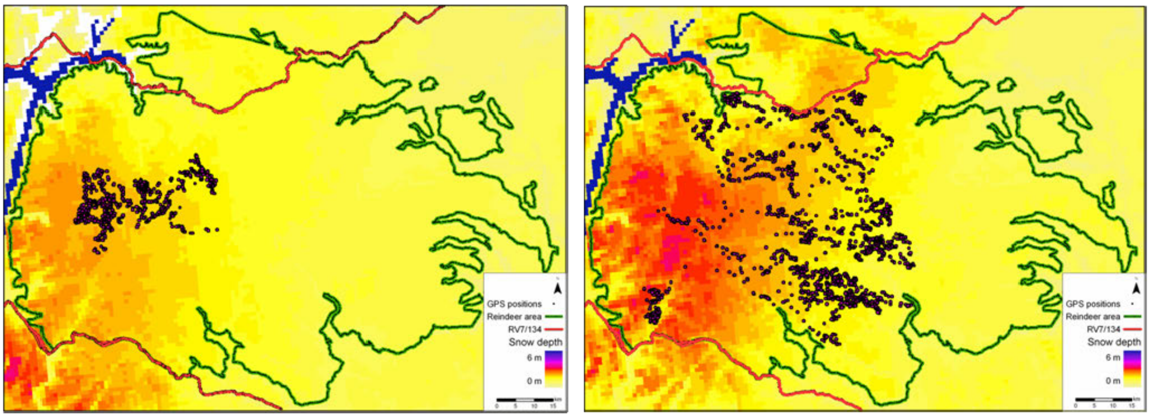
A visual interpretation of the various maps suggests a dependency of the selected locations on snow depth. Especially within the upper bound years 2002 and 2005 with snow depth over 5 m within the western parts over Hardangervidda, the selected winter habitats were shifted to the more eastern areas, demonstrating lesser snow depth values. In contrast, during lower bound years (2003 and 2006) reindeer appear to have used more central and western parts within the study area. This especially holds true during LATE WINTER 2001 when areas within the north-western range of Hardangervidda, which had exceptionally low snow depth values during that year, were used more intensely by reindeer.

In contrast to the snow depth results, LWC showed a far lesser impact on winter distribution of reindeer and results indicated no clear correlation between the two.



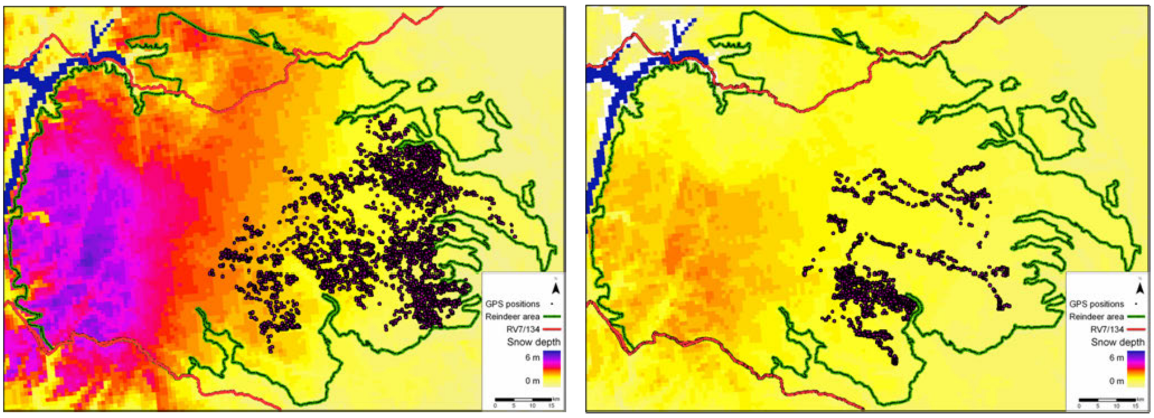
Snow depth late winter 2001

Snow depth late winter 2002



Snow depth late winter 2003

Snow depth late winter 2004



Snow depth late winter 2005

Snow depth late winter 2006

Map 2-5: Snow depth and reindeer distribution in Hardangervidda late winter 2001 to 2006

2.4 Discussion

Annual cycle of sub-seasonal movement patterns

The observed and profound differences in the annual cycle of reindeer’s movement patterns suggest a cyclic change in their behavioral strategy. This probably is because reindeer optimize habitat use through making specific decisions for the four parameters described above (directionality and regularity of movement, activity level and size/stability of seasonal home range). Four major factor groups are discussed as possible explanations for these shifts in behavioral strategy: (i) climate (energy expenditure, insect harassment), (ii) differences in spatial distribution and quality of resources between seasons (forage availability, snow depth), (iii) predator avoidance and reaction to human disturbance (recreational activities, hunt, predators) and (iv) social behavior of reindeer (mother-offspring behavior, mating, herd behavior, etc.).

Reduced activity level of reindeer during “calving” (CALVING) can be explained by mother-offspring behavior and a reduced mobility of neonates (see. e.g. Skogland 1989b). Both factors are also seen as a possible reason for site fidelity and irregular movement patterns during this time period, possibly amplified by females controlling for energy expenditure within the still harsher climate during calving. Both, forage availability and predator avoidance, are known to influence habitat selection of reindeer during calving significantly (Barten, Bowyer & Jenkins 2001). In case of the results from Hardangervidda, reindeer’s selection of the western and south-central parts might therefore also be due to these two factors. First, predator avoidance within these areas is fostered by the ruggedness of the terrain. Second, the western and south-central parts of Hardangervidda are characterized by high variability of elevation and thereby allow for closeness to areas with early green-up (Klein 1970, 1990; Skogland 1980, 1984a), important for reindeer’s protein intake (Barboza & Parker 2009). Thus these two qualities of the selected terrain are likely to cause inter-year site fidelity of (large-scale) calving ground selection. The observed annual spatial differences in small-scale calving ground selection, however, can partially be caused by the local variation in snow conditions.

During “summer” (SUMMER, LATE SUMMER), high activity rates[54] are expected to result from an altered trade-off between energy intake and expenditure. Intake possibilities are favored through the abundance of high value forage plants (protein rich herbs, green plants), the lack of snow cover and longer daytime hours. Climatic conditions, on the other hand, impose significantly less restrictions on movements. Activity rates are further raised through insect harassment. For insect relief reindeer are well known to alter their behavior and to form large groups (Helle & Aspi 1983; Skogland 1989b; Helle *et al.* 1992). Areas with insect relief (higher elevation, snow covered terrain, wind exposure) are actively selected for (Hagemoen

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[54] Note, that the activity patterns of reindeer have also been described as a major determinant for growth and fattening of *Rangifer* (Reimers 1980). Increased activity levels due to (cumulated) human disturbance can therefore directly affect population dynamics.

& Reimers 2002; Colman *et al.* 2001, 2003; Skarin *et al.* 2004). Movements between these areas and rich forage pastures are believed to generate the overall higher activity levels observed in the data. Both, site fidelity and irregularity of movements, within “summer” periods could potentially be explained by unique spatial qualities of summer habitats (distribution of vegetation, insect relief, etc.). Such factors could therefore also (partially) explain the restricted habitat use during “summer” and the high inter-year stability of summer home ranges. On the other hand, little quantitative knowledge on such factor uniqueness for the south-central areas of the study area is available to strengthen this hypothesis. To further assess this possibility it will be necessary to formulate a habitat selection model incorporating all potentially important factors and habitat characteristics for the area (see chapter 5). An alternative explanation for “summer” confinement of reindeer within habitat depicted could be human disturbance and/or natural barrier effects (see below).

The observed movement patterns during “winter” (EARLY WINTER, WINTER, LATE WINTER) are hypothesized to result from a critical trade-off between energy expenditure and intake: as forage resources are scare (phenological state of vegetation, deep snow cover, etc.) and climatic conditions extreme, reindeer have to limit movements to save energy during winter (Loe *et al.* 2007). This is reflected by the observed low activity rates. At the same time energy intake has to be maximized through both, regular and directed movements. Low observed fractal dimensions and under-prediction of CRW models are a result of this strategy. Findings from other studies have shown similar results (e.g. Ferguson, Rettie & Messier 1998). The scarcity of resources is also believed to explain the use of larger areas and a more extensive use of home ranges during winter. The eastward shift of the winter home ranges also seems plausible since the east-west gradient within the study area (see Bakkestuen, Erikstad & Økland 2008) follows lesser snow depth and higher lichen volumes within eastern Hardangervidda (see chapter 1.3). The low stability of home ranges between years is likely to be caused by spatial differences in the availability of lichen biomass due to shifts in snow depth on a year-to-year basis. As for the “summer” situation it seems necessary to model the habitat use of reindeer during “winter” in order to better understand the relative impact on single factors like forage availability and snow depth on reindeer habitat selection (see chapter 5). A preliminary discussion of the potential impact of spatial differences in snow depth follows below.

Directionality of movements was found to be highest during “migration” (SPRING; AUTUMN). This result seems plausible with respect the migratory behavior of reindeer and has been confirmed for other reindeer/caribou populations (see e.g. Bergman, Schaefer &

Luttich 2000). Although activity levels during these periods are relatively low (probably caused by a need to keep energy expenditure low during the still/already harsh climatic conditions during migration), the distances covered are significantly under-predicted by CRW. This confirms a clear tendency of reindeer in Hardangervidda to actively select for seasonal habitats providing important time-specific resources and that this process is generating a migratory lifestyle with seasonal shifts between geographically distinct home ranges.

Both, activity level and regularity of movement during “hunt” (HUNT), are significantly different from other periods of the annual movement pattern cycle. Compared to LATE SUMMER (predecessor) and RUT (following sub-season) the activity level is relatively high (see Figure 2-8: Cycle of annual movement patterns). This might be caused by hunting stress and frequent flight behavior during this period (Skogland & Grövan 1988; Reimers *et al.* 2009; Baskin & Hjälten 2001). This hypothesis is also strengthened by the low inter-year stability during HUNT, as seasonal home ranges both, before (LATE SUMMER) and after (RUT), are significantly more concentrated and located in similar parts of the study area (west-central Hardangervidda).

The results suggest that both, “early summer” (EARLY SUMMER) and “pre/post-calving” (PRE CALVING, POST CALVING), might be seen as transitional periods within reindeer’s annual movement cycle (see Figure 2-8: Cycle of annual movement patterns). While PRE CALVING bridges parameter values between AUTUMN and CALVING season, POST CALVING resembles parameter values between CALVING and EARLY SUMMER. EARLY SUMMER, on the other hand, clearly demonstrates parameter values between POST CALVING and SUMMER.

Altogether reindeer in Hardangervidda appear to have a migratory lifestyle with seasonal shifts in habitat preferences and thereby an annual cycle, where animals are returning to similar habitats and habitat utilization strategies on a year-to-year basis. As such the migration in Hardangervidda appears to be driven by a "bottom-up" process, where the suitability of the habitat is driving the migratory shift in habitat use und utilization.

Selection and calculation of single parameters

The proposed parameters used to describe seasonal movement patterns of reindeer (directionality and regularity of movement, activity level and size/stability of seasonal home range) incorporate several essential qualities within movement theory. Significant differences within the annual cycle thus also highlight the decisive character of the selected parameters. Nevertheless, the applied parameter composition cannot be regarded as definite or complete, since other decisive factors describing movement are not included: Especially behavioral aspects (being vs. doing) are not addressed within this quantitative approach[55].

Calculation of movement patterns is dependent on scale (e.g. Johnson *et al.* 2002a/b). Especially activity level, fractal dimension and CRW models are dependent on the measurement scales selected for the GPS units. It is thus important to note, that, given the decision for a three-hour fix-rate interval, the resulting movement pattern parameters can only be interpreted within the corresponding scale. E.g. movement patterns depicted to optimize selection within feeding sites (patch-level) cannot appropriately be detected or described. It thus follows that measurement scale decisions have to be carefully considered dependent on research scale.

Empirical definition of sub-seasons can clearly be regarded as a desirable starting point for detection and description of reindeer's seasonal movement patterns. Results from floating cut-off points using linear regression on CRW calculated for individuals can be seen as a potential means to do so. On the other hand, even though the proposed method offers a significant increase in objectivity, it still leaves a certain amount of freedom for defining cut-of points. Furthermore, as the following results depend on prior cut-off point decisions, definition of sub-seasons following this method can be seen as interdependent. CRW results only represent one dimension of an individuals movement patterns. It would therefore be desirable if sub-seasons could be defined empirically based on a model including more than just this factor (e.g. to include one or all of the other three parameters used to describe movement patterns). On the other hand, cut-off point decisions interdependent between four or more parameters are difficult to determine. Against this background the decision to focus on one parameter alone, is a practical one.

So far this chapter has tried to disentangle the movement patterns of reindeer in Hardangervidda. In order to further understand the factors underlying the different movement patterns, and to prepare for the later habitat modeling, the GPS data were held up against some environmental data sets that might serve to explain the observed differences in movement patterns.

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[55] For the importance of behavioral studies in conservation biology see Sutherland (1998). See e.g. Colman *et al.* (2001, 2004) as examples for twenty-four-hour behavioral studies of reindeer during summer.

Impact of cumulated human disturbance

As discussed above, seasonal distribution reindeer during “summer” (EARLY SUMMER, SUMMER, LATE SUMMER) was clustered within the south-central parts of the study area (see above). This clustering could potentially be explained by both, the spatial feature qualities within the selected summer habitats and/or cumulated human disturbance.

Visual overlays of the disturbance map with the seasonal reindeer distributions suggest a disturbance related effect restricting reindeer from utilizing smaller undisturbed spatial entities. However, the spatial distribution of reindeer during SUMMER also suggests other potential factors as possible explanations for the observed clustering effect: Even though undisturbed areas do continue flawlessly further north from the preferred (used) areas and no clear disturbance related barrier should prevent reindeer from accessing these areas, these potential summer habitats were not utilized (see Map 2-3). It can therefore be argued that either habitat qualities within these more northern undisturbed areas are significantly different and less attractive, or that other and so far unknown factors do play a significant role in reindeer habitat selection and thus also distribution patterns (e.g. natural barriers). As northern areas were indeed used during both, EARLY and LATE SUMMER (see Map 2-2 and Map 2-4), the earlier explanation seems less likely. Terrain analysis, on the other hand, suggests Kvennedalen as a major natural east-west facing valley/river system to indeed impose a natural barrier effect for locomotion during “summer”. In order to further assess the relative importance of various factors on reindeer habitat selection and distribution during summer an explicit and quantitative model incorporating the potential relevant factors is formulated in chapter 5.

Impact of snow depth

As expected, snow depth seems to influence reindeer distribution during winter significantly. While the visual overlays seem to support this initial hypothesis, reindeer’s functional response to snow has to be estimated in conjunction with other relevant factors determining habitat selection. This will be done in chapter 5.

The smaller impact of LWC seems plausible since this parameter is describing snow density and behavioral studies suggest surface condition of snow to be of much more importance for forage availability as icing can prevent reindeer from cratering (Skogland 1978; Kohler & Aanes 2004; Chan *et al.* 2005; Hansen, Aanes & Sæther 2010; Stien *et al.* 2010). Due to a lack of spatially explicit data for the selected study area, this hypothesis could not be examined further.

Conclusion

The proposed approach to detect and quantify the seasonal distributions and movement patterns of reindeer in Hardangervidda can be seen as fully independent of any prior assumptions regarding reindeer behavior and seasonality (empirical method). As a quantitative approach it holds a reasonable degree of objectivity and comparability both, trough time and between species and/or populations. It can therefore be regarded as a potential baseline for a possible change detection and impact assessment of e.g. an altered degree of disturbance or population density.

Weaknesses and possible improvements of this method include a dependency of the detectable movement patterns on the measurement scale. Hence some careful considerations are necessary to find an appropriate scale corresponding to the relevant research questions under consideration (e.g. feeding site vs. migration). Furthermore, an empirical definition of sub-seasons within the proposed approach is based on a single parameter only (floating cut-of points within CRW) and an interesting approach for further studies would be to include several parameters simultaneously in the process of defining cut-of points. In order to directly compare home range sizes between sub-seasons, the utilized areas should be normalized by period lengths and number of individuals. For future purposes it would be desirable to calibrate the contribution of the single disturbance related factors to the overall layer empirically, both, the search radii and the individual weights for overlaying. Finally, it is important to note that seasonal distributions and movement patterns of reindeer within the study area are likely to depend on population density. Future studies either of comparative populations or at higher population densities would give valuable insights on the influence of reindeer density on behavioral strategies.

3 Land cover classification

3.1 Introduction

Habitat selection of reindeer dependent on land cover

Land cover composes a core input factor for the explanation of habitat use by reindeer and numerous hypotheses on reindeer's seasonal selection patterns of vegetation have been presented and tested by researchers over time (see e.g. Warenberg 1977; Hansen *et al.* 2001; Ihl & Klein 2001; Johnson et al. 2003; Johnson, Parker & Heard 2001; Skogland 1984a or Warenberg *et al.* 1997).

Ridges dominated by lichen heaths communities are known to be the most important grazing resource for reindeer during winter (Skogland 1984a; Gaare, Tømmervik & Hoem 2005). A study carried out in Hardangervidda by Østbye *et al.* (1975) found reindeer to spend between 80 – 100% of their total grazing time on lichen ridges during the winter period. Graminoid ridges as described by Fremstad (1997) dominated by *Festuca ovina*, *Juncus trifidua*, *Deshampsia flexuosa*, *Carex bigelowii*, together with lichens like *Cetraria nivalis*, *Cladonia mitis* and *Cladonia rangiferina* cover significant areas of Hardangervidda and are considered important winter grazing habitats.

Pellet-group counts carried out by Edenius *et al.* (2003) and Skogland (1984a) suggested snowbed vegetation to be the most intensively selected vegetation type by reindeer during summer. Reindeer are believed to select areas containing snowbed vegetation for a variety of reasons: Snowbed vegetation provides highly nutritious food both, during the upbringing of the calves and summer, important for resupplying reindeer with protein (Barboza & Parker 2009). Lye (1975) found species like *Salix herbacea* and on more "eutrophic" localities *Salix polaris* to be very important grazing species for reindeer. Before snowmelt snowbed vegetation can also provide relief from both, insect harassment (Gaare, Thomson & Kjos-Hanssen 1975; Downes, Theberge & Smith 1986; Walsh *et al.* 1992) and high temperatures (Ion & Kershaw 1989; Andersen & Nilsen 1998). Virtanen (2000) concluded snowbed vegetation to be a limiting factor for reindeer summer ranges due to both, their scarcity and their sensitivity to grazing pressure (Virtanen 2000).

Depending on the snow cover, leeside vegetation can be utilized by reindeer in early as well as in late winter, during calving and in winter with thin snow covers (Gaare, Thomson & Kjos-Hanssen 1975). Mires, on the other hand, are believed to be an important forage resource for reindeer during late spring to late summer (Gaare, Tømmervik & Hoem 2005).

Reindeer can use forests as a grazing resource in autumn (Gaare, Tømmervik & Hoem 2005). It is also here where reindeer find most of the mushrooms, which are known protein contributors in the diets of cervids (see. e.g. Inga 2007; Launchbaug & Urness 1993). Unproductive areas like snow and ice fields or areas dominated by rocky terrain can provide refuge from flies and high temperatures for reindeer during warm and sunny summer days with little wind (Hagemoen & Reimers 2002). Wide and deep water bodies are believed to function as migration barriers for reindeer herds when uncovered by ice from early summer throughout the rut.

Snow cover and elevation determine distribution of alpine vegetation

In general, snow cover and elevation have a major influence on the distribution of alpine vegetation in mountainous areas.

Annual snow cover patterns in the mountainous areas of Scandinavia are mostly dependent on the terrain. Due to their wind exposure, mountain ridges exhibit sparse or no snow cover during most part of the winter with a maximum snow depth of 50 – 60 cm (Lye 1975). Extreme winter temperatures, thin soil covers and dry summer conditions due to concave terrain lead to restrictive conditions favoring lichen or grass heath dominated vegetation communities depending on snow cover. Generally ridges with thin snow cover are dominated by *Loiseleuria procumbens*, *Alectoria ochroleuca* and *Cetraria nivalis* (Carlsson, Karlsson & Svensson 1999). On the other hand, more accumulated snow cover favor *Alectoria ochroleuca* and *Cetraria nivalis* disappear while *Cladonia stellaris* together with *Cladonia rangiferina* and *Cladonia mitis* tend to dominate. Due to thicker snow depths ranging between 1 – 3 m, slopes within the more intermediate mountain parts provide better protection from cold winter temperatures. At the same time they still allow for a long enough vegetation period suitable for more demanding plants due to an early snow melt in summer. The resulting leeside vegetation composition is determined by water and nutrition level. While mostly oligotrophic bilberry and dry grass heaths communities dominate, richer plant communities develop within Cambro-Silurian phyllitic rocks ranging form dry heath over cushion pillow grasses, herbs and meadows dominated by willows to eutrophic mires, depending on water-conditions (Fremstad 1997). At the bottom of mountain slopes deep snow covers between 4 – 10 m can accumulate during winter (Lye 1975) protecting vegetation from cold winter temperatures. Snow cover often lasting till July favors snowbed vegetation tolerant both, to short vegetation and cryoturbation. While water provision is good, plant composition is mainly dependent on nutrition levels with *Salix herbacea* and mosses prominent at oligotrophic and *Salix polaris* at eutrophic sites.

Analogue to snow cover, elevation has a profound impact on vegetation composition in Hardangervidda: With trees requiring summer average temperatures above 7.3^0 C Wielgolaski (2000) draws the timberline at app. 1,050 m on the eastern side and often lower on the more oceanic western side of Hardangervidda. The distribution of willow-shrubs is limited by an average summer temperature of about 5.5^0 C resulting in an altitudinal threshold at about 1,320 – 1,350 m (Wielgolaski 2000).

Satellite-based methods for mapping alpine vegetation

Remote sensing from satellites has provided wildlife researchers and managers with new and innovative possibilities for the surveillance of critical parameters, such as distribution of vegetation, snow cover, infrastructure and pasture quality, crucial for the monitoring and risk mapping of populations. For mapping the arctic-alpine vegetation satellite-based methods have shown substantial advantages over traditional methods like aerial surveys because they allow for mapping the distribution of cover types over large spatial areas like Hardangervidda which are difficult to access. Furthermore, satellite-based remote sensing offers detailed spectral information with sufficient spatial resolution needed for land cover classification. Landsat, IRS-1C/D and SPOT imagery has therefore been widely used in Alaska, Canada and Fennoscandia to produce vegetation and land cover maps of tundra and mountain areas (e.g. Walker 1999; Tømmervik & Lauknes 1987; Stow, Burns & Hope 1989; Mikkola 1996; Tømmervik, Johansen & Lauknes 1997; Toutoubalina & Rees 1999; Nordberg & Allard 2002; Edenius *et al.* 2003; Tømmervik *et al.* 2003; Tømmervik, Høgda & Solheim 2003; Tømmervik *et al.* 2004; Nordberg & Evertson 2005; Théau, Peddle & Duguay 2005; Ferguson 1991; Johansen *et al.* 2004; Makela & Pekkarinen 2004; Muller, Racoviteanu & Walker 1999 or Joria & Jorgensen 1996). These approaches have generally used field-based validation of supervised and hybrid supervised–unsupervised classification methods. Although they give a sufficient classification accuracy of more than 80% for the densest lichen dominated types (Colpaert, Kumpula & Nieminen 2003; Tømmervik *et al.* 2003; Nordberg & Evertson 2003), these methods give poorer results concerning snowbeds and mires, which are important summer and autumn pastures for reindeer (Manseau, Huot & Crete 1996; Edenius *et al.* 2003; Sandström *et al.* 2003). When an expert classification is required to combine and allocate classification results, the process becomes time consuming and difficult to repeat.

Classification methods

A broad variety of classification methods has been developed with promising results during the last 20 years (see. e.g. Dwivedi, Kandrika & Ramana 2004; Tso & Mather 2001; Albertz 2001). Tow main groups are commonly distinguished:

Unsupervised methods like e.g. ISODATA (LEICA Geosystems 2003) use algorithms that are independent of training data for classification (e.g. Lillesand, Kiefer & Chipman 2007). Similar pixels are grouped into unlabeled classes (clusters) with the analyst having to later combine those clusters and label them with the appropriate land cover category. This method is technically easy to apply but it requires profound local knowledge on land cover classes for post processing and the results can be highly dependant on the analyst's interpretation. Examples are Tømmervik *et al.* (2003), who used ISODATA clustering to identify reindeer ranges in Forollhogna, Norway, or Rees, Williams & Vitebsky (2003), who used ISODATA clustering in combination with dendogram analysis for mapping land cover change in a reindeer herding area of the Russian Arctic based on Landsat TM and ETM+ imagery and indigenous knowledge.

Supervised classification methods use sample data for training (e.g. Lillesand, Kiefer & Chipman 2007). Classes can therefore directly be defined according to later application needs. While parametric supervised classification algorithms (e.g. parallelepiped, minimum distance, maximum likelihood and Mahalanobis distance) are based on statistically gained class-profiles, non-parametric methods like decision tree, kNN or neuronal networks (NN) are instead utilizing reflectance vectors of individual sample points for classifier training. Parametric classifiers – while considered easy to use and reasonably efficient – often demonstrate difficulties in handling heterogeneous classes and in integrating ancillary data. Accuracies using maximum likelihood classification are often superior to other parametric methods, as both, the variance/covariance matrix between classes and features a-priori class probabilities are utilized. On the other hand, it is dependent on normal distribution of band histograms within classes, whereas minimum distance is not. The implementation of non-parametric supervised classification methods is usually more complicated and time consuming as compared to parametric classification methods, as they often require advanced editing skills. On the other hand, they tend to yield superior results as they are more robust to class distributions and ancillary data can be integrated more easily. Both, the decision tree and the kNN method, have been frequently tested with high accuracies (e.g. Holmström & Fransson 2003; Franklin *et al.* 2001; Rogan *et al.* 2003) with decision trees being more controllable whereas kNN is considered easier to use. While Neural Networks have demonstrated promising results by being robust and fault tolerant and partially compensating for minor class variability (Tso & Mather 2001), they can be both, difficult to model and to repeat. Examples of parametric supervised classification are Nordberg & Allard (2002), who used maximum likelihood classification to identify land cover classes based on Landsat TM data, or Colpaert, Kumpula & Nieminen (1995), who classified reindeer ranges in Finland based on Landsat TM data. Supervised non-parametric classifiers have e.g. been applied by Hansen, Dubaya & DeFries (1996); Rogan *et al.* (2003) or Avci & Akyurek (2004), who all used decision trees for land cover mapping based on Landsat TM imagery.

Furthermore, hybrid classification methods use a combination of supervised and unsupervised classifiers. These hybrid classifiers are often used in praxis to break the compromises of single classifiers (e.g. Beaubien *et al.* 1999). Likewise, numerous meta classifiers have been developed and successfully implemented (Tso & Mather 2001). Meta classifiers assign pixels to classes by using second order classification rules (e.g. winner, voting, weighted probabilities, bagging, boosting) based on results from first order classifiers (see e.g. Tso & Mather 2001 or Manly 1997).

Ancillary data can improve classification accuracy

Although remote sensing using satellite images has become a widely used tool in habitat mapping, Arctic and high mountain vegetation still composes specific challenges for satellite analysis (Edenius *et al.* 2003): Small-scale vegetation patterns dominate as topography can differ largely within small areas. Furthermore, plant phenology is extremely variable due to both, a compressed and highly dynamic growing season and local as well as temporal differences in snow conditions and soil moisture. Altogether these parameters generate a fine-scaled vegetation mosaic with large spatial and temporal variations. In order to address these challenges various authors have applied methods including ancillary data independent from phenological variations (e.g. topography; snow cover, etc.) and thereby improved the classification accuracy significantly (e.g. Nilsen *et al.* 1999). By using ancillary data it is also possible to allow a differentiation in finer and more precise classes (habitats) (Edenius *et al.* 2003; Nilsen *et al.* 1999; Schardt & Gallaun 1999; Boresjo-Bronge & Wester 1999).

Digital elevation models (DEM) and its derivates (e.g. slope and aspect) are well known examples of ancillary datasets, which can be used to support the image classification process. DEMs are often used to supplement satellite data (e.g. Janssen, Jaarsma & Linden 1990) since plants (and thereby also vegetation classes) often are limited to specific elevations or aspects. Second sources of ancillary data are various thematic maps. Examples of such are climatic data (snow cover, rainfall, temperature, etc.) or vector overlays such as roads or rivers. In addition, satellite imagery from other seasons has proven useful since some of the more similar and confusing vegetation classes can be separated by utilizing time specific differences in plant phenology in the classification process (e.g. McRoberts *et al.* 2006).

While ancillary data provides crucial information to increase classification accuracy it can also increase classification complexity and/or result in serious sample size limitations as it often increases feature space dimensionality. Several methods or utilization rules have been developed and used in order to incorporate ancillary data into the classification process (see e.g. Hutchinson 1982): Most straight forwardly ancillary data can just be added to the models as additional variables (and thus increasing feature space dimensionality). While significant accuracy improvements can be achieved by this approach, both, weighting problems and over proportional increases in sample size requirements, can be prohibitive depending on the classifier used.

An alternative method is to use ancillary data to stratify the study area into masks based on one or more environmental threshold values (e.g. for elevation and/or snow cover). The classification can then be carried out within each of the individual strata. This method reduces the variability of the input data and allows the classifier to operate with a limited number of classes for each mask (Boresjö-Bronge & Rud 1995). Some of the problems connected with an increased feature space dimensionality are thereby reduced. Furthermore, the resulting strata can also be used to adjust the overall a-priory probabilities or to construct a spatially differentiated probability-layer for each class that can later be utilized by the classifier. Using this method Edenius *et al.* (2003) achieved an accuracy in mapping snow-bed vegetation between 69 – 77 %, depending on the data used. They concluded that small-scale, pixel-wise classification modeling may be useful for depicting sparsely occurring cover types considered as important determinants of range quality for reindeer. Another use of ancillary data within the classification process is to correct misclassified pixels in the post classification process. E.g. a rule-based inclusion of topographical data can help to correct pixels above the tree-line falsely classified as forest to the most likely class heather vegetation (Tso & Mather 2001).

Objectives

In order to organize and formulate the overlaying research questions of this dissertation (compare chapter 1.2), three main objectives were followed within this chapter:

i. The first aim was to accurately classify land cover in the alpine region of Hardangervidda as a central input factor for modeling the habitat selection of reindeer later. It is asked: What are the relevant land cover classes for resource selection of wild reindeer in the study area? How do they distribute spatially?

ii. The second aim was to compare and test selected parametric (maximum likelihood) and non-parametric (kNN and decision tree) supervised classification methods in terms of accuracy and feasibility. Questions in focus are: Which classifiers work best for vegetation classification within a mountainous area in Northern Europe?

iii. Finally, the third aim was to test the impact of including ancillary data on both, the overall classification accuracy and average user's-/builder's accuracies of the single classes. It was asked: Can the classification accuracy be improved by using ancillary data?

3.2 Methods

Land cover classification within this thesis followed a three-step approach. An overview is given in the following before describing the proposed methods in detail below.

a. Definition of relevant classes for training and testing within supervised classification: This was done based on their assumed relevance for the spatial behavior of reindeer, on class detectability by satellites as well as on existing classification systems and available vegetation samples from earlier studies (2000 to 2004). Sample points for training and testing were then collected in the field during the summers of 2005 and 2006. Outliers were removed and sample points were weighted with prior possibilities before classification in order to correct for biases in sample size between the single classes.

b. Selection and preparation of satellite images and ancillary data: Landsat imagery, DEM and derivates as well as satellite imagery from late winter and early summer were chosen. Preparation included orthorectification of images using high-resolution aerial photographs. Images were corrected for topography induced distortions using c-correction. Landsat was chosen as primary data as a trade off between image resolutions and the spatial extend of a single scene as well as image availability and backlog for a possible later change detection (past and future).

c. Land cover classification and accuracy assessment: Maximum likelihood, kNN and decision tree method were chosen as classifiers. Classification was carried out with and without ancillary data. As utilization rules for ancillary data a combination of homogeneous subsets creation (snow cover in early summer, relative pixel elevation compared to its neighbors) with adjusted prior possibilities and implementation of post classification rules for misclassified pixels (elevation, slope, snow cover in late winter) was chosen. Accuracy assessment and quantification of accuracy gains by using ancillary data were done using independent testing data collected in the field.

Distribution of vegetation classes in Hardangervidda

Understanding vegetation zones within the study area including their underling factors (topography, geology, temperature, precipitation and snow cover) is vital for class definition. In the following a brief description is given based on earlier studies, including distribution estimates when available:

As described in chapter 1.3, the Hardangervidda mountain plateau is situated in the range of 780 – 1,300 m a.s.l., and the topography is fairly level at the plateau itself, with differences of height in the range of 100 – 400 m, although there are some high peaks (above 1800 m) in the northern and south western part of the plateau. The bedrock consists mainly of gneissic bedrock of the Precambrian Baltic shield (Sonesson, Wielgolaski & Kallio 1974).

A substantial part of the area consists of unproductive habitats and Gaare, Tømmervik & Hoem reported that app. 30% of the total range holds no or very little vegetation (2005). The western parts and the southern parts of the Hardangervidda plateau are considered as humid with an annual precipitation of 1,200 – 1,800 mm. The eastern and the northern parts are considered under a more continental influence with 600 – 800 mm annual precipitation. In the central and eastern parts the annual precipitation is less than 1000 mm and lichen dominated vegetation entities prevail (Gaare, Tømmervik & Hoem 2005).

On a macro scale, temperature is the most important limiting factor to primary production and vegetation structure in the Fennoscandian tundra, e.g. for the altitudinal belts described by Dahl (1975) and Wielgolaski (1975). In addition to temperature and precipitation, soil moisture, snow cover and nutrient conditions of the soil are also very important to both, vegetation structure and production. Snow cover and temperature are the main factors influencing the length of the growing season in this area (Hesjedal 1975a/b). Much of the annual precipitation occurs as snow, which blows off the macro and micro ridges by the often strong wind in the treeless areas and accumulates in the depressions or snow beds. In western Norway the depth of snow may be several meters thick in the snow beds, but often less than 50 cm on the ridges (Wielgolaski 1975).

In the following a description and area estimates for the most important vegetation types/entities is presented. The cover estimates are based on visual point estimation from aircraft in summer 2004 (Gaare, Tømmervik & Hoem 2005) or aerial photographs from an old investigation in 1973/74 (Hesjedal 1975a/b) covering only 1% of the total area of Hardangervidda. These estimations are therefore considered to be very coarse and not significant estimates for the different vegetation types.

The most important vegetation types in Hardangervidda are obviously the oligotrophic *Vaccinium myrtillus* and the chionophilous *Nardus stricta* heath which covers about 30% of the total area (Hesjedal 1975a/b, Gaare, Tømmervik & Hoem 2005). They are located in habitats with a snow cover of 1 – 3 meter during winter and they are dominated by *Vaccinium myrtillus*, *Deshampsia flexuosa, Festuca ovina* and *Carex bigelowii*. Graminoid ridges (Fremstad 1997) dominated by *Festuca ovina*, *Juncus trifidua*, *Deshampsia flexuosa*, *Carex bigelowii*, together with lichens like *Cetraria nivalis*, *Cladonia mitis* and *Cladonia rangiferina* cover significant areas of Hardangervidda and are considered also as important winter grazing habitats which also contribute proteins and other nutrients for the reindeer. In western parts there are communities with *Carex bigelowii* and *Cetraria nivalis* which can occur together in combination with *Vaccinium myrtillus* and *Empetrum herrmaphroditum* in areas with intermediate snow cover which can be utilized by the reindeer in the early as well as late winter and in the calving time. The moss cover is usually more abundant than in typical lichen heaths. Soil moisture is still probably the strongest limiting factor for growth in these types of heaths (Wielgolaski 1975).

Lichen heaths are mostly oligotrophic and occur in localities with very sparse snow cover and cover about 18% of the total area (Gaare, Tømmervik & Hoem 2005). The maximum snow cover in the lichen heaths is usually less than 50 – 60 cm (Lye 1975). The communities with thin snow cover are dominated by *Loiseleuria procumbens*, *Alectoria ochroleuca* and *Cetraria nivalis*. In habitats with more accumulated snow cover during winter, *Alectoria ochroleuca* and *Cetraria nivalis* disappear while *Cladonia stellaris* together with *Cladonia rangiferina* and *Cladonia mitis* tend to dominate. The lichen heaths are best developed in the central and eastern parts of Hardangervidda and they are considered as the best winter grazing habitats for reindeer (Gaare, Tømmervik & Hoem 2005). In the western parts of the Hardangervidda, the moss *Racomitrium lanuginosum* occasionally dominates this community together with some *Cetraria nivalis* and *Cladonia mitis* (Lye 1975; Gaare, Tømmervik & Hoem 2005). There is also an east-western gradient in the pattern of the most dominating lichen species with more coverage and frequency of *Cladonia stellaris* in the eastern parts than in the central and western parts due to dryer climate in east (Gaare, Tømmervik & Hoem 2005). This type of lichen heath is, however, more related to oligotrophic heaths and grasslands of intermediate snow cover (Lye 1975). In Hardangervidda these vegetation types are used by the reindeer for 80 – 100% of the total grazing time during winter period (Østbye *et al.* 1975). At the central Hardangervidda plateau lichen dry weight biomass is usually of the order 200 – 400 gm^{-2}, often dominated by *Cetraria nivalis*. Visually, much of the highly grazed and trampled lichen mat seems to be dead, but radioautographs have shown that only about 2% were not assimilating CO_2 and were unable to recover (Wielgolaski 1975).

In areas with cambro-siluraian phyllitic rocks, richer plant communities due to species diversity develop. If the water is not scarce (e.g. near streams, depressions with available ground water and edges of mires), meadows dominated by willows (*Salix glauca*, *Salix lapponun*) and herbs (*Geranium sylvaticum*, *Alchemilla glomerulans*, *Deschampsia caespitose*) are found. In dry eutrophic habitats, a very low-growing community rich in cushion plants, herbs and grasses develops. This community called Dryas heath are dominated by species like *Dryas octopetala*, *Salix reticulata*, *Salix herbacea*, *Salix polaris* and *Polygonum viviparum*. The distribution of eutrophic mires corresponds well to that of eutrophic heaths and meadows. These mires are dominated by species like *Carex nigra*, *Comarum palustre* and *Polygonum viviparum* (Lye 1975).

The majority of mires on Hardangervidda is mesothrophic, and is usually dominated by *Eriophorum angustifolium*, *Eriophorum scheuchzeri* and *Carex rostrata*. The oligotrophic communities are dominated by *Eriophorum vaginatum*, *Rubus chamaemorus*, *Empetrum hermaphroditum* and *Betula nana*. In Hardangervidda, macrophytic water communities are rare, although important reindeer grazing species like *Carex rostrata* and *Ecquisetum fluviatile* sometimes form pure stands in open water (Lye 1975). Mires cover 12% of the total area of Hardangervidda (Hesjedal 1975a/b).

Oligotrophic snowbed communities in Hardangervidda are found in habitats with 4 – 10 meter snow depth. Species like *Salix herbacea* dominate and is considered as a very important grazing species for the reindeer. On more “eutrophic” localities *Salix polaris* occurs. Moderate snow bed vegetation covers about 14% of Hardangervidda while extreme snowbeds cover about 5% of the total area (Lye 1975).

The Hardangervidda plateau is fringed by rather extensive sub-alpine forests on its western and eastern side and these forests cover about 9% of the total area (Hesjedal 1975a/b). These forests are dominated by *Betula pubescens*, *Juniperus communis*, *Vaccinium myrtillus*, *Empetrum hermaphroditum* and the mosses *Pleurozium schreberi* and *Hylocomium splendens* (Lye 1975).

Definition of land cover classes

In addition to available information on class distribution of vegetation from earlier studies class definition has to be relevant for reindeer, must be detectable by satellites and preferably should be in line with existing classification systems:

Class definition which is relevant for the spatial behavior of reindeer has to answer some principal questions: What is the perception of the environment from a reindeer perspective, which land cover classes does a reindeer recognize as homogeneous entities and which of these are relevant for their spatial behavior? As described earlier, some indirect indication on these matters is given from existing studies on seasonal differences in forage intake (Gaare, Tømmervik & Hoem 2005; Østbye *et al.* 1975; Edenius *et al.* 2003; Skogland 1984a; Lye 1975; Gaare, Thomson & Kjos-Hanssen 1975; Downes, Theberge & Smith 1986; Walsh *et al.* 1992; Ion & Kershaw 1989; Andersen & Nilsen 1998; Virtanen 2000; Hagemoen & Reimers 2002): Ridge vegetation is the predominant winter forage. Snowbed vegetation is believed to be over proportionally used during summer. Mires are used between late spring to late summer as grazing pastures. Forests are used during autumn. Snow patches and rocky terrain are utilized as refuge areas in summer against insect harassment. Finally, larger rivers can pose a migration barrier during summer.

Theoretically reindeer’s perception of its environment should be in focus of any land cover classification. Unfortunately such information is rather coarse and to a large extent unknown at this stage (although there is some indication for a start). Therefore the reindeer perspective is to some extent rather a result of than a starting point for classification.

Satellite detectability is important for class definition, because it is a crucial limiting factor of what can be reliably seen and separated by the available sensor systems. More specific, two questions are in scope: Which land cover classes have similar spectral characteristics and which differ from others? What becomes separable using the available spectral bandwidths and pixel sizes?

Unsupervised classification is a means of classifying strictly from a satellite perspective, but results are often difficult to relate to existing classification systems and can often be inferior (Loveland *et al.* 1991). Typical limitations for sensor detectability are: Too many and/or too similar classes. Heterogeneous classes are especially problematic for parametric classifiers, as they work with average reflectance values. Furthermore, mixed pixels can be a serious obstacle for classification depending on the relation between spatial resolution and the patchiness of the vegetation. Finally, the minimum classification unit is dependant on pixel size. As a result, the satellite perspective is a serious limitation to the level of detail achievable within classification. On the other hand, an aggregation of classes is a feasible solution of a possible misclassification due to similarity of classes and different classifiers tolerate a different amount of heterogeneity within classes. It is therefore desirable to collect training and testing data in a sufficient level of detail to allow for merging of classes during classification later.

A feasible definition of vegetation classes is reliant to existing classification systems suitable for alpine vegetation in arctic areas. Selection follows crucial questions: What are the existing classification schemes? How applicable are they in the field? How detailed are they for possible later alterations? Which criteria do they follow? What kind of classification systems were used in the past on Hardangervidda? In general two approaches of vegetation classification can be distinguished (Dierschke 1994): While European ecologists mostly follow a phytosociological hierarchy or composition, a combination of non-floristic criteria (climate pattern, habit, phenology and dominant species) is often preferred in North America.

In this thesis the classification code following Fremstad (1997) was selected as an appropriate classification system for the Hardangervidda reindeer area due to multiple reasons: First, it incorporates all major land cover classes which seem relevant for reindeer habitat selection. Second, a sufficient degree of detail allowed for re-classing and aggregation during the classification process. Third, it is relatively easy to use for fieldwork and a well established ‘standard’ within Norwegian vegetation mapping allowing for possible later comparisons for different regions and/or change detection. Finally, the available historical sample points from earlier studies collected between 2000 and 2004 followed the Fremstad systematic. In the following a brief description of the Fremstad code is given based on Fremstad (1997):

The Fremstad classification key for vegetation types follows the concept of ecological gradients, such as changes in soil type, moisture, nutrition availability and regional or local climate. Fremstad defines 24 main vegetation groups. These are divided into a number of vegetation types (137 in total) and again in sub types (379). Although the Fremstad code is not based on the Central European phytosociological system for classification of vegetation (Dierschke 1994), the 24 main vegetation groups operate mainly at the level of one or more classes in the phytosociological systems. The more detailed the level becomes the more important become the ecological gradients. On the group level, the ecological gradients were used to define among others heath/poor fen vegetation according to the moisture conditions and mires according to the nutrition level and further on to water conditions. Concerning the alpine vegetation, most important for this study, the group classification in ridge, leeside (early snow patch), and snowbed (late snow patch), follows ecological gradients determined mainly by the lengths and the depths of the snow cover but also the moisture and nutrition conditions and topographical and climatic aspects.

Collection of sample data used for training and testing

The sampling scheme used during fieldwork contained eight main land cover classes, divided into 28 sub types (see Table 3-1).

Sub Class	Fremstad Code	Main Class
Ice	-	**SNOW**
Snow	-	
Water	(O-Q)	**WATER**
Rocky shoreline at reg. lakes	(R1 Berg)	
Rock	(R1 Berg)	**ROCK**
Trailing Azaliea/Diapensia st.	R1a	
Lichen st.	R1b	**RIDGE**
Cladonia alpestris st.	R2a	
Cladonia st.	R2b	
Graminoid ridge	R5	
Mixed ridge vegetation	R1a/R1b/R2a/R2b/R5	
Other ridge vegetation	R1cde/2c/R3/R4/R6-R8	
Meadow-leeside	S4, S5 (S6, S7)	
Tall herb/scrub-leeside	S6, S7	**LEESIDE**
Poor juniper/dwarf birch heath	S2ab	
Bilberry/mount. crowberry heath	S3ab	
Other leeside vegetation	S1	
Grass-/meadow snowbed	T1, T2, T3	**SNOWBED**
Dwarf willow/bryophyte snowbed	T4 / T5	
Dwarf willow/Net willow snowbed	T4 / T6	
Bryophyte snowbed	T5 / T7	
Mixed snowbed vegetation	T1/T2/T3/T4/T5/T6	
Other snowbed vegetation	T8, T9, T10	
Dry mire	J2,3(4),K2-3, L2, M2-3	**MIRE**
Shrub mire	J1,K1,L1,M1	
Wet mire	(J4), K4, L(3)4, (M4)	
Bilberry woodland	A4	**FOREST**
Tall herb/birch/spruce forest	C2	

Table 3-1: Systematic of vegetation classes: sub classes used in the field and aggregation to main classes

The sub types are composed of one or more Fremstad vegetation types. Adjustments were made (i) by adding non-vegetation land cover types that are not covered by Fremstad (snow/ice), (ii) by aggregating classes that cannot be distinguished by Landsat. Sampling was conducted on a detailed level in order to keep as much information as possible (while still being able to merge classes later, if necessary). Lichen ridges were mapped with qualitative (species, vegetation type) and quantitative parameters (lichen height and coverage in %) for modelling lichen biomass (see chapter 4.2).

Fieldwork was carried out during late July and August between 2000 and 2005 with the majority of sample points collected in 2004 and 2005. A random sampling design for testing and training points was considered unpractical in the field due to both, the large area size/inaccessibility of Hardangervidda and the risk of getting insufficient sample sizes for less frequent vegetation classes. To address these obstacles a stratified sampling design was applied with estimated prior class probabilities, geographical distribution (east-west/north-south gradient), elevation and grazing pressure, based on Gaare, Tømmervik & Hoem (2005), as covariates. For sampling classes in the field a minimum size of 30x30 sqm, possibly 50x50 sqm, was selected in order to avoid mixed pixel problems[56]. Additional sample points for snow/ice, water, rock and forested areas were derived from secondary data (N50 topographical map together with a visual interpretation of aerial photos).

Aggregation of vegetation classes

Empirical testing[57] and sample size considerations (see below) lead to an aggregation of sample data to eight different classes (see Table 3-1). Although theoretically one might prefer to maintain the highest level of detail possible, the decision was made to reduce the number of classes significantly. Three reasons were decisive for this choice:

First, using land cover classes as dummy variables within spatial habitat selection models later, required large enough classes to allow for significant results. The decision was therefore made to limit the number of classes to a maximum of ten, preferably less. (Temporary) snow and (perennial) ice were therefore merged to a single class (SNOW), so were subtypes of mires as well as classes S4 to S7 (leeside meadows).

Second, results from preliminary classification with different classifiers indicated limitations for fine scale separation of classes as recorded in the field, especially between different lichen types within ridge communities (see also Rees, Tutubalina & Golubeva 2004), different forest classes as well as separation between classes S2/3 (leeside).

Finally, a limitation in sample sizes lead to further reduction of classes (see below). Especially the aggregation of different subtypes of snowbed vegetation to a single class (SNOWBED) seemed imperative. While this was judged to be justifiable from a reindeer perspective, it lead to some in-class heterogeneity possibly affecting some of the (parametric) classifiers. For the same reason the decision was made to merge the S classes to a single class LEESIDE.

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[56] Given an average GPS-accuracy of 5 m and a pixel size of 30x30 m^2 with a geometric inaccuracy of maximal 15 m, the training point should ideally be situated in the middle of a homogeneous area that covers at least 50x50 m^2, in order to secure that the training point is representative for the land cover of the pixel. In praxis it was often difficult to find homogeneous areas that cover 50x50 m^2, especially for snowbed and ridge vegetation, therefore a minimum size of 30x30 m^2 was chosen.

[57] To do this a preliminary maximum likelihood classification of Hardangervidda was carried out using the single vegetation classes and the first three components of a PCA based on the 2003 Landsat summer image (see e.g. Tso & Mather 2001). Classes were later merged based on their confusion matrix.

Description of classes

In the following a short description of the aggregated classes selected for land cover classification of Hardangervidda is given based on Fremstad (1997):

The land cover class RIDGE is characterized by low, often sparse vegetation dominated by mostly oligotrophic lichen heath and grass communities and only a thin, unstable snow cover during winter usually less than 50 – 60 cm resulting in high variations in temperature. It is predominant in low to high alpine areas of Hardangervidda especially in the (south) central areas. Characteristic plant communities for the R1 subclass (Trailing Azale – lichen/bryophyte st.) are *Arctostaphyllus alpinus*, *Loiseleuria procumbens, Thamnolia vermicularis*, *Alectoria ochroleuca*, *Alectoria nigrans*, *Bryocaulon divergens*, *Ochrolechia frigida, Coelocaulon aculeatum, Cetraria cuculata* and *Cetraria nivalis*. R2 (Dwarf birch - mountain crowberry st.) is dominated by *Betula nana*, *Diapensia lapponica*, and *Cladonia spec.* whereas R5 (Graminoid ridge) is specified by *Carex bigelowii*, *Festuca ovina*, *Hieracium alpinum*, *Juncus trifidus*, *Luzula spicata*, *Salix herbacea* and *Solidago virgaurea*.

Class LEESIDE is defined as heather-, tall herb- or scrub-dominated, dense vegetation with a stable snow cover and a relatively long vegetation period due to an early snow melt. It is predominantly situated on hillsides with balanced temperature and moisture. Within Hardangervidda leeside vegetation occurs in low- to middle alpine regions. Characteristic plant communities according to Fremstad (1997) for the S2 subclass (Juniper - dwarf birch heath) are *Betula nana*, *Juniperus communis*, *Empetrum nigrum coll.*, *Barbilophozia lycopodioides*, *Hylocomium splendens*, *Cetraria islandica* and *Cetraria nivalis*. S3 (Bilberry - blue heath and mountain crowberry heath) demonstrates *Deschampsia flexuosa*, *Diphasiastrum alpinum*, *Empetrum nigrum ssp. hermaphroditum*, *Pedicularis lapponica*, *Vaccinium myrtillus*, *Dicranum fuscescens*, *Hylocomium splendens*, *Pleurozium schreberi*, *Cetraria islandica*, *Betula nana*, *Festuca ovina*, *Cornus suecica* and *Vaccinium uliginosum*. Subclass S6 (poor tall-herb meadow and scrub) is characterized by *Salix lapponum*, *Salix phylicifolia*, *Cirsium helenioides*, *Deschampsia cespitosa*, *Filipendula ulmaria*, *Geranium sylvaticum* and *Pedicularis sceptrum-carolinum*.

The class SNOWBED is defined as low grass-, moss- or fern-dominated vegetation with a thick and stable snow cover (4 – 10 m) during winter. A short vegetation period due to late snowmelt is characteristic. Snowbed vegetation is predominantly situated in depressions with north-east exposition and high soil-moisture. Disturbances due to landslides are common. Within Hardangervidda snowbeds are mainly found in the western and south central areas.

Characteristic plant communities differ between subclasses. T1 (grass snowbed) demonstrates *Nardus stricta*, *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Carex bigelowii*, *Phylodoce caerulea* as well as *Juncus trifidus*. Within T2/3 communities (poor/rich snowbed meadow) R*anunculus acris*, *Anthoxanthum odoratum* and *Alchemilla glomerulans* dominate. T4 (dwarf willow snowbed) shows *Salix herbacea*, *Ranunculus glacialis* and *Luzula spec.* T5 (poor, bryophyte snowbed) is characterized by *Polytrichastrum sexangulare* and *Anthelia juratzkana* whereas T6 (net-leaved willow – polar willow st.) is dominated by *Salix reticulate* and *Salix polaris*.

The land cover class MIRE is characterized by moist bog- and fen vegetation build up on turf and other organic material. Vegetation is mostly dominated by moss- and grass-species, situated in water accumulating slopes, often former lakes. Plant composition is depending on nutrition and moisture-values. Mires are distributed throughout the entire Hardangervidda. Characteristic plant communities are described following Lye (1975): Mesotrophic mires (majority of mires in Hardangervidda) encompass *Eriophorum angustifolium*, *Eriophorum scheuchzeri* and *Carex rostrata*. Oligotrophic communities demonstrate *Eriophorum vaginatum*, *Rubus chamaemorus*, *Empetrum hermaphroditum* and *Betula nana*. Macrophytic water communities are scarce in Hardangervidda. They hold *Carex rostrata* and *Ecquisetum fluviatile* sometimes to form pure stands in open water. Finally, eutrophic mires are defined through *Carex nigra*, *Comarum palustre* and *Polygonum viviparum*.

FOREST is defined by open to dense birch-forest with bilberry- or tall-herb dominated ground cover. The study area is fringed mainly by sub-alpine birch forests on its western, southern and eastern borders at lower altitudes (< 1,200 m). Characteristic plant composition for the A4 subtype (bilberry woodland) are *Betula pubescens*, *Vaccinium myrtillus*, *Picea abies*, P*inus sylvestris*, *Deschampsia flexuosa*, *Vaccinium vitis-idaea*, *Dicranum majus*, *Hyloconium splendens*, *Pleurozium schreberi*, *Ptilium crista-catrensis*, *Empetrum nigrum*, *Phyllodocaea caerulea* and *Pedicularis lapponica*. On the other hand, subclass C2a (tall-herb, downy birch st.) is dominated by *Betula pubescens*, *Salix glauca*, *Deschampsia cespitosa*, *Alchemilla ssp.*, *Aconitum septentrionale*, *Athyrium filix-femina*, *Cicerbita alpina*, *Geranium sylvaticum*, *Millium effusum*, *Myosotis decumbens*, *Stellaria nemorum* and *Trollius europaeus*.

ROCK as a land cover class is defined by bare, exposed rock and soil at extreme locations. The class has only scarce vegetation in sheltered crevices accounting for < 15% of its extent. It mainly occurs in the high western and south-central areas of Hardangervidda showing extreme climate conditions and/or steep terrain. Existing plant communities are dominated by Epilithic lichen vegetation mixed with other ridge communities in more protected areas (R7). More specific: *Rhizocarpon*, *Umbilicaria*, *Parmelia-Arctoparmelia-Pseudephebe-Brodoa*, *Xanthoria elegants*, *Physconia*, *Ramalina polymorpha*, *Arcarospora* and *Dermatocarpon*.

The class SNOW mainly consists of Hardangerjøkull and smaller glaciers as well as permanent ice- and snowfields[58] with a minimum diameter of approximately 20x20 sqm. The class is predominantly found in the high areas in the western parts of the study area.

WATER is composed by natural and artificial lakes, rivers and streams, with the class being equally distributed throughout Hardangervidda.

In addition to the eight above described classes it was necessary to operate with a class SHADOW as an auxiliary class for unclassifiable pixels due to shadow as cast in the master image (see below). This problem foremost was relevant for steep slopes in north-west exposition, mainly occurring in the western areas of Hardangervidda.

Sample size and preprocessing of sample data

Sample size for both, training data and data used to test the classification accuracy, is crucial. This is since the minimum sample size for training data is dependent on the dimension of the feature space used for classification, the number of classes and the in-class variability as well as the spatial scale/resolution (Tso & Mather 2001).

As a rule of thumb for low dimensional data, that is few variables (bands) used for classification, Mather (1999) concludes that the minimum amount of training-data per class should be at least thirty times the number of features used for classification.

More precise, Congalton and Green (1999) calculated the necessary total sample n size for training as:

$$n = B\prod_i (1-\prod_i)/b_i^2 , \qquad (3\text{-}1)$$

where b_i is the required precision level (expressed as a proportion), $\prod_i$ is the proportion of area covered by class i, i should be the class with the largest proportion of area covered, B is the upper (α/k) x 100th percentile of the chi-square distribution with one degree of freedom, with α as the required confidence level and k as the number of classes.

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[58] Reference data: Landsat TM5 (path/row: 199/18; 9th Aug. 2003)

The amount of training data per class should be proportional to its expected land cover (as expected from random sampling), which also is an assumption of the kappa coefficient used for accuracy assessment.

When applying the above measures, the necessary sample size for statistically valid training ranges between 599[59] (Congalton and Green 1999) and 1080[60] (Mather 1999).

Sample points collected in the field were filtered by excluding observations with a GPS accuracy less than 15 m RMS (root mean square of location error) to ensure sufficient congruence between field data and Landsat pixels. Furthermore, sample points were excluded and classified as outliers if their satellite reflectance values exceeded 95% confidence intervals of class means within all single bands. In total a number of n=5,700 sample points from fieldwork and aerial photos remained (see Table 3-2):

Main Class	Sample-points	Apriori prob.
SHADOW	*570*	*0,5*
SNOW	359	1,2
WATER	1 395	9,1
ROCK	489	9,5
RIDGE	1 345	26,5
LEESIDE	360	21,5
SNOWBED	275	18,0
MIRE	554	9,0
FOREST	443	4,7

Table 3-2: Prior probabilities and number of sample points per main class

Since the number of collected sample points allowed for independent datasets for training and testing, it was opted against cross-validation for accuracy assessment. For testing, a stratified random sample of n=100 sample points per class was used (900 testing points in total). This left a more than satisfactory sample size of n=4,900 training points in total and a minimum number of n=260 training points per class with the exception of snowbed vegetation (n=175 training points). Both the above estimated requirements for minimum sample sizes were hence considered satisfied.

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[59] Assuming RIDGE as the class with the largest proportion of area covered (0.265 derived from prior possibilities), k=9 classes, a confidence level α of 95% and a desired precision b of 0.05

[60] Assuming an average feature space dimension of 4 (within subgroups created from ancillary data) and k=9 classes.

In order to compensate for a skewed distribution of sample points between classes and to approximate a random sampling scheme, data used for training and later testing were weighted by their prior probabilities (see Table 3-2). This was considered necessary, as especially non-parametric classifiers (e.g. kNN) can be sensitive to a skewed distribution of training data (Chen *et al.* 2009). Prior probabilities describe the expected class distribution before classification and can therefore provide additional decision support for classifiers, when the spectral characteristics of a pixel do not allow for a clear allocation to a unique class (Chen *et al.* 2009). Estimation of prior probabilities for the land cover classes in Hardangervidda (see Table 3-2) was based on Gaare, Tømmervik & Hoem (2005), who used airborne vegetation classification along transects during summer 2004 based on visual interpretation.

Image selection

For land cover classification the selection of the appropriate satellite system is a critical choice. It foremost can be seen as a trade of between resolution and other image related factors (e.g. spatial extent of acquired scene, number of bands together with bandwidths, backlog or price). An overview of commonly available systems with resolution and image related factors is given in Table 3-3:

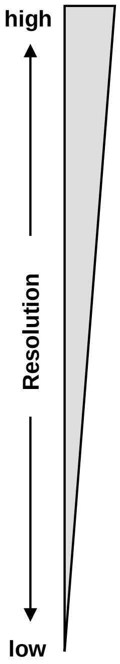

		Image related factors			
System	**Res.**	**Swath**	**Backlog**	**Price**	**Bands (nm)**
Quickbird 2	**2.4**	**16,5x 16,5**	**2001**	**high**	**4 (450-890)**
IKONOS 2	**4**	**11,3x 11,3**	**1999**	**high**	**4 (450-900)**
IRS-P6 Liss 4	**5,8**	**23.9x 23,9**	**2003**	**medium**	**3 (520-860)**
SPOT 5 HRG	**10**	**60x 60**	**2002**	**medium**	**4 (500-1750)**
SPOT 4	**20**	**60x 60**	**1998**	**medium**	**4 (500-1750)**
IRS-P6 Liss 3	**23.5**	**141x 141**	**2003**	**medium**	**4 (520-1700)**
Landsat ETM+	**30**	**185x 172**	**1999**	**low**	**7 (450–12500)**
Landsat TM	**30**	**185x 172**	**1982**	**low**	**7 (450–12500)**

Table 3-3: Overview of selected Satellite systems: Spatial resolution and image related factors[61]

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[61] Based on Lillesand, Kiefer & Chipman (2007).

Choosing a sensor with the appropriate spatial and spectral resolution is a crucial factor and foremost dependent on the degree of spatial detail that will be required from the resulting land cover map later.

High-resolution images can be problematic for several reasons: First, the precision of the available ground control points for orthorectification might not meet the requirements of high-resolution images (Aguilar *et al.* 2007). Second, depending on the terrain of the study area, topographic correction can be essential to compensate for a spatial mismatch between the (flat) acquired satellite scene and the (three-dimensional) surface in the field. Again a gain in satellite resolution might not necessarily translate into a real accuracy gain, as the required spatial resolution of the available DEM might not be suitable for high-resolution images. Third, training point accuracy can be a limiting factor for image resolution, as both have to correspond reasonably. And, finally, a higher spatial resolution is generally bound to a reduction of band numbers and spectral resolution and can lead to a greater spectral variability and increase the boundary-effects or mixed pixel problems (Martin & Howart 1989).

In this study Landsat TM/ETM+ imagery was chosen for land cover classification as a suitable compromise between the above factors for the following reasons:

In contrast to most of the competitive systems with higher spatial resolutions (e.g. SPOT; IKONOS or IRS) Landsat TM/ETM+ has a large enough extent to cover the entire study area within a single acquisition scene. Hence a compilation of different scenes associated with accuracy loss due to the necessity of radiometric correction could be avoided. Landsat shows the highest continuity over the last decades with a number of usable scenes since 1984. This favors a possible later detection of (historical) changes. The spatial resolution of 30x30 sqm seems sufficient for most of the above classes, even though some problems with patchy snowbed vegetation are to be expected. A further increase in spatial resolution seems to be of limited value due to the accuracy of the available corresponding data: Available ground control points depict a root mean square (RMS) of location error of 1 – 7 m, while training and testing points have an average RMS of 5 m ranging from 2 – 15 m. Within the mountainous terrain of Hardangervidda topographic correction is crucial for accuracy. The 25 m spatial resolution of the available DEM already can be considered critical for Landsat resolution (Richter 1997) and thus seems prohibitive for the use of high-resolution images. It has also been shown that Landsat’s available spectral channels are appropriate (number and wavelength) for vegetation mapping including biomass assessment (Beaubien *et al.* 1999; Nordberg & Allard 2002; Petzold & Goward 1988). The relatively high band number (7) allows for numerous combinations and specific selections tailored for individual classes and a large amount of experience from other studies have indicated promising results (Nordberg & Alland 2002; Tømmervik, Johansen & Aira 1990). Not the least the acquisition of numerous scenes for ancillary data and possible later change detection has to be cost efficient. Landsat fulfills this requirement. Most important: for a later modeling attempt of reindeer habitat selection (see chapter 5) the spatial resolution of the land cover map has to correspond with the average RMS from GPS radio collars. As those fall between 4 – 15 m, a spatial resolution beyond Landsat values thus seemed inappropriate for this study.

Three Landsat images from different seasons have been acquired for land cover classification. They are shortly described within the following:

The main image for classification is a Landsat TM5 summer scene acquired on Aug 9th 2003 (path/row: 199/18). It is completely cloud free (cloud cover: 0%) and has been resampled using the nearest neighbor method instead of cubic convolution in order to preserve the initial reflectance values (see e.g. Atkinson 1985). At this time of the year the snow cover has melted down to a large extend and the phenological stage of the vegetation allows to discriminate between different land cover types (Tømmervik, Høgda & Solheim 2003). The second image acquired was an early summer image dating from Jun 12th 1988 (Landsat TM5; path/row: 199/18; cloud cover: 0% also with nearest neighbor resampling). It was used as an ancillary image[62] to differentiate between patches with late snow coverage and early snowmelt (snowbed vs. leeside/ridge vegetation). In addition a late winter image dating from May 4th 2000 was selected (Landsat ETM+7; Path/row: 199/18; cloud cover: 0 – 10%) as an ancillary image to define snow-free lichen ridges, the main source of winter forage for reindeer.

Preprocessing of images

As pointed out earlier orthorectification and topographic normalization is a crucial prerequisite for satellite-based land cover classification (see e.g. Lillesand, Kiefer & Chipman 2007; Colby 1991). Landsat images have been orthorectified on WGS84 UTM 32N by Geodatasenteret AS using ERDAS Imagine 8.7 (LEICA Geosystems 2003) on base of a digital elevation model (DEM) and ground control points (GCP) (LEICA Geosystems 2003). GCPs have been derived from a formerly corrected Landsat image (Landsat ETM+7; Path/row: 199/18; Sep 25th 2000) that was georeferenced using Vexcel aerial photos and a water mask

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[62] See also McRoberts *et al.* (2006) for the use of satellite imagery as ancillary data within the classification process.

compiled from 1:50.000 topographical map data (Hjeltnes 2006). Nearest neighbor resampling was chosen in order to preserve the initial reflectance values, which is essential for patchy vegetation patterns (Rogan, Franklin & Roberts 2002; Dirnböck *et al.* 2003). The estimated root mean square error (RMS) falls between 5 – 7 m in relation to the reference image. Considering the inaccuracy of the DEM and the ground control points, the total RMS error accounts for about 13 – 14 m and could thereby be limited to less than half a pixel size.

Topography normalization was used to control for relief induced differences in ground reflectance (Schardt 1987; Parlow 1996). In this study c-correction was preferred over alternatives (e.g. cosine), as it, together with Minnaert-correction (see e.g. Blesius & Weirich 2005), has been found to show the best performance for illumination correction (McDonald *et al.* 2000) but coefficients for c-correction are easier to obtain. C-correction uses a parametric model accounting for non-lambertian reflectance by introducing ground cover specific correction factors (c-factor) (e.g. Civco 1989; Meyer *et al.* 1993; Schardt 1987). Within the model radiance observed for the horizontal surface is calculated using the equations below (Teillet, Guindon & Goodenough 1982; Meyer *et al.* 1993):

$$L_H = L_T\left(\frac{\cos(sz)+c}{\cos(i)+c}\right), \tag{3-2}$$

where L_H is the radiance observed for horizontal surface, L_T is the radiance observed over sloped terrain, sz is the sun's zenith angle, i is the sun's incidence angle and c is the correction parameter, obtained through:

$$c = \frac{b}{m}, \tag{3-3}$$

where m is the inclination of the regression line and b the intercept of the regression line within the equation:

$$L_T = m\cos(i) + b, \tag{3-4}$$

In order to obtain c-factors for individual bands and classes a preliminary classification was carried out using maximum likelihood classification based on bands 1 – 3 of a principal component analysis of L5, Aug 09th 2003. C-factors were derived for each class from the regression coefficients of the digital number against the sun incidence angle as calculated from DEM (based on 30.000 random points). For all classes bands with significant topography effect on reflectance were corrected (RIDGE, LEESIDE, SNOWBED, MIRE, FOREST, ROCK within bands 2 – 5 and 7). Due to the good quality of the main image, no radiometric correction was carried out.

Selection of classifiers

Three parametric and non-parametric classifiers have been selected for method comparison among the potential options (see Figure 3-1), following the rational described below:

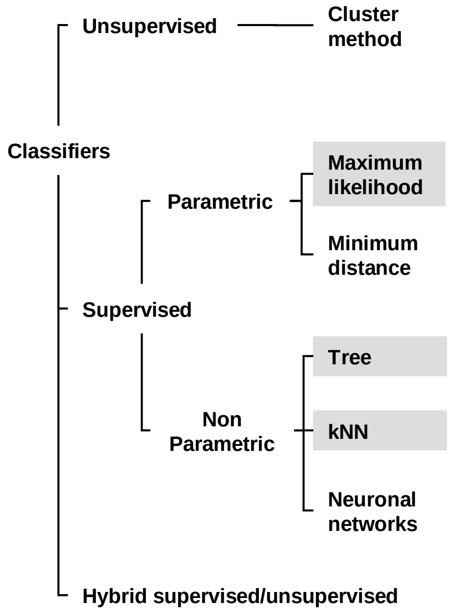

Figure 3-1: Systematic of selected classifiers – overview

The accuracy levels achieved in the land cover mapping was considered to be an important side condition as the primary objective of the land cover classification was to obtain a suitable land cover map for later modeling of reindeer habitat selection. Supervised classification methods often show superior results as compared to unsupervised methods, mainly because of better interpretability (Gilichinsky *et al.* 2011).

Among supervised methods especially non-parametric classifiers (tree and kNN) have shown promising results in patchy habitats characterized by considerable within-class heterogeneity (Sandström *et al.* 2003). For comparative reasons and as a basis for possible reapplication in other reindeer areas and/or later change detection it was decided to run the results of the above methods against the frequently used maximum likelihood classifier, which is known to be superior as compared to other parametric classifiers like minimum distance (Gilichinsky *et al.* 2011). For practical reasons the number of classifiers had to be limited. Within the non-parametric group the tree and kNN classifier were preferred over neuronal network in order to foster easy repeatability, even though results from other studies applying neuronal networks were promising with respect to classification accuracy (Sandström *et al.* 2003). Finally, the majority classifier was used as a baseline for significance testing of the above classifiers.

Image classification

Maximum likelihood classification follows the decision rule of allocating pixels to the class with the highest statistical probability (maximum likelihood) (e.g. Swain & Davis 1978; Richards & Xiuping 1999). In order to do so, the probability density functions for each pixel and class were computed from the pattern vector of the pixel to be classified, the mean pattern vectors of classes and their covariance matrix as calculated from training data, the prior probabilities for individual classes and optional misclassification costs per class. Under the assumption of a class-wise Gaussian distribution of training data the response pattern of a class can be fully described by the above statistical parameters (hence parametric). In order to reduce the dimension of the feature space (and thereby sample size requirements) a subset selection of Landsat TM bands 1 – 5 and 7 was programmed using a forward/backward loop as empirical algorithm. This was done by iteratively adding/removing single bands using the gain in classification accuracy as controlling parameter.

The kNN classifier allocates a pixel to the (weighted) majority class of the k-nearest neighbors (kNN) within the feature space (Sandström *et al.* 2003). In order to follow this decision rule a nearest neighbor ranking of the pixel to be classified was performed using Euclidean distance in a multidimensional feature space. Nearest neighbors were weighted by prior probabilities. Again, feature space dimensionality was reduced empirically using a forward/backward loop for subset selection of Landsat TM bands 1 – 5 and 7. In addition the parameter k was calibrated empirically through multiple iterations using the gain in classification accuracy as selection criteria. Pixels were assigned to the class which the majority (weighted by a priory possibilities) of training data points selected as nearest neighbors belonged to. Class probabilities were hence calculated from the proportion of the weighted majority class.

Tree classifiers commonly allocate a pixel according to its pattern vector following successive decision rules derived from the training data (Tso & Mather 2001). To achieve this, a top-down hierarchal split of training data (stem) into multiple leafs was performed. Training data points were weighted by prior probabilities. In order to select the most beneficial splitting criteria at each internal tree node, the Gini-coefficient was chosen (see e.g. Bratko 2011). To stop further splitting at nodes, the minimum number of examples per node criterion (minEx) was used (see e.g. Bratko 2011). For post pruning the m-parameter was applied by comparing m-estimates of static and dynamic error as defined in Bratko (2011). Both, minEx and parameter m, were calibrated empirically using multiple iterations. Class probabilities were derived from class distribution within leafs.

Classification and empirical calibration of all classifiers was obtained in Orange (Demsar & Zupan 2004) using Python scripting (Van Rossum 1995). Following the basic classification scheme using the above classifiers a subset of potential ancillary data was derived from Landsat imagery and DEM and tested for further accuracy gains. Spatial information layers derived from Landsat imagery included different band indices, context and texture (see e.g. Caetano, Navarro & Santos 1997), snow masks, bands derived from principal component (see e.g. Tso & Mather 2001) and Tasseled cap (Kauth & Thomas 1976) analyses. DEM derivates included elevation, relative elevation, aspect, curvature, ruggedness, hill shade and solar radiation. Tested utilization rules for ancillary data included increasing feature space dimensionality through additional layers of information, generating homogeneous subsets prior to classification as well as correcting misclassified pixels based on normative logical rules in post classification.

Preliminary testing revealed significant improvements of classification accuracies by using snow masks and relative elevation for defining homogeneous subgroups prior to classification with adjusted prior probabilities. Additional gains in accuracy could be reached using snow masks, elevation, relative elevation and slope as knowledge based information for normative correction of pixels after classification. No additional improvements could be achieved through additional ancillary data, hence those data was later dropped. Also bagging and boosting[63] of selected classifiers did not significantly raise classification accuracy. Nor did meta-classification using majority voting of classifiers or the classification result of the classifier with the highest relative probability (probability layer).

Selection of ancillary data

In the following, ancillary data sources selected after pre-testing (elevation, relative elevation, slope and snow masks form late winter and early summer) together with selected utilization rules (homogeneous subset creation with adjusted prior probabilities, normative post-classification rules) are described in more detail:

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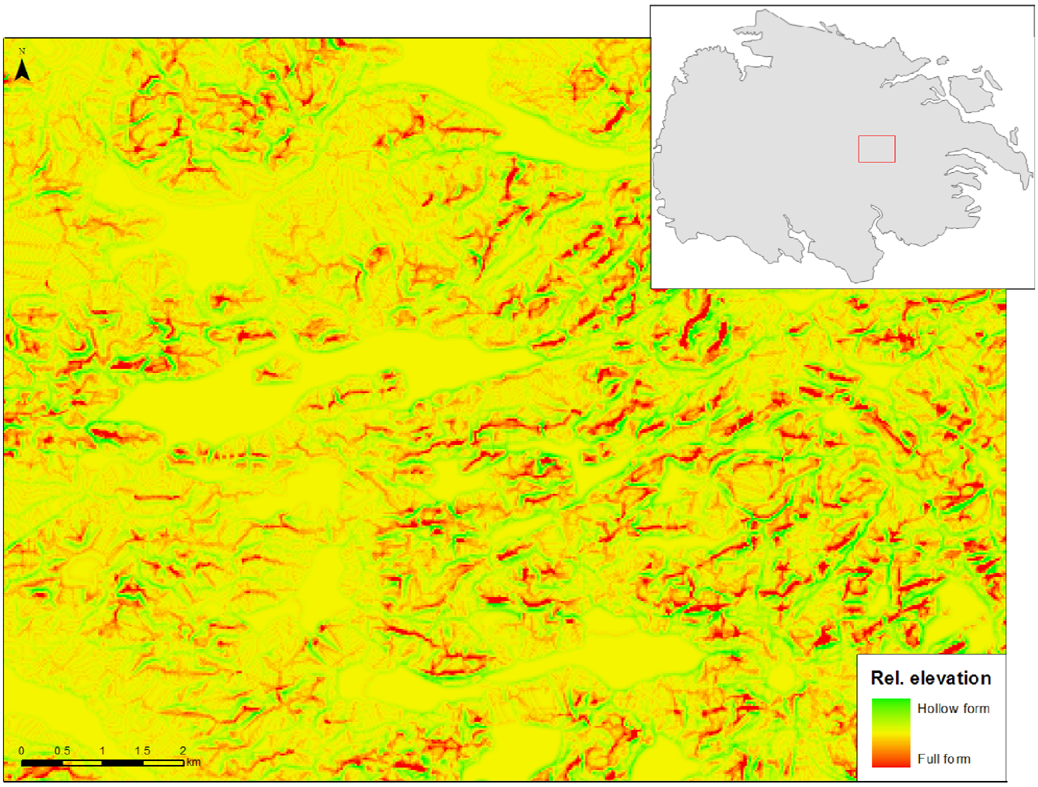
[63] For a more detailed discussion of meta classifiers see e.g. Tso & Mather (2001) or Manly (1997).

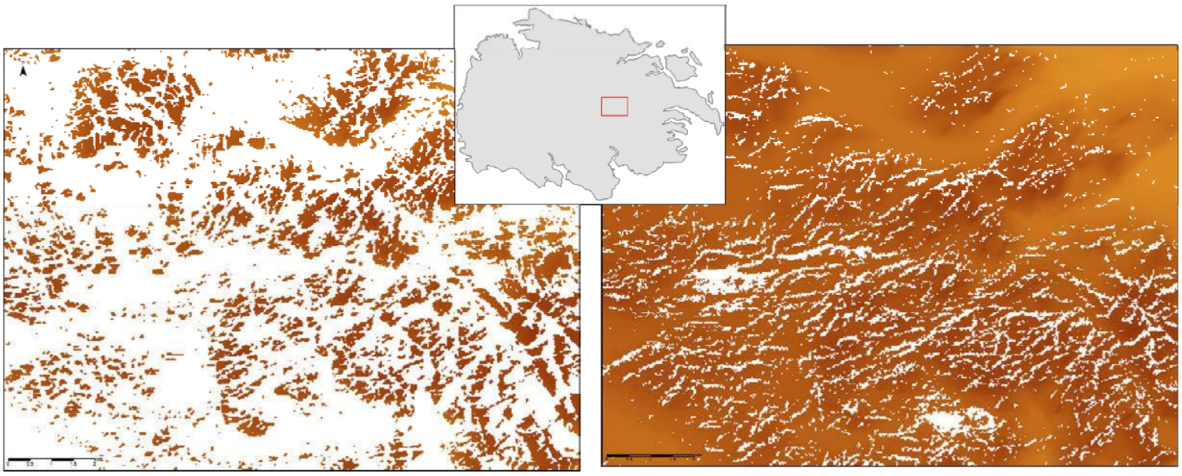
Several studies have found that classes with similar satellite reflectance profiles can be separated by utilizing class characteristics obtained from DEM derivates. Examples as such are Paracchini & Folving (1994), Gallaun *et al.* (1998) and Buchroithner *et al.* (2002) who found that elevation and slope significantly improved classification results for vegetation in alpine habitats. Similarly Edenius *et al.* (2003) found relative elevation especially valuable for differentiation between ridges and snowbed vegetation.

Relative elevation, elevation and slope were all derived from a digital elevation model (DEM) covering the Hardangervidda area. The model has been compiled by Statens Kartverk (2006) based on contour lines, terrain points, water of the 1:50.000 topographical map and road data. It has a spatial resolution of 25x25 sqm with 90% of its contour lines falling into a tolerance of 5 meter accuracy (Statens Kartverk 2006). In order to match the DEM to Landsat pixels a bilinear resampling to 30x30 sqm was applied. DEM derivates for the study area were calculated using ArcView GIS (ESRI 2005). A 5x5 pixel roving window (see Wilson 2000) was used to calculate the relative elevation (full form/ridge vs. hollow form/depression) of pixels with regard to neighboring pixels. See Map 3-1 for example:



Map 3-1: Relative elevation: distribution patterns of hollow and full forms – illustrative example central Hardangervidda

Spatial information on typical snow conditions can also help to avoid misclassification. E.g. lichen vegetation, the primary winter forage for reindeer, is found predominantly on wind blown ridges with little or no snow cover (Hesjedal 1975a/b). In contrast, snowbed vegetation, which might easily be misclassified as ridge or leeside vegetation due to similar reflection characteristics (Edenius *et al.* 2003), is usually bound to stands with long lasting snow cover up to summer (Edenius *et al.* 2003). In order to utilize this information two snow masks were derived from Landsat images from late winter[64] (Landsat ETM+7; Path/row: 199/18; May 4th 2000) and early summer (Landsat TM5; path/row: 199/18; Jun 12th 1988). Technically this was done using a matrix classification of a normalized difference index for the bands 2 and 5 together with threshold values for band 3 (normalized difference snow index; Riggs & Salomonson 1994; Salomonson & Apple 2004)[65]. An example for snow cover during seasons under regard is given in Map 3-2:



Map 3-2: Snow cover in late winter/early summer: distribution patterns – illustrative example central Hardangervidda

Creation of homogeneous subsets

Four different homogeneous subsets were created using the early summer snow mask and relative elevation as dichotomous variables (see Map 3-3):

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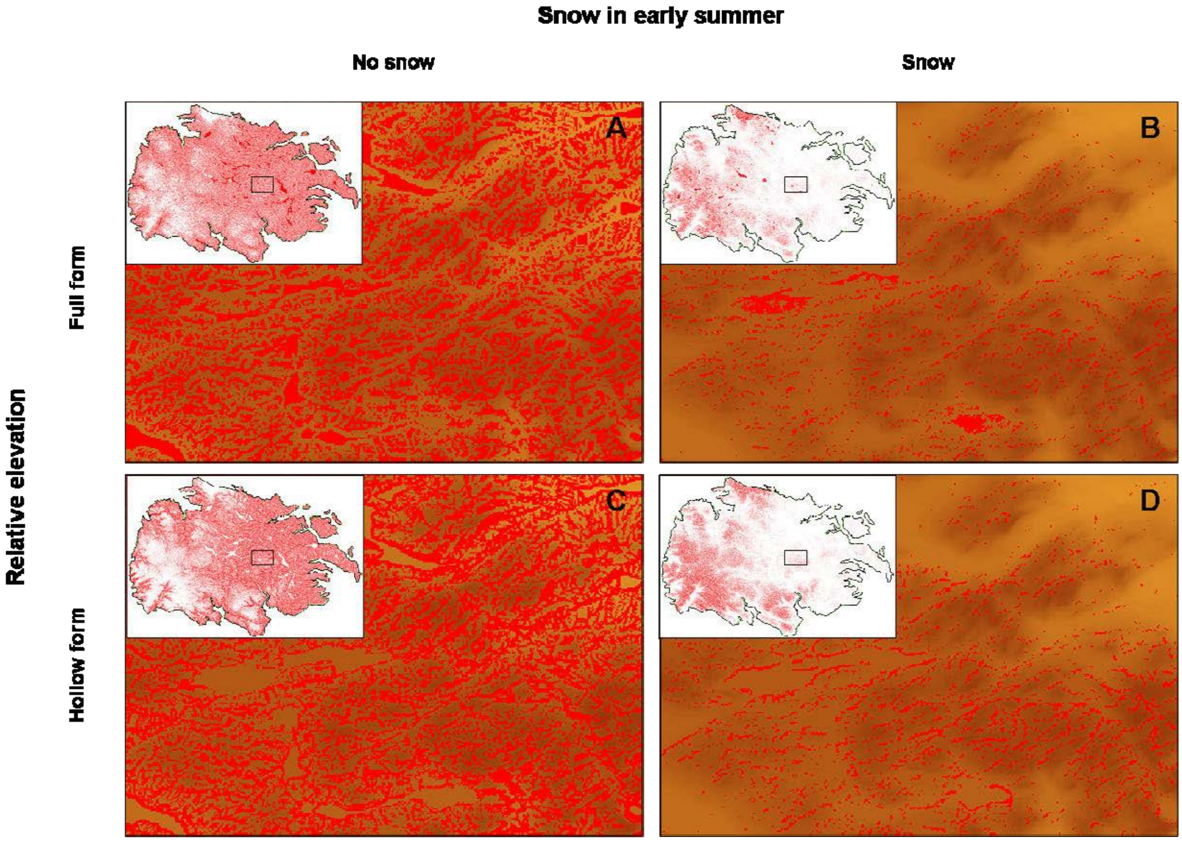
[64] For the spectral signature of alpine snow cover from Landsat TM see also Dozier (1989).

[65] An alternative approach for residual snow patch mapping was used by Gray *et al.* (1989). Alternative snow indices were applied by Pruitt (1997) and Xiao, Shen & Qin (2001). See also Vogel (2002) for the usage of high resolution Landsat 7 band 8 for single band snow-cover classification.



Map 3-3: Overview of subsets used for classification: four possible cases depending on relative elevation and snow distribution in early summer – illustrative example central Hardangervidda

The assumption was made that the relative class distributions would dependent on subsets. For example the relative probability of a pixel to be classified as snowbed vegetation was assumed to be significantly higher if the pixel would be snow covered during early summer and located in a hollow form or depression (subset D in Map 3-3) as compared to snow free pixels with high relative elevation (subset A in Map 3-3). In contrast, it is assumed that ridge vegetation are more likely to be found within pixels which are snow free during early summer and at high relative elevations. Following these assumption the prior class probabilities were altered depending on the respective subsets. Information on prior probabilities were taken from within subset distribution of sample points.

Post-classification rules

In order to further reduce misclassification likelihoods, a set of normative post-classification rules was designed, again based on ancillary data. The following reclassification rules were implemented: If pixels were located above 1,150 m a.s.l. and classified as FOREST they were assumed to be falsely classified and hence reclassified to LEESIDE, as analysis of preliminary confusion matrices revealed considerable confusion between this pair of classes. Similarly MIRE was reclassified to LEESIDE if the pixels were located to areas with a slope higher than 10 deg. Likewise, WATER was reclassified to SHADOW (unclassified) if slope exceeded 10 deg. Within full form subsets showing no snow cover in early summer (subset A in Map 3-3) pixels classified as SNOWBED were reclassified to ROCK if they were not snow covered in late winter as to be expected from snowbed vegetation.

In addition to this, a water mask was generated from a topographical map 1:50.000 (Statens Kartverk 2006). The post-classification of pixels with this water mask seemed necessary mainly for two reasons: First, a considerable number of the larger lakes in Hardangervidda are regulated for hydroelectric purposes and thus have a high variability in water levels. The water level shown in the satellite image of Aug 09th 2003 is very low, so that it does not represent the average expansion of the land cover class WATER. Second, pixel reclassification using a water mask could significantly reduce the misclassification of smaller lakes (<30 m diameter) due to the resolution of the Landsat image (mixed pixels).

Accuracy assessment

A reliable accuracy assessment is crucial for any satellite-based classification (Congalton 2001). In this study a combination of confusion matrixes and kappa coefficients was used, calculated from a set of independent testing data (see above). In the following a brief description and criticism of the two concepts is presented based on Congalton (2001):

The confusion matrix is a square array of n by n dimensions, where n is the number of classes, showing the relationship between selected testing data sampled from the field as columns and its label assigned by the classifier as rows. Accuracy assessment is divided into three different types: Overall accuracy gives the correctly classified pixels over all classes calculated as the fraction of (weighted) summed diagonal cases from the (weighted) total sample size used for testing. The builder’s accuracy is defined as the per class proportion of (weighted) testing data being correctly labeled by the classifier (calculated by dividing the entry (i,i) for an information class i by the sum of column i). Finally, the user’s accuracy gives the per class proportion of (weighted) classified pixels representing the correct classes that is the probability that the classified pixel actually represents the specific information class on the ground (calculated by dividing the entry (i,i) for an information class i by the sum of row i).

As an evaluation method the confusion matrix is an easy to use method for accuracy assessment, allowing for direct comparisons between different classifiers. Comparisons between user’s and builder’s accuracy per class can reveal tendencies weather a classifier tends to act too “greedy” or “selective” for a particular class. As a drawback it is often stated that within the concept of overall, builder's and user's accuracy only partial information of the confusion matrix at a time is utilized. Therefore this concept does not account for correctly classified pixels occurring by chance (Foody 1992).

The Kappa coefficient is often implemented to heal these discrepancies. The Kappa value k is an accuracy statistic that represents the proportion of agreement obtained after removing the proportion of agreement that could be expected to occur by chance (Foody 1992). Congalton & Mead (1983) defined the Kappa coefficient by the equation:

$$\hat{k} = \frac{N\sum_{i=1}^{r} x_{ii} - \sum_{i=1}^{r}(x_{i+} \times x_{+i})}{N^2 - \sum_{i=1}^{r}(x_{i+} \times x_{+i})}, \tag{3-5}$$

where $\hat{k}$ is the estimated kappa coefficient, r is the number of columns/rows in the confusion matrix, x_{ii} is the entry (i,i) of the confusion matrix, x_{i+} is the marginal total of row i, x_{+I} is the marginal total of column i and N is the total number of observations.

The Kappa coefficient typically falls on a scale between 0 and 1, where the latter indicates complete agreement. Values are often split into 3 groupings for interpretation: a value greater than 0.80 (80%) represents strong agreement, a value between 0.40 and 0.80 (40 to 80%) represents moderate agreement and a value below 0.40 (40%) represents poor agreement (Congalton 1996). The Kappa value is widely used because all elements in the classification error matrix, and not just the main diagonal, contribute to its calculation and because it compensates for agreement by chance (Rosenfield & Fitzpatrick-Lins 1986).

3.3 Results

Method comparison

The results of the land cover classification process were largely promising, with the overall classification accuracies (CA) including ancillary data ranging between 71.5 to 79.6% depending on classifier. Kappa values showed similar results with values falling in the interval between 0.65 and 0.75. For an overview of classification results see Figure 3-2:

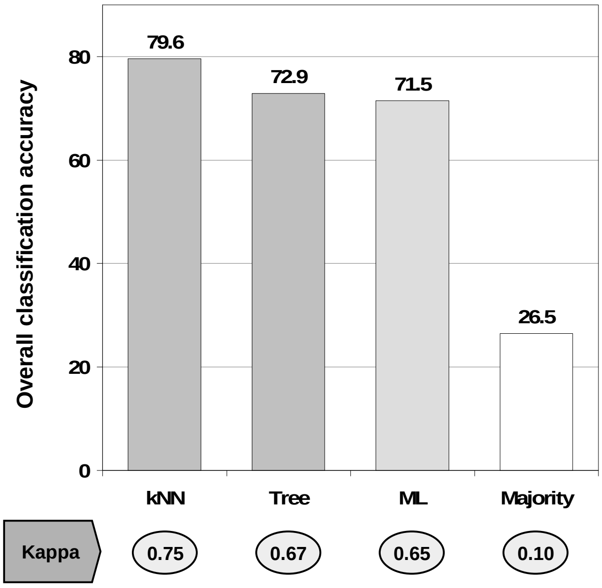


Figure 3-2: Overall classification accuracy by classifier – overview

The best results could be achieved with the kNN classifier (overall CA: 79.6; Kappa: 0.75). The tree classifier fell short of this (overall CA: 72.9; Kappa: 0.67), while the maximum likelihood approach showed slightly lower results (overall CA: 71.5; Kappa: 0.65). All classifiers performed significantly better as compared to a majority classification (overall CA: 26.5; Kappa: 0.10).

All tested classifiers gained significantly in accuracies from including ancillary data using homogeneous subset creation and normative post-classification rules (see Figure 3-3):

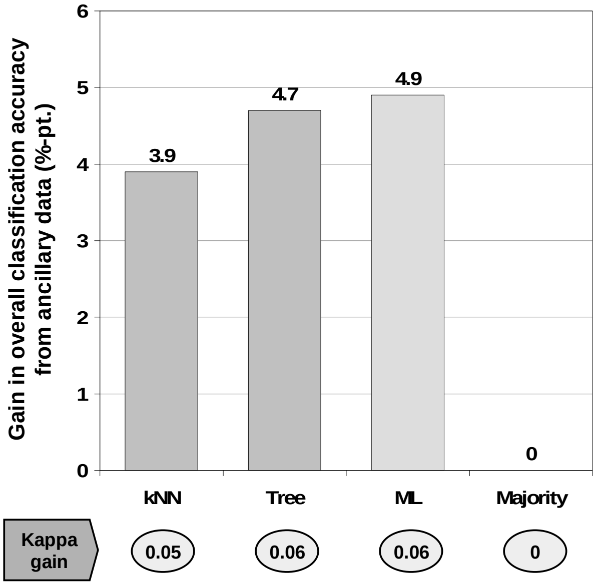


Figure 3-3: Gain in overall classification accuracy from ancillary data by classifier – overview

The maximum likelihood classification demonstrated the highest gains (overall CA: +4.9%-pt.; Kappa: +0.06). The tree classifier showed similar gains (overall CA: +4.7%-pt.; Kappa: +0.06), whereas the kNN classifier benefited slightly less (overall CA: +3.9%-pt.; Kappa: +0.05) but still considerably.

The analysis of average user's/builder's accuracies as well as the gains from ancillary data by class showed similar tendencies between the classifiers, but with significant differences between classes (see Figure 3-4), suggesting that the additional support provided from the snow mask and the DEM was more important for the classification accuracy of some of the vegetation classes:

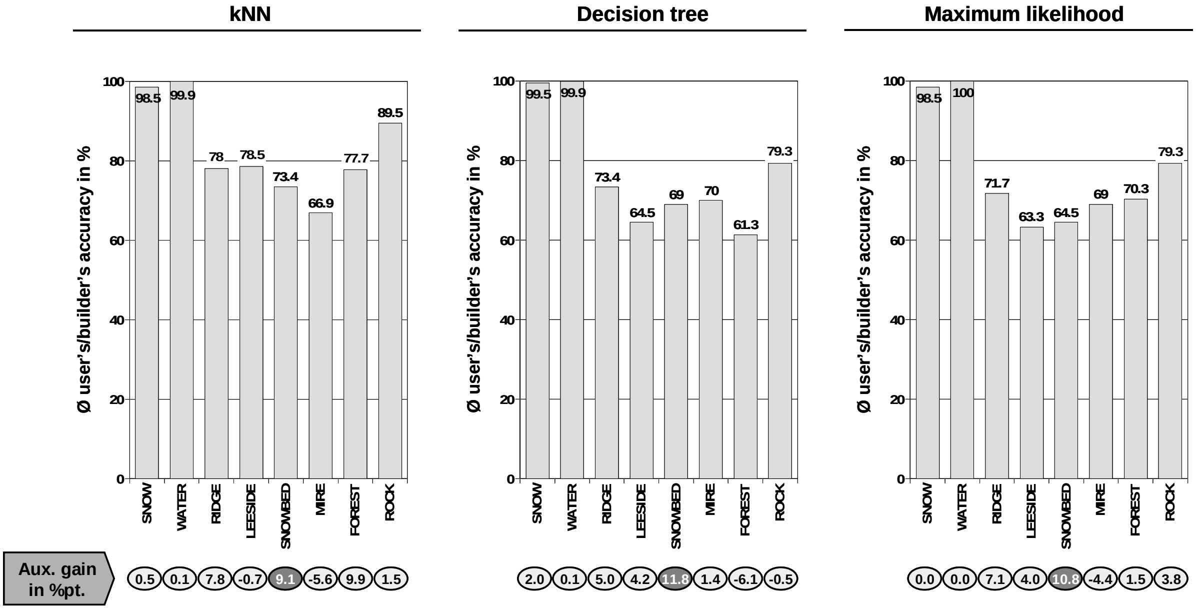


Figure 3-4: Classification accuracy by class and classifier – overview

For all classifiers the highest accuracy values were found for the classes SNOW and WATER (SNOW: 98.5 to 99.5%; WATER: 99.9 to 100%). The gain from ancillary data for these classes was low for all classifiers (SNOW: +0.0 to +0.5%-pt.; WATER: +0.0 to +0.1-pt.). The land cover class ROCK could also be classified with very high accuracies (kNN: 89.5% vs. Tree/ML: 79.3%) with low to modest accuracy gains from incorporating ancillary data (-0.5 to +3.8%-pt.). Also ridge vegetation (RIDGE) could be classified with satisfactory accuracies (ranging from 71.7% (ML) to 78% (kNN)) and this category significantly benefited from ancillary data for all selected classifiers (ML: +7.1%-pt.; Tree: +5.0%-pt.; kNN: +7.8%-pt.). Leeside vegetation (LEESIDE) still demonstrated very satisfactory results for the kNN classifier (78.5%), but did not gain significantly from ancillary data. Results from the tree and ML classifiers were significantly lower (64.5% and 63.3%), but benefited more from ancillary data (+4.2% and +4.0%-pt.). Given the difficulties with heterogeneous subclasses, the SNOWBED category showed promising results for both non-parametric classifiers (kNN: 73.4%; Tree: 69%). This was in contrast to results from the maximum likelihood classification, which fell short with a modest class accuracy of only 64.5%. For all three classifiers snowbed vegetation demonstrated by far the highest gain from creating homogeneous subsets based on early summer snow conditions and relative elevation (kNN: +9,1%-pt.; Tree: +11.8%-pt.; ML: +10.8%-pt.). Classification results for the classes MIRE and FOREST were ambiguous depending on classifiers: While kNN gave satisfactory results for FOREST (CA: 77.7%; gain from AD: +9.9%-pt.), MIRE demonstrated rather poor results (CA: 66.9; negative gain from AD: -5,6%-pt.). Maximum likelihood classification showed the same tendencies with a satisfactory accuracy for FOREST (70.3%) gaining from AD (+1.5%-pt.), MIRE with CA of 69% but not gaining from AD (-4.4%-pt.). The tree classifier showed the best results for MIRE classification (CA: 70%; gain from AD: +1.4%-pt.) but gave poor results for FOREST classification (CA: 61.3%; gain from AD: -6.1%-pt.).

Comparison of the confusion matrices for the selected classifiers revealed superior results for the kNN classifier for all overall accuracies, kappa coefficients and user's/builder's accuracies (see Figure 3-5). Values given within the matrices represent testing data (n=100 per class) weighted by prior probabilities (see chapter 3.2.).

kNN

	SNOW	WATER	RIDGE	LEESIDE	SNOWBED	MIRE	FOREST	ROCK	Total	User's
SNOW	**9.2**								9.2	**100.0**
WATER	0.2	**72.8**							73.0	**99.7**
RIDGE			**146.3**	12.3	31.7	13.0		1.5	204.8	**71.4**
LEESIDE			23.3	**153.1**	11.5	13.7	13.2		214.8	**71.3**
SNOWBED			33.9	7.0	**90.7**	3.6		3.0	138.3	**65.6**
MIRE			2.1			**39.6**	1.5	0.8	44.0	**90.0**
FOREST			2.1	3.5		2.2	**22.9**		30.7	**74.6**
ROCK	0.2		4.2		10.1			**70.7**	85.2	**83.0**
Total	9.6	72.8	212.0	176.0	144.0	72.0	37.6	76.0	**800.0**	**Ø: 76.2**
Builder's	**96.0**	**100.0**	**69.0**	**87.0**	**63.0**	**55.0**	**61.0**	**93.0**	**Ø: 75.7**	**O: 75.7**
Ø U/B	**98.0**	**99.9**	**70.2**	**79.1**	**64.3**	**72.5**	**67.8**	**88.0**		**k: 0.7**

Decision tree

	SNOW	WATER	RIDGE	LEESIDE	SNOWBED	MIRE	FOREST	ROCK	Total	User's
SNOW	**9.1**								9.1	**100.0**
WATER	0.2	**72.8**							73.0	**99.7**
RIDGE			**144.2**	22.9	30.2	9.4		3.0	209.7	**68.8**
LEESIDE			36.0	**110.9**	10.1	19.4	15.8		192.2	**57.7**
SNOWBED			27.6	37.0	**89.3**	3.6		12.9	170.3	**52.4**
MIRE	0.2			1.8	4.3	**39.6**	0.8	1.5	48.1	**82.3**
FOREST			2.1	3.5			**21.1**		26.7	**78.9**
ROCK	0.1		2.1		10.1			**58.5**	70.8	**82.6**
Total	9.6	72.8	212.0	176.0	144.0	72.0	37.6	76.0	**800.0**	**Ø: 69.6**
Builder's	**95.0**	**100.0**	**68.0**	**63.0**	**62.0**	**55.0**	**56.0**	**77.0**	**Ø: 68.2**	**O: 68.2**
Ø U/B	**97.5**	**99.9**	**68.4**	**60.3**	**57.2**	**68.6**	**67.4**	**79.8**		**k: 0.61**

Maximum likelihood

	SNOW	WATER	RIDGE	LEESIDE	SNOWBED	MIRE	FOREST	ROCK	Total	User's
SNOW	**9.3**								9.3	**100.0**
WATER		**72.8**							72.8	**100.0**
RIDGE			**144.2**	31.7	46.1	7.2		6.1	235.2	**61.3**
LEESIDE			44.5	**110.9**	17.3	17.3	7.9	1.5	199.4	**55.6**
SNOWBED			19.1	15.8	**72.0**	2.2		16.0	125.0	**57.6**
MIRE				3.5	1.4	**44.6**	1.5	1.5	52.6	**84.8**
FOREST			2.1	14.1		0.7	**28.2**		45.1	**62.5**
ROCK	0.3		2.1		7.2			**50.9**	60.5	**84.1**
Total	9.6	72.8	212.0	176.0	144.0	72.0	37.6	76.0	**800.0**	**Ø: 67.7**
Builder's	**97.0**	**100.0**	**68.0**	**63.0**	**50.0**	**62.0**	**75.0**	**67.0**	**Ø: 66.6**	**O: 66.6**
Ø U/B	**98.5**	**100.0**	**64.6**	**59.3**	**53.8**	**73.4**	**68.8**	**75.6**		**k: 0.59**

kNN with ancillary data

	SNOW	WATER	RIDGE	LEESIDE	SNOWBED	MIRE	FOREST	ROCK	Total	User's
SNOW	**9.3**								9.3	**100.0**
WATER	0.1	**72.8**							72.9	**99.9**
RIDGE			**169.6**	15.8	18.7	15.8		3.0	223.0	**76.0**
LEESIDE			17.0	**144.3**	11.5	10.1	9.8		192.7	**74.9**
SNOWBED			17.0	10.6	**102.2**	2.2		3.0	135.0	**75.8**
MIRE			6.4	1.8	4.3	**42.5**	1.1	0.8	56.8	**74.8**
FOREST				3.5		1.4	**26.7**		31.7	**84.3**
ROCK	0.2		2.1		7.2			**69.2**	78.7	**87.9**
Total	9.6	72.8	212.0	176.0	144.0	72.0	37.6	76.0	**800.0**	**Ø: 79.6**
Builder's	**97.0**	**100.0**	**80.0**	**82.0**	**71.0**	**59.0**	**71.0**	**91.0**	**Ø: 79.6**	**O: 79.6**
Ø U/B	**98.5**	**99.9**	**78.0**	**78.5**	**73.4**	**66.9**	**77.7**	**89.5**		**k: 0.75**

Decision tree with ancillary data

	SNOW	WATER	RIDGE	LEESIDE	SNOWBED	MIRE	FOREST	ROCK	Total	User's
SNOW	**9.5**								9.5	**100.0**
WATER	0.1	**72.8**							72.9	**99.9**
RIDGE			**159.0**	26.4	21.6	8.6	0.4	5.3	221.3	**71.8**
LEESIDE			25.4	**114.4**	13.0	14.4	11.3		178.5	**64.1**
SNOWBED			14.8	17.6	**100.8**	2.9		12.2	148.3	**68.0**
MIRE			2.1	5.3	2.9	**44.6**	1.5	0.8	57.2	**78.1**
FOREST			4.2	12.3		1.4	**24.4**		42.4	**57.6**
ROCK			6.4		5.8			**57.8**	69.9	**82.7**
Total	9.6	72.8	212.0	176.0	144.0	72.0	37.6	76.0	**800.0**	**Ø: 73.2**
Builder's	**99.0**	**100.0**	**75.0**	**65.0**	**70.0**	**62.0**	**65.0**	**76.0**	**Ø: 72.9**	**O: 72.9**
Ø U/B	**99.5**	**99.9**	**73.4**	**64.5**	**69.0**	**70.0**	**61.3**	**79.3**		**k: 0.67**

Maximum likelihood with ancillary data

	SNOW	WATER	RIDGE	LEESIDE	SNOWBED	MIRE	FOREST	ROCK	Total	User's
SNOW	**9.3**								9.3	**100.0**
WATER		**72.8**							72.8	**100.0**
RIDGE			**159.0**	28.2	30.2	8.6		6.1	232.1	**68.5**
LEESIDE			31.8	**116.2**	15.8	18.0	7.5	2.3	191.6	**60.6**
SNOWBED			14.8	15.8	**90.7**	1.4		14.4	137.3	**66.1**
MIRE			6.4	1.8	1.4	**43.2**	1.9	0.8	55.4	**78.0**
FOREST				14.1		0.7	**28.2**		43.0	**65.6**
ROCK	0.3				5.8			**52.4**	58.5	**89.7**
Total	9.6	72.8	212.0	176.0	144.0	72.0	37.6	76.0	**800.0**	**Ø: 72.3**
Builder's	**97.0**	**100.0**	**75.0**	**66.0**	**63.0**	**60.0**	**75.0**	**69.0**	**Ø: 71.5**	**O: 71.5**
Ø U/B	**98.5**	**100.0**	**71.7**	**63.3**	**64.5**	**69.0**	**70.3**	**79.3**		**k: 0.65**

Figure 3-5: Confusion matrices by classifier

For all classifiers very little confusion was found within non-vegetation classes (SNOW, WATER and ROCK) and between non-vegetation classes and classes containing vegetation

(RIDGE, LEESIDE, SNOWBED, MIRE and FOREST). Some confusion was found between the categories ROCK, SNOWBED and RIDGE depending on the classifier, however (see Figure 3-5). Highest absolute confusion was found between RIDGE and SNOWBED without ancillary data. Confusion was significantly less for all classifiers when ancillary data was included. The matrices in Figure 3-5 also show significant confusion between MIRE with LEESIDE and RIDGE vegetation. Some confusion was also found between LEESIDE and FOREST, depending on the classifier. In absolute numbers confusion between RIDGE and LEESIDE vegetation was also noticeable, but of lesser importance when related to weighted sample size within those classes.

Class distribution within the study area

As stated above, classification results were superior using the kNN method incorporating ancillary data. In the following the distribution of land cover classes will hence be described based on those results. Class distribution after classification is presented in Figure 3-6. For comparative reasons prior probabilities are depicted below.

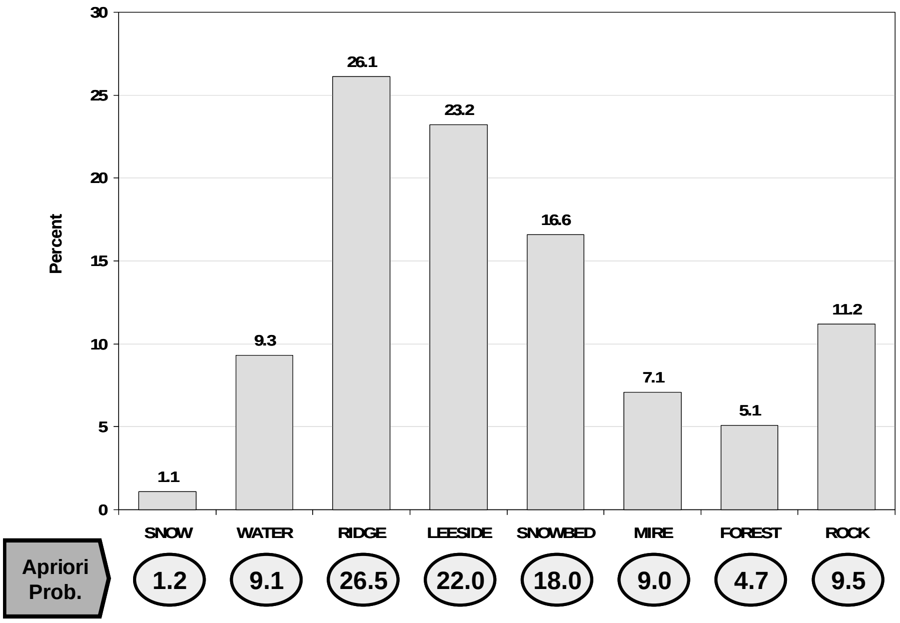


Figure 3-6: Distribution of land cover classes and comparison to prior probabilities – overview

Results from kNN indicated RIDGE to account for the largest proportion of Hardangervidda (26.1%), followed by LEESIDE (23.2%), SNOWBED (16.6%) and ROCK (11.2%). While the proportions of land cover classes suggested from kNN results seemed to generally be inline with prior probabilities, slightly lower proportions were found for RIDGE and SNOWBED classes (-0.4% and -1.4%), while both, LEESIDE and ROCK, showed higher proportions of land cover within the study area (1.2% and 1.7%) than prior probabilities suggested.

Results from kNN showed significant differences in class distributions with respect to elevation (see Figure 3-7).

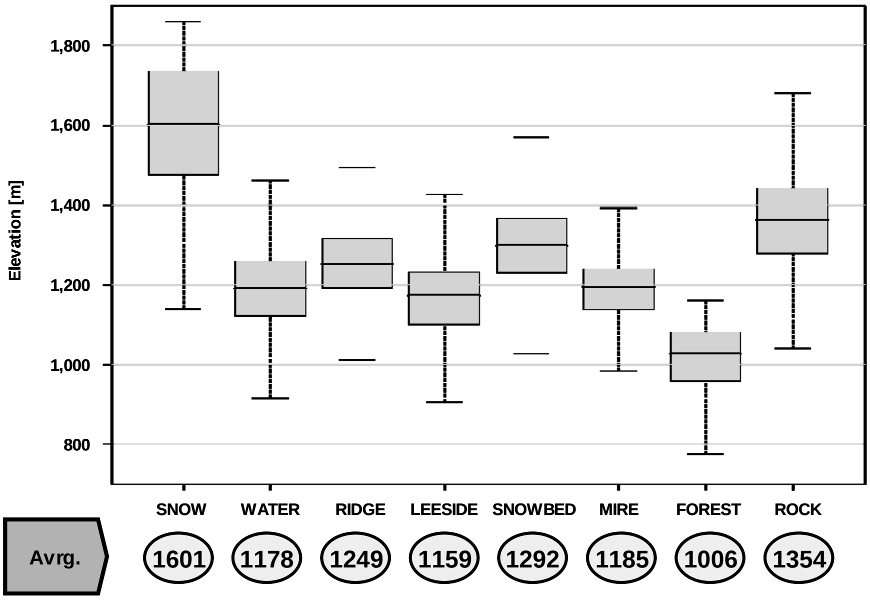


Figure 3-7: Elevation distribution by land cover class

Unproductive areas (SNOW and ROCK) showed the highest average elevations (SNOW: 1,601 m; ROCK: 1,354 m), followed by SNOWBED (1,292 m) and RIDGE (1,249 m). FOREST (1,006 m), MIRE (1,185 m) and LEESIDE (1,159 m), on the other hand, showed below average mean elevations.

Significant differences in average area sizes between classes as classified from kNN were found (see Figure 3-8). As expected, the classes WATER and SNOW yielded the largest average area sizes from classification (app. 17,600 sqm and 13,600 sqm), with SNOW showing significantly larger standard deviation. While RIDGE, FOREST and LEESIDE demonstrate intermediate average area sizes classified as homogeneous (5,100 sqm to 6,100 sqm), SNOWBED, ROCK and MIRE were characterized by small average areas (2,300 sqm to 3,700 sqm), indicating possible accuracy gains from larger image resolution.

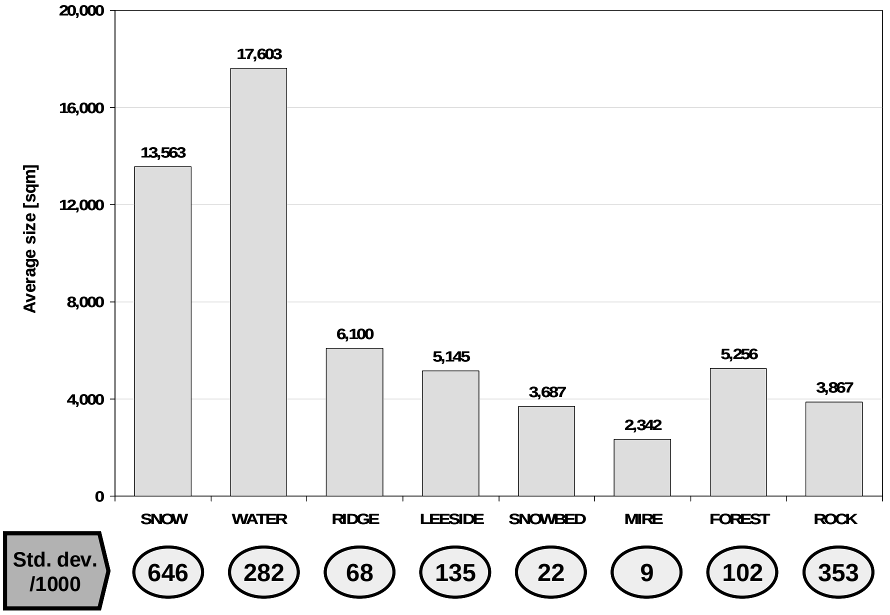
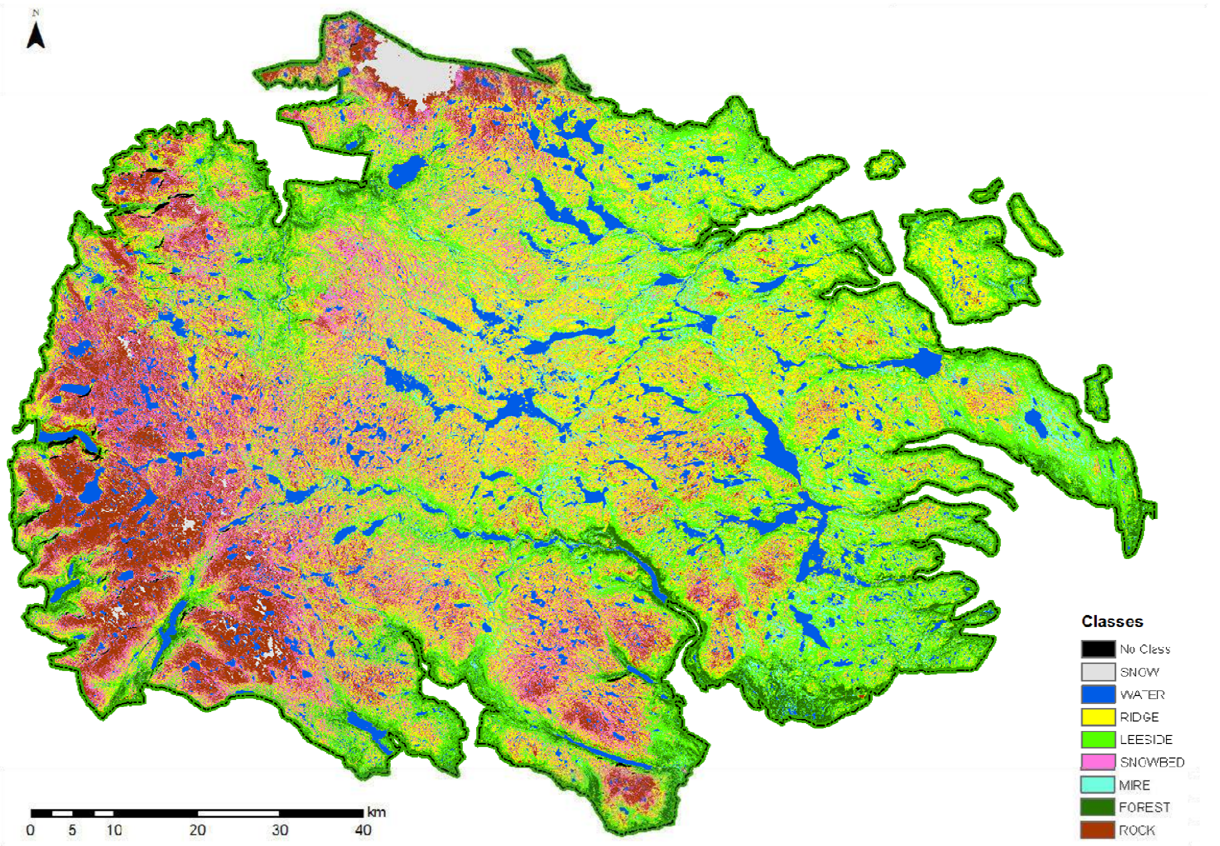


Figure 3-8: Average size of patches by land cover class (with standard deviation)

Spatial class distribution in overview is given in Map 3-4 (see below) and, for enhanced visibility, class-specific distribution patterns were compiled in Map 3-5 (further below).



Map 3-4: Hardangervidda land cover map 2003 – classification result

The class SNOW covers app. 1.1% (prior 1.2%) of the total study area with Hardangerjøkull accounting by far for the largest proportion (hence the high standard deviation). Larger areas covered by glaciers or permanent snowfields are also found in high western and partially in southern areas of Hardangervidda. The class mean elevation is app. 1,600 m (std. dev.: 153 m) and well above average. Spectrally SNOW is an extremely characteristic class resulting in a very high overall accuracy (98.5% for kNN). Very little confusion is found with rock and water (probably due to remaining snow/ice and/or mixed pixels). Therefore only minor improvements through ancillary data could be reached (accuracy gain of 0.5% for kNN).

Approximately 9.3% (prior 9.1%) of Hardangervidda's total land cover consists of WATER. A homogeneous distribution of lakes and rivers was found both, over the entire study area and elevation zones (mean elevation: 1,178 m; std. dev: 152 m). The class is characterized by a very high overall class accuracy (99.9% for kNN) due to both, a spectrally characteristic class profile (Tso & Mather 2001) and post-classification correction of misclassified pixels using ancillary data (slope derived from DEM, N50 water mask). Minimum initial misclassification occurred between water and shadow cast as well as for small water bodies under 20 m diameter. The low water level of regulated lakes at the time of image acquisition (Aug 09th 2003) resulted in partially exposed lake beds.

With 26.1% (prior 26.5%) RIDGE represents the largest proportion of land cover within the study area. This land cover type occurs in all parts of Hardangervidda but is slightly more abundant in the more central areas (number and extension) possibly following an altitudinal gradient. The class shows a mean elevation of 1,249 m (std. dev.: 101). Classification results for RIDGE were best using kNN (78.0%), while Tree and ML had significantly lower accuracies (73.4% and 71.7%). Some confusion between RIDGE and LEESIDE/SNOWBED was documented and is most likely to be caused by the patchiness of this class leading to some mixed pixel problems. With a 7.8%-pt. gain in accuracy (kNN) lichen ridges benefited considerably from incorporating ancillary data due to lower confusion with both, SNOWBED and LEESIDE categories.

The class LEESIDE covers app. 23.2% (prior 22%) of the total area. It is mainly found on wind-sheltered, southern slopes and at a mean elevation of 1,159 m (std. dev.: 115 m). LEESIDE is only sparsely found at higher altitudes in the western and southern areas. The class could be identified with an accuracy of 78.5% by the kNN classifier, who performed significantly better as compared to the tree (64.5%) and ML classifier (63.3%). LEESIDE was found to be a spectrally heterogeneous vegetation class, leading to confusion with other classes, mainly RIDGE, SNOWBED, MIRE and FOREST. Accuracy gains through ancillary data were modest (-0.7%-pt. /4.0%-pt. /4.2%-pt. for kNN/ML/Tree).

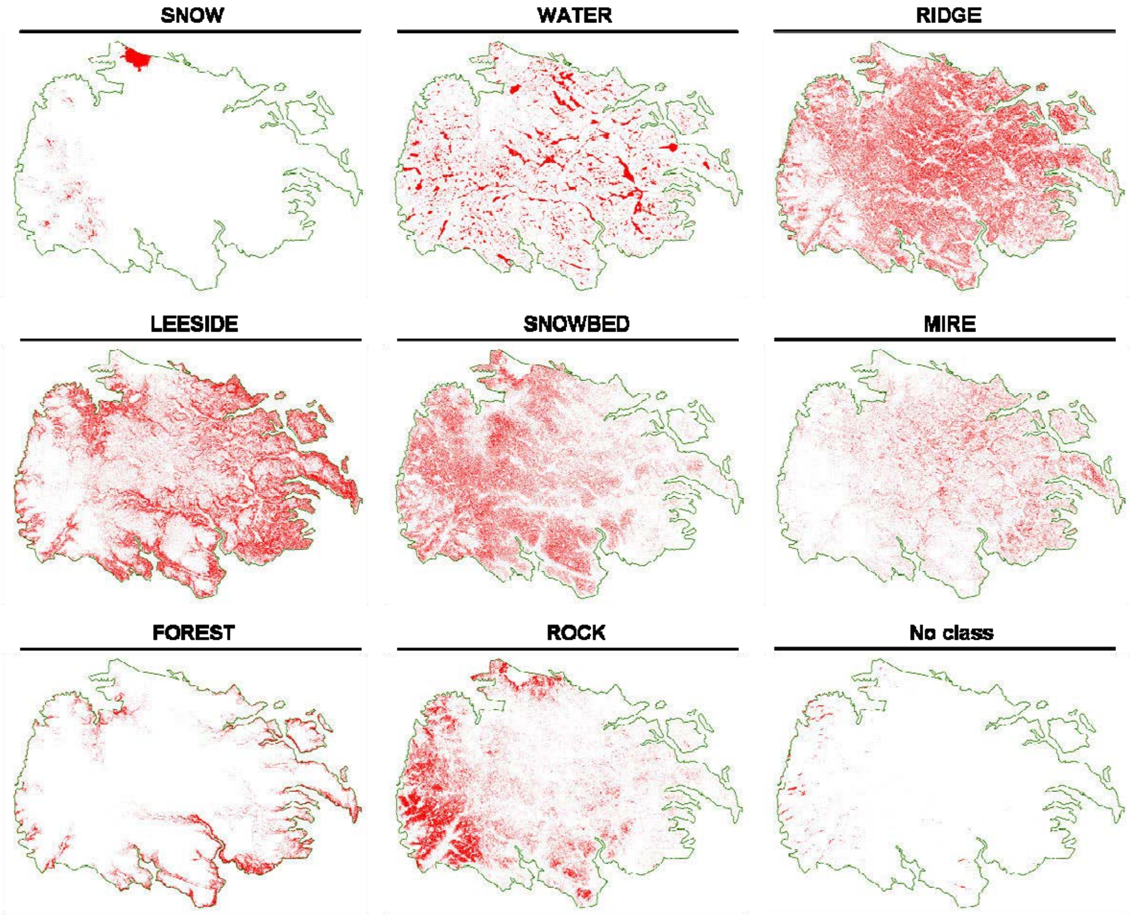
SNOWBED composes app. 16.6% (prior 18%) of the Hardangervidda reindeer area. They foremost occur on the colder northern and eastern slopes and within depressions, well above average altitude (mean: 1,292 m; std. dev.: 113 m). SNOWBED distribution follows both, an east-west and an altitudinal gradient, resulting in highest densities within the upper western areas of Hardangervidda. Due to heterogeneous vegetation composition together with a small-scaled distribution pattern of snowbed communities the spectral variance of this class is high. This creates high challenges for land cover classification. Confusion occurs mainly with RIDGE, LEESIDE and ROCK classes. Ancillary data proved to be especially helpful for SNOWBED with a class accuracy gain of 9.1%-pt. (kNN). This gain mainly results from a lower confusion with both, RIDGE and ROCK classes.

7.1% (prior 9%) of Hardangervidda land cover was classified as mires. Mires are more abundant in the middle and eastern parts of Hardangervidda and show a below average mean elevation of 1,185 m (std. dev.: 94 m). In contrast, to all other classes kNN shows the lowest overall accuracy for mires (66.9%) while Tree and ML yielded higher class accuracies (69% and 70%). While Tree could slightly gain in accuracy from ancillary data (+1.4%-pt.) both, kNN and ML, could not (-5.6%-pt. and -4.4%-pt.). Considerable confusion between MIRE and LEESIDE was found. Some confusion was found between MIRE and forest (possibly bush-mires).

FOREST (birch forests) composes 5.1% (prior 4.7%) of the Hardangervidda area and is, mainly located on the lower edges of the study area, primarily within the southern and eastern slopes. FOREST depicts significantly lower mean elevations as compared to the other vegetation classes (1,006 m; std. dev.: 108 m). It could be classified with an overall accuracy of 77.7% by kNN, while Tree (61.3%) and ML (70.3%) gave significantly lower results. With a class accuracy gain of 9,9%-pt. (kNN) birch forests could benefit significantly from ancillary data, mainly due to reduced confusion with LEESIDE vegetation (possibly shrubs). Still some confusion with scrub dominated mires and leeside vegetation was found.

ROCK dominated terrain covers app. 11.2% (prior 9.5%) of the study area, predominantly in high altitudes within the western, southern and northern parts of Hardangervidda, often surrounding snow and ice fields. With an average class altitude of 1,354 m (std. dev.: 135 m) ROCK yields the highest values next to SNOW. The class could be identified by the kNN-classifier with an overall accuracy of 89.5% – remarkably better than from Tree and ML (both with 79.3% accuracy). ROCK could gain about 1.5% (kNN) in accuracy through implementation of ancillary data, caused by less confusion with both, RIDGE and SNOWBED vegetation. Generally rocks are fairly easy to separate from vegetation with reflection increasing with wave-lengths (Tso & Mather 2001) but confusion between light epilithic lichen and other yellow lichen (e.g. *Cladonia spec.*, *Cetraria spec.*) can lead to misclassification of rocks as ridges.

App. 0.4% of the total study area could not be allocated to the above classes. These pixels were mainly dark shadows caused by steep slopes in the western and southern part of Hardangervidda. Their mean elevation was at about 1,109 m (std. dev.: 239 m). Shaded areas were initially confused with water; post-classification rules based on topographic data helped to correct misclassified pixels: dark shadows that were misclassified as water could be corrected by using slope derived from DEM.



Map 3-5: Spatial distribution of land cover classes n Hardangervidda

3.4 Discussion

In this chapter selected parametric and non-parametric classifiers were used to map the alpine mountain plateau of Hardangervidda, Norway, into eight different land cover classes based on Landsat imagery and ancillary data. The achieved overall accuracies varied from 71.5% to 79.6% depending on the classifier in use.

Accuracy comparison with other studies

Compared to similar studies the results of the above approach are well within range of classification accuracies documented. For example Théau, Peddle & Duguay (2005) mapped terrestrial lichens in a caribou habitat of Northern Quebec, Canada, using an enhancement-classification method and spectral mixture analysis. With the enhancement classification method, they reached an overall accuracy of 74.5% (kappa=0.70) across 10 land cover classes. Ostendorf & Reynolds (1998) developed a model for arctic tundra vegetation derived from topographic gradients. They mapped six different vegetation classes for Northern Alaska using two types of models with overall class accuracies ranging from 71 to 78%. Nordberg (1998) achieved an overall accuracy of 85% for vegetation classification of alpine heath based on ML and Landsat TM. Boresjo-Bronge & Wester (1999) mapped land cover in Swedish mountain areas using a knowledge based mixed classification approach (ML classification with strata based on spectral and biomass ratios). The overall accuracy obtained in their study for 12 land cover classes ranged from about 80 to 90% for different images. Colpaert, Kumpula & Nieminen (1995) classified reindeer ranges in Finland into three different classes based on Landsat TM data using maximum likelihood with overall accuracies between 83% and 92% for three selected areas.

As presented above, the average user’s/builder’s accuracy for snowbed vegetation in this study could be significantly increased from 64.3% to 73.4% using both, images from different seasons and DEM derivates as ancillary data. These findings correspond with results from Edenius *et al.* (2003), whom achieved an average class accuracy between 69% and 77% for snowbed vegetation, depending on the ancillary data used. Dahlberg (2001) could classify snowbed vegetation with an accuracy of 74% using a combination of IRS 1S-LISS satellite imagery and data on spatial structure plus DEM in an auto-logistic regression model.

Comparison of classifiers

The kNN classifier was found to yield superior results for both, overall accuracy (kNN: 79.6% vs. Tree: 72.9% and ML: 71.5%) and the majority of average users'/builder's class accuracies. The advantages of the non-parametric classifiers over ML are assumed to be partially explained by considerable within class variances of reflectance profiles for some of the more heterogeneous classes. Especially for snowbed and leeside vegetation the assumption of normal distribution within bands and classes made by the ML method does not seem to be completely justified. While this can cause both, estimation biases and inefficiency within ML theory due to its dependence on the variance-covariance matrix, kNN and decision tree seem to be less affected, as they make use of individual reflectance profile of single sample points (Gilichinsky *et al.* 2011; Thessler *et al.* 2005).

Ancillary data

Ancillary data derived from both DEM and different seasonal satellite images proved to be highly beneficial for all selected classifiers. Overall accuracies could be increased by 3.9 to 4.9 percentage points depending on classifier. More specific, the chosen approach led to a significantly better separation between snowbed and ridge vegetation for all classifiers. As a result the average user's/builder's accuracies of snowbed vegetation could be improved by +9.1%-pt. to 11.8%-pt., depending on classifier, while ridge vegetation yielded accuracy gains between +5.0%-pt. and +7.8%-pt. percentage points.

These results reflect the selection of ancillary data sources and their implementation within the classification models. Primary interest was to cluster Hardangervidda in land cover classes relevant for reindeer in order to test for spatial selection patterns using habitat selection models later. Earlier studies indicated both, ridge and snowbed vegetation, to be of predominant importance for reindeer habitat selection in winter/summer, respectively (Tømmervik *et al.* 2004; Edenius *et al.* 2003). As preliminary results indicated considerable confusion between those two classes (compare 3.2) it was opted for stratified classification using early summer snow cover and relative elevation as ancillary data to create homogeneous sub areas to allow for adjusted prior class probabilities. Classification results seem to confirm the appropriateness of the above approach to enhance class separation between snowbed and ridge vegetation. This, since snowbed vegetation should be indicated by both, snow cover during early summer and convex terrain, ridges – on the other hand – should be free of snow and concentrated on concave terrain.

Other classes do not benefit evenly from this implementation approach: While some classes like SNOW, WATER and ROCK already yield high average class accuracies without ancillary data (89.5% to 99.9% for kNN) and therefore seem less likely to experience further gains, classes like MIRE might have required an alternative approach to increase separability[66].

Ancillary data can enhance satellite-based land cover classification significantly through providing additional information relevant for classes characterized by similar reflectance profiles. While increased data availability and computational capabilities have favored this development over the last years, data abundance and implementation possibilities require efficient selection and combination methods to develop approaches suitable for the underlying objective. Future research in this context is needed.

Landsat imagery vs. high-resolution data

As argued above, Landsat imagery was chosen for land cover classification in Hardangervidda as a reasonable compromise between spatial resolution, scene extent, historic backlog, suitability of spectral channels as well as cost efficiency. While satisfactory accuracies were achieved with respect to overall results and for most of the classes, results for single classes seem to suggest further improvement potential by using high-resolution images. More specific, rather small average homogeneous area sizes (vegetation fragments) were found for snowbed vegetation (3,687 sqm) and mires (2,342 sqm), corresponding to an average of 2.6 to 4.1 Landsat pixels. As this patchiness directly relates to accuracy reductions due to mixed pixel problems, an increase in spatial resolution would most likely be beneficial to these vegetation classes currently yielding lowest accuracies from kNN (snowbed = 73.4%; mires = 66.9%).

In order to detect small-scale vegetation patterns in alpine vegetation Schardt & Gallaun (1999) recommend a spatial resolution of at least 5 m using multi-spectral satellite images. On the other hand, Käyhkö & Pellika (1994) concluded that SPOT multi-spectral (XS) imagery, while providing high-resolution data, was not entirely suitable for vegetation mapping of reindeer habitat due to spectral confusion between vegetation and lichen in the near infrared band. Furthermore, Tso & Mather (2001) emphasized that an increase in spatial resolution inevitably implies a loss of radiometric resolution as the signal to noise ratio decreases. Furthermore, the number of good quality images available for vegetation mapping in Hardan-

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[66] E.g. the normaliyed difference water index (NDWI) for remote sensing of vegetation proposed by Gao (1996) could potentially increase the seperability of mires from other vegettaion classes.

gervidda was limited. This is since first, rapid phenological developments in the vegetation limits the potential period for image acquisition and second, that a frequent cloud cover during summer also reduces the potential number of high quality images largely (compare also Dahlberg 2001). This is even more restrictive for high-resolution images as several scenes would have to be compiled in order to compensate for smaller scene sizes (e.g. 60x60 sqkm for SPOT 5 vs. 185x172 sqkm for Landsat).

In addition a further separation of different lichen heaths types would have been desirable. During field work it became apparent that it was difficult to find enough suitable training points for each type, due to the inhomogeneous, small-pattern distribution and a blending of the different vegetation classes. Rees, Tutubalina & Golubeva (2004) showed that the Landsat 7 ETM+ sensors do not form an ideal basis for the spectral discrimination of lichen-species. A higher spectral resolution and coverage in the range from 900 to 11,300 nm would be desirable. Nordberg & Allard (2002) found that only *Cladonia stellaris* with a reflectance of about 65% of the NIR could be separated from the other analyzed species (*Cladonia rangiferina*, *Cladonia arbuscula*, *Cetraria islandica* and *S. saxatile*), because they reflected in a similar way in the MIR and can hardly be separated from each other.

In order to further assess potential gains in overall accuracy and separability between vegetation classes within alpine mountain areas, a comparative study using high-resolution satellite imagery should be conducted within a smaller area to avoid problems due to radiometric corrections.

Sample data for training and testing

Parametric and non-parametric classifiers depend on ground truth data for training and testing. As shown earlier, the requirements in sample size are dependent both, on number of classes and feature space dimensionality (which can be significantly increased by using ancillary data). By limiting the classification to eight classes and by using empirical forward/backward selection to reduce feature space dimensionality it was possible to keep the necessary amount of field data for training and testing at a feasible level (and thereby costs). Nevertheless, collection of sample points in the field was found to be severely limiting for satellite-based land cover mapping in Hardangervidda. In this context more efficient sampling methods could be highly beneficial in order to allow for utilization of potential accuracy gains from ancillary data. Especially opportunities for collecting sample points by helicopter/airplane and from aerial photographs should be tested and assessed (compare also Théau, Peddle & Duguay 2005).

Class distribution

The overall distribution of land cover/vegetation classes in Hardangervidda derived from 2003 Landsat imagery and ancillary data using kNN classification seems to be in-line with results from previous studies. Using slightly different class definitions Gaare, Tømmervik & Hoem (2005) concluded a similar class distribution based on visual point estimation from aircraft in summer 2004 for snow/ice, water, mire and forest. They suggested higher values for rock and snowbed vegetation (18.7% vs. 11.2% and 22.3% vs. 16.6%) while both, leeside and ridge vegetation, were estimated with lower proportions (16.2% vs. 23.2% and 17.5% vs. 26.1%).

Hesjedal (1975a/b) used aerial photographs from an old investigation in 1973 – 74 covering only 1% of the total area of Hardangervidda. As the training data in Hesjedals study over-represent the sub alpine and low alpine zone, while the mid alpine zone (1,250 – 1,500 m) is underrepresented and the high alpine zone (>1500 m) is not included, results are not directly comparable to this study. This explains the higher proportion of forest (11.3% vs. 4.9%) and leeside vegetation (36.1% vs. 23.2%), while the classes rock and ridge, which occur more in the higher alpine zones, yield lower proportions (0.5% vs. 11.2% and 12.1 vs. 26.1%). Snow/ice and water were not covered in the Hesjedal study.

Conclusion

In this chapter the kNN classifier was documented to deliver superior results as compared to two selected parametric and non-parametric methods for land cover classification in a mountainous terrain in Scandinavia. Both, the sufficient number of sample points collected in the field (n=5,700) and the limited number of land cover classes (8), enabled statistically valid training and testing of all classifiers. Empirical calibration of classifier parameters together with the proposed forward/backward selection of satellite bands ensured classification efficiency. Empirical testing of accuracy gains through implementation of different types and utilization alternatives for ancillary data proved to be not only beneficial within the given context but might also be helpful for other studies.

The proposed approach is limited by a number of factors, however. Defining appropriate land cover classes was difficult and always represents a compromise between different perspectives (scientific purpose, satellite detectability and existing vegetation classification schemes). The amount of sample data required for training and testing demanded a considerable amount of fieldwork. Skewed distribution of sample points from fieldwork with regard to prior class probabilities required weighting of sample points for training and testing. While land cover classification using Landsat TM data seemed to be an appropriate compromise between resolution, scene extent, historic backlog and cost efficiency, on the one hand, and proved to yield satisfying overall results, the patchiness of the vegetation classes within the study area (especially for snowbed vegetation) indicated, that potential accuracy uplifts can be achieved from higher spatial resolution. C-correction lead to a significant reduction of terrain induced reflectance but still was limited by the 25 m spatial resolution of the available DEM for Hardangervidda. Finally, the proposed methods for implementation of ancillary data requires profound hypothesis on prior probabilities (distribution of vegetation classes), which might not be available for other areas.

4 Estimation of lichen biomass

4.1 Introduction

Lichen ridges and reindeer

Lichen ridges are the most important winter pastures for reindeer (e.g. Klein 1968; Skogland 1984a). Reindeer, in contrast to all other ruminants, have developed the ability to utilize lichens, which mainly contain carbohydrates, through symbiosis with bacteria capable of digesting lichens (Warenberg 1997). Access to winter forage has also been regarded as one of the major limiting factor determining population growth in some populations (Gaare, Thomson & Kjos-Hanssen 1975; Skogland 1984a). The spatial distribution of lichen biomass is therefore considered to have a major impact on reindeer's (winter) habitat selection (Skogland 1989).

Snow conditions (snow depth/surface condition) limit the forage availability for reindeer during winter, as cratering is only possible up to a threshold of app. 50 – 70 cm snow depth (Skogland 1978)[67]. Such snow conditions are most frequently found on wind exposed mountain ridges, especially associated with a more continental climate (short vegetation period, high annual differences in temperature and low precipitation). Extreme sites like these only allow for development of very poor or no soil at all, further limiting possible vegetation types. Lichens show competitive advantages over other plants for windblown ridges with dry climate, as they are not dependent on soil and can cope with extreme temperatures as well as short vegetation periods (Nordhagen 1943).

Spatial differences in grazing pressure

Wild reindeer are sensitive to anthropogenic changes in the environment, and in Norway the combination of land cover/land use changes, the construction of roads as well as the development of infrastructure for the tourist industry (e.g., hotels, tourist cabins) is a significant threat in recent years for this species (Nellemann *et al.* 2001a/b). More specific, hydroelectric power development including power lines together with the development of the tourist industry and the construction of roads are increasing on reindeer pastures and migratory routes in southern Norway, often blocking pathways to traditional pasturelands (Vistnes *et al.* 2004)[68].

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[67] Note, however that other authors have reported different thresholds (Pruitt 1959; Bergerud 1974c; LaPerriere & Lent 1977; Helle 1984; Thing 1984; Adamczewski *et al.* 1988; Brown & Theberge 1990)

[68] See also Mahoney & Schaefer (2002).

It has been shown that these cumulative disturbances not only directly affect migration routes (Wolfe, Griffith & Wolfe 2000) but can also lead to spatial alterations of reindeer densities within traditional habitats since disturbed areas are used significantly less as compared to areas under little or no influence by human disturbance (Vistnes & Nellemann 2008). These spatial changes in reindeer habitat use can additionally be enhanced by environmental and climate changes including alterations in precipitation, snow condition, increased insect harassment and vulnerability to predators and pollution (Nellemann *et al.* 2001a; Vistnes *et al.* 2004; Mörschel 1999) and can themselves lead to increases in spatial heterogeneity of resources within habitats (Abrams 2000).

The carrying capacity according to Caughley (1979) of a habitat for herbivores is dependent on the growth rate of vegetation, both, in harvested (Hadwen & Palmer 1922) and non-harvested systems (Leopold 1933). In the case of lichens, the highest growth rates are found at intermediate biomass values, as growth rates are reduced both, when lichen biomass is low due to overgrazing and when biomass is high in the absence of grazing (Gaare & Skogland 1975). The hypothesis exists that in a situation, where the average lichen growth rate is reduced by artificial spatial differences in grazing pressure induced by human disturbance, the maximum sustainable yield (MSY) is lowered significantly (Vistnes & Nellemann 2008). Due to the slow recovery rate of the fragile lichen beds (see e.g. Sveinbjornsson 1990; Kumpula, Colpaert & Nieminen 2000), overgrazing of lichen winter pastures can result in density dependent population crashes for reindeer. Such crashes have e.g. been published for Greenland and Canada (Gunn 2003; Gunn, Miller & Berry 2003)[69].

Overgrazing and density dependent population crashes

Populations of wild reindeer sometimes experience pronounced population fluctuations (e.g. Tyler 2010; Morneau & Payette 2000; Cuyler 2007) with corresponding periods of overgrazing when populations are at high numbers. As lichens do not replace biomass annually, high population densities have the potential to deplete winter food resources and lichen biomass can be suppressed for long time periods (Klein 1968, 1987). In such situations (high populations, depleted lichen beds), environmental stochasticity (icing of remaining pastures) has been suggested to lead to extreme population crashes (Klein 1968; Cuyler 2007), especially, if migration is prevented (e.g. through insularity (Klein 1999) or anthropogenic habitat fragmentation).

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[69] See also Olofsson (2001) for the long-term effect of herbivory on tundra ecosystems.

Klein (1968, 1999) has shown that caribou and reindeer are less likely to overgraze fragile winter lichen beds and therefore less likely to experience density-dependent population crashes at higher latitudes, where snow cover is more persistent. In this context avoiding density dependent population crashes for Hardangervidda, carrying a wild reindeer population at its southern edge of existence, can be a considerable challenge for management.

Lichen monitoring important for reindeer management

Lichen can be regarded as an indicator for the ecological status of alpine vegetation because of its sensitivity to overgrazing and trampling. This is also fostered by the fact that lichens – in contrast to other vegetation – show little variation in biomass between seasons (Kershaw 1985)[70]. As it is protecting the soil from erosion and washout of nutrition (Brown & Mikkola 1974), damage of lichen cover is the beginning of soil erosion. Since lichens are almost exclusively used by reindeer and caribou, the evidence of overgrazing and trampling is accepted as a good indicator of habitat condition (Théau, Peddle & Duguay 2005).

While lichen biomass has been shown to correlate negatively with reindeer density through increased grazing pressure and trampling, it can be affected by numerous other factors: Alterations in precipitation and temperatures (caused by climate change, see Arctic Climate Impact Assessment 2004; Roald *et al.* 2003) can alter vegetation periods and/or change the composition of species (within lichens and in relation to other plants) and thereby affect the maximum potential lichen biomass (Leader-Williams, Smith & Rothery 1987). In addition increases in human land use and recreational activities can reduce lichen biomass (e.g. trampling). More specific, the use of off-road vehicles has been shown to affect lichen volumes significantly (Tømmervik *et al.* 2012; Swanson & Barker 1992). Finally, as lichens directly obtain nutrients from the air, atmospheric pollution can severely affect their growth (Leader-Williams, Smith & Rothery 1987).

As described above, the crucial impact of reindeer/caribou on lichens and the slow recovery of this vegetation (e.g. Klein 1987) make plausible the hypothesis of a long-term, cyclic/fluctuating dynamic (Messier *et al.* 1988). While the overall process has been discussed, little is known about its spatiotemporal dynamics, especially within an unequally disturbed habitat. It is therefore important to map and assess lichen resources for reindeer both, in a current and historic perspective. Spatially explicit information on pasture qualities through time together with temporal data on population development and human disturbance could for

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[70] For further aspects of the ecology of mat-forming lichens see also Crittenden (2000).

example contribute significantly to a better understanding of habitat use, both, for the past and present. Additionally spatial differences in lichen volume development over the past could allow for basic ex post impact assessment on infrastructure development for reindeer habitat use. In a longer perspective ongoing monitoring of winter grazing resources could provide valuable measures for future reindeer management.

Lichen biomass assessment based on single predictor models

The use of simple classification methods to characterize the amount and the status of high-latitude vegetation has been shown to be potentially misleading for a variety of reasons (Rees, Golubeva & Williams 1998), including the prevalence of lichens, for which the normal correlation between NDVI and biomass does not apply. The problem using a NDVI-based method in estimation of biomass is that its results are dependent on vegetation or land cover type. Arctic and high mountain phenology is also extremely rapid, with growing seasons compressed into a few weeks, and exceptionally variable in their timing from year to year (Rees, Golubeva & Williams 1998; Karlsen *et al.* 2006). Although traditional methods like supervised or hybrid supervised–unsupervised classification methods give a sufficient classification accuracy of more than 85% for the most dense lichen dominated types (Colpaert, Kumpula & Nieminen 2003; Tømmervik *et al.* 2003), they do not provide sufficient estimates for different categories of lichen density/coverage as well as thickness categories.

Nevertheless, the general possibility to separate lichens from other land cover types and also to differentiate between discrete lichen biomass classes, has been confirmed by laboratory measurements carried out by Nordberg & Allard (2002). While the spectral shapes were partially influenced by lichen species, lichen height, presence of humus and moisture content proved to be dominant (Nordberg & Allard 2002). Nordberg & Allard (2002) concluded that changes in lichen cover can be classified and mapped using NDVI-methods in three classes: unchanged, moderate decrease, and high decrease. The classes can be regarded as three risk-assessment classes for vegetation degradation and ensuing soil erosion. Nordberg (1998) developed a new normalized difference index for mapping of lichen biomass called the Normalized Difference Lichen Index (NDLI) which showed to be quite good ($R^2 = 0.73$ using visual interpretation of color-infrared (CIR) aerial photos with an overall sample size of n=30 for accuracy assessment), but in a later study by Nordberg & Allard (2002) the NDVI-index showed to be better than the NDLI-index. Dahlberg (2001) concluded that it was not always obvious whether the model described the biomass or some ground variable (e.g. rock cover, topography) recommending topography and other ground variables as ancillary data or estimate biomass by vegetation cover types.

Objectives

This puts forward the importance for improved methods as well as “new” vegetation indices for detection and monitoring of lichen dominated vegetation entities.

i. The first objective of this study is therefore to establish a method for a continuous estimation of lichen biomass within lichen dominated mountain heath communities using a multivariate prediction model to increase both, overall accuracy and stability towards misclassified or mixed pixels. It is asked: Is it possible to quantify lichen biomass using satellite based remote sensing? And, if so: To which degree can the proposed method support the management of reindeer (and possibly other species)?

ii. The second objective is than to create a lichen biomass map of Hardangervidda, which - within the greater context of this dissertation - will later be used as a crucial input factor for modeling reindeer habitat selection (see chapter 5). Three questions are in focus: What is the current status of lichen biomass in Hardangervidda and how does it translate spatially? How does this current distribution of lichen biomass coincide with the spatial distribution of reindeer?

4.2 Methods

The proposed method for the estimation of lichen biomass is based on a three-step approach:

a. First, the distribution of lichen ridges within the study area is described and discriminated from potentially confusing vegetation classes.

b. Second, the collection of training and testing data including preparation (outlier removal and weighting) is presented and the selected Landsat image and its preprocessing (orthorectification, topographic correction) are described.

c. Based on sample points and reflection indices from the selected image a prediction model for lichen biomass is developed in a third step. The distribution of lichen biomass within the study area is estimated employing the above established prediction model.

Lichen pastures in Hardangervidda

The general distribution of land cover classes within Hardangervidda has been described in chapter 3.2. In the following a closer description of lichen ridges and heath, graminoid ridges and oligotrophic bilberry and dry grass heaths as well as grasslands of intermediate snow cover is presented:

Most lichen heaths on Hardangervidda are oligotrophic and occur in localities with very sparse snow cover. The maximum snow cover in the lichen heaths is usually less than 50 – 60 cm (Lye 1975). Because of poor snow cover, the winter temperatures may be < -15° C in upper vegetation layers. This, together with the often extreme dry conditions (2 – 5% soil moisture measured as wet weight in northern Finland and southern Norway (Hesjedal 1975a/b)), and high soil-surface temperatures in summer (40 – 50° C observed in both areas (Hesjedal 1975a/b)) strongly limits the number of vascular plant species on exposed ridges (*Festuca ovina* and a few other monocotyledons, and some dwarf shrubs, e.g. *Empetrum hermaphroditum*, *Vaccinium vitis-idaea* and *Arctostaphylos alpine*). In Hardangervidda lichen heaths are best developed in the central and eastern parts and they are considered to be the best winter grazing habitats for reindeer (Gaare, Tømmervik & Hoem 2005)[71]. These vegetation types (Loiseleurio-Arctostaphylion alliance in phytosociological terminology) cover about 10% of the area (Hesjedal 1975a/b; Gaare, Tømmervik & Hoem 2005) and were used by the reindeer for 80 – 100% of the total grazing time during the winter period (Østbye *et al.* 1975)[72]. At the central Hardangervidda plateau lichen dry weight biomass is usually of the order 200 – 400 g/sqm, often dominated by *Cetraria nivalis*. Visually, much of the highly grazed and trampled lichen mat seems to be dead, but radioautographs have shown that only about 2% were not assimilating CO_2 and were unable to recover (Wielgolaski 1975).

In habitats with more accumulated snow during winter, *Alectoria ochroleuca* and *Cetraria nivalis* disappear while *Cladonia stellaris* together with *C. rangiferina* and *C. mitis* tend to dominate. In the western parts of Hardangervidda the moss *Racomitrium lanuginosum* occasionally dominates this community together with some *Cetraria nivalis* and Cl*adonia mitis* (Lye 1975; Gaare, Tømmervik & Hoem 2005). There is also an east-western gradient in the pattern of the most dominating lichen species with more coverage and frequency of *Cladonia*

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[71] Lichens are consumed by reindeer even in summer, but comprise a lower percentage of the total intake than in winter; they have a high digestibility, about 70% of dry matter, for reindeer, which therefore utilize the energy in lichens far better than, for instance, sheep (Østbye *et al.* 1975).

[72] Although lichens, mainly *Cladonia spp.* and yellow *Cetraria spp.* are the main reindeer diet in winter, graminoids and woody plants of the wind-blown communities make up about 40% of the intake even in this period, based on rumen samples (Gaare & Skogland 1975).

stellaris in the eastern parts than in the central and western parts due to dryer climate in east (Gaare, Tømmervik & Hoem 2005). This type of lichen heath is, however, more related to oligotrophic heaths and grasslands of intermediate snow cover (Lye 1975). In Hardangervidda the maximum lichen biomass, about 1,100 – 1,800 g/sqm, is found on un-shaded, but not too dry, ridges in the more continental areas (Gaare, Tømmervik & Hoem 2005). In the western districts lichens are restricted by shading from bryophytes which grow under the better moisture conditions, e.g. *Racomitrium lanuginosum*; here the maximum lichen biomass is probably not above 500 g/sqm (Gaare, Tømmervik & Hoem 2005).

Graminoid ridges (Fremstad 1997) dominated by *Festuca ovina*, *Juncus trifidua*, *Deshampsia flexuosa*, *Carex bigelowii*, together with lichens like *Cetraria nivalis*, *Cladonia mitis* and *C. rangiferina* cover significant areas of Hardangervidda and are considered to be important winter grazing habitats providing proteins and other nutrients for the reindeer. In western parts there are communities with *Carex bigelowii* and *Cetraria nivalis* which can occur together in combination with *Vaccinium myrtillus* and *Empetrum herrmaphroditum* in areas with intermediate snow cover which can be utilized by the reindeer in the early as well as late winter and in spring.

If the snow cover is somewhat deeper (0.5 – 1.5 m maximum snow cover in the relatively moist south-western alpine Norway) and the soil-moisture content slightly higher (as compared to typical lichen heaths), increasing amounts of vascular plant biomass and production are observed even if the nutrient conditions are poor. In these very important heath communities (covering about 1/3 of the total area of Hardangervidda (Hesjedal 1975a/b)), a number of characteristic species appear like bilberry (*Vaccinium myrtillus*), *Deschampsia flexuosa*, *Festuca ovina*, *Carec bigelowii*, *Juncus trifidus*, *Hieracium alpinum*, *Nardus stricta*, and on slightly better soils also *Anthoxanthum odoratum* and *Alchemilla alpinum* (Lye 1975; Wielgolaski 1975). The bilberry heaths are considered as the most important vegetation type in Hardangervidda with respect to area coverage (Hesjedal 1975a/b). Lichens are still important in this heath community and in Hardangervidda *Cladonia stellaris* together with *C. rangiferina* and *C. mitis* dominate in these communities. The moss cover is usually more abundant than in typical lichen heaths and soil moisture is still probably the strongest limiting factor for growth in these types of heaths (Wielgolaski 1975). These types of vegetation are mainly used by reindeer in the beginning of the winter and in winter with thin snow cover.

Field data and lichen measurements

For training and testing lichen coverage and height of n=1345 sample areas were recorded in the field during late July/August 2000 – 2005, with most of the fieldwork carried out between 2003 and 2005. These sample areas were placed within areas classified as ridge vegetation (see chapter 3.2), following a stratified sampling design with prior class probabilities, geographical distribution (east-west/north-south gradient), elevation and estimated grazing pressure as covariates. Areas selected for collection of training/testing data had a minimum size of 30x30 sqm (possibly 50x50 sqm) in order to reduce mixed pixel problems in satellite analysis.

Within each sampling area a sampling point close to its center and four additional sampling points at 10 m distance from the central point in the four cardinal directions were randomly selected. Within a radius of 2 m around the center of each sampling point a 0.5x0.5 m grid was placed, consisting of 25 10x10 cm squares, within which the percentage area covered with lichen as well as the lichen height was measured (see Figure 4-1).

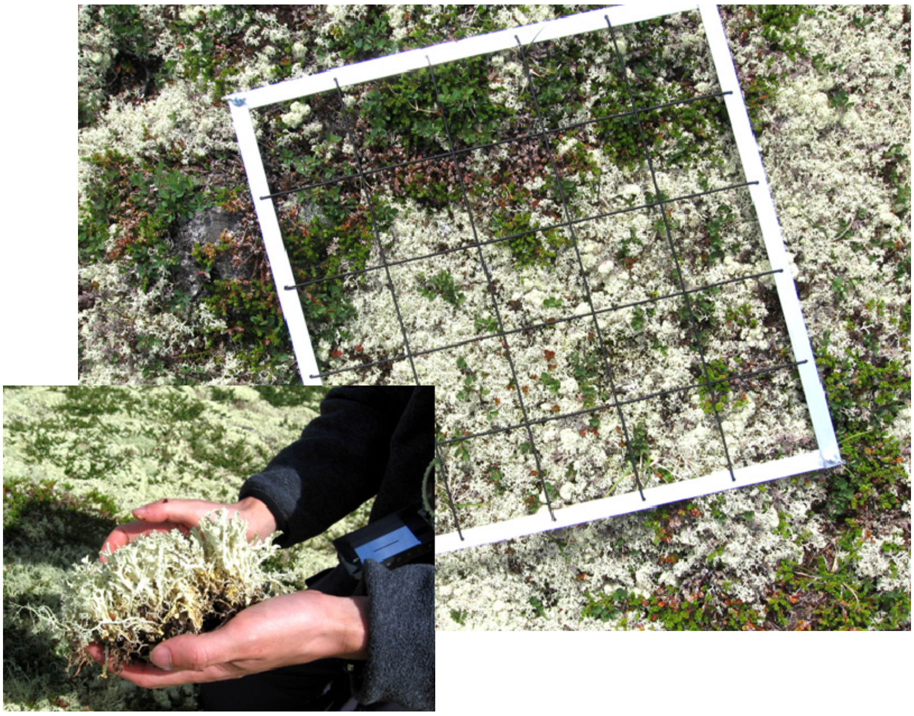


Figure 4-1: Collection of lichen volume sample points – example

For each sampling area all five measurements of lichen coverage and height were averaged, and used to calculate lichen volumes.

Empirical data form Gaare (unpublished) suggests a strong correlation between lichen volume and biomass within Norwegian alpine areas depending on species and water content (average R-square: 0.90). As many of the available lichen samples did not encompass estimations on lichen water content during recording it was decided to use lichen volume as a proxy for biomass. For examples of differences in lichen volume within sample points see Figure 4-2:

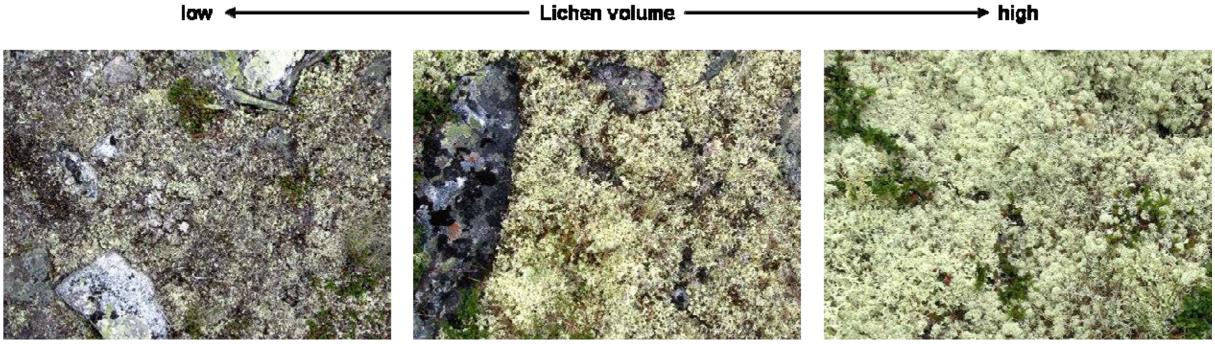


Figure 4-2: Differences in lichen volume – examples

Sample areas with atypical reflectance profiles (mismatch between GPS accuracy of sample areas and orthorectified master image) were excluded from the study. Preliminary analysis suggested a skewed sample design due to severe over sampling of areas with low lichen volumes (see Figure 4-3):

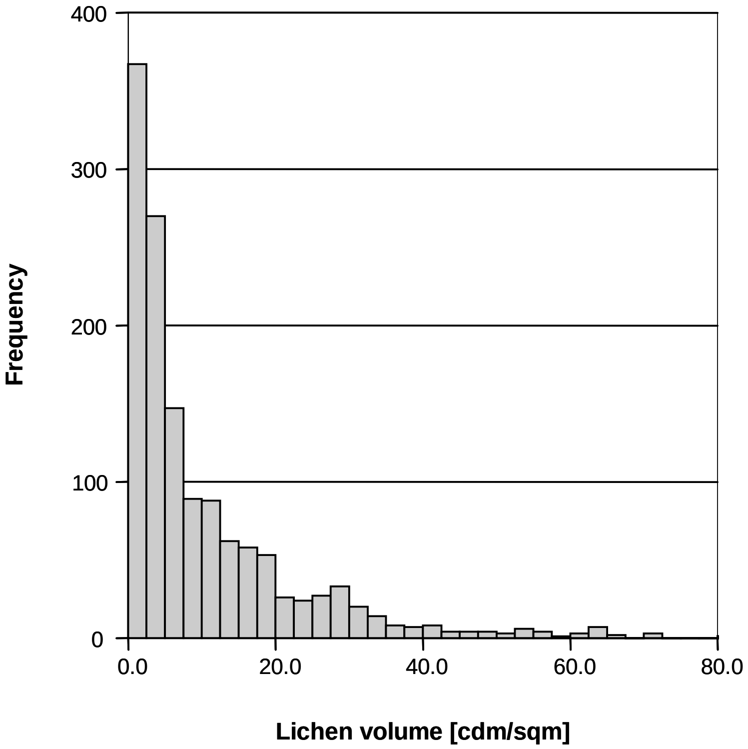


Figure 4-3: Frequency distribution of lichen sample points by volume

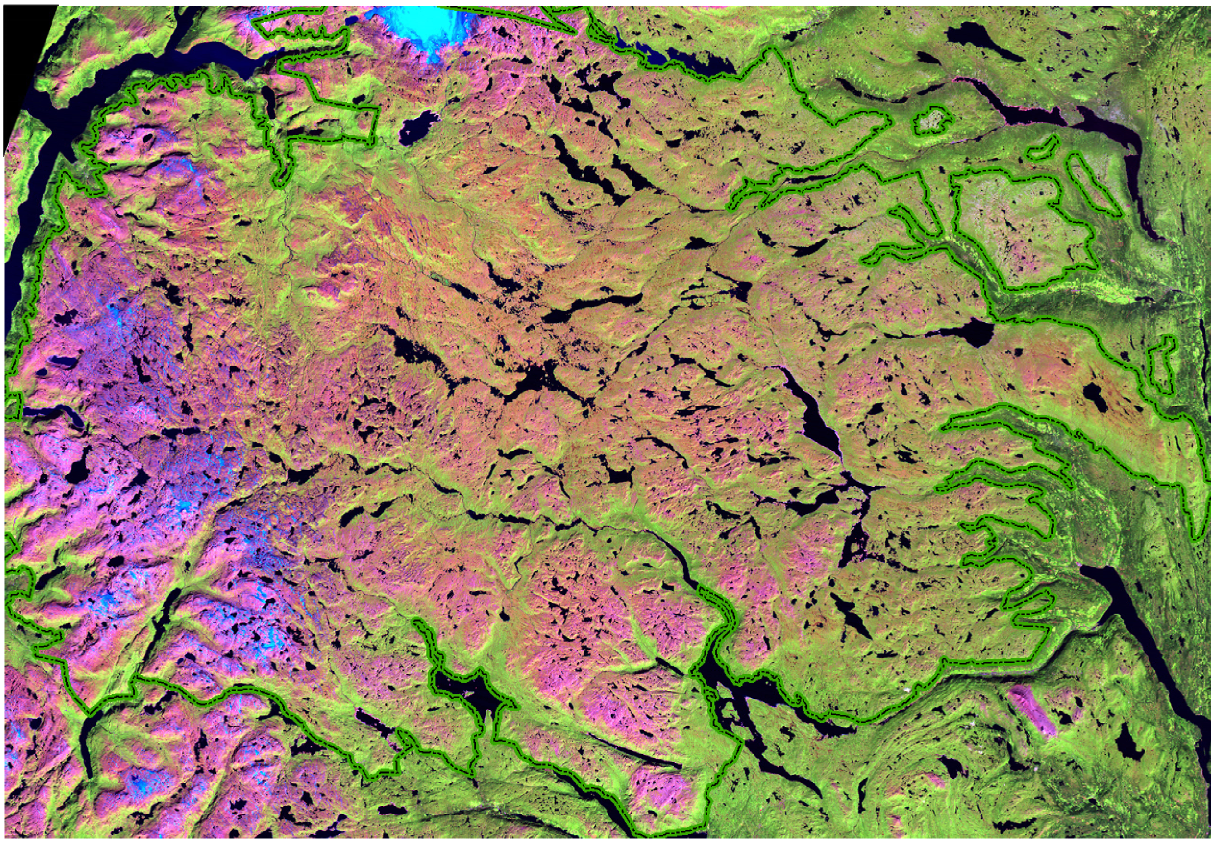
It was therefore decided to use a binned sub-sampling design with 32 equidistant classes of lichen volume to achieve a more leveled distribution of sample areas for later model building. Using a random draw of 10 areas per bin, sample size was reduced to n=202 lichen volume samples in total, as some of the bins contained less than ten sample areas. Within the sub-sample lichen volume showed a more equal distribution ranging from 0 to 80 liters of lichen volume per square meter. While the remaining sample size (n=202) was considered to be large enough for model building it was decided to use a ten fold cross validation for accuracy assessment rather than to split sample areas in training and testing data which would have further reduced sample size.

Image selection

Analogue to land cover classification Landsat TM/ETM+ data was chosen as the best compromise between spatial resolution and other factors (compare chapter 3.2). The spatial extent of one Landsat scene is sufficient to cover the entire study area. Hence no compilations of different scenes were necessary, which would have required prior radiometric corrections between scenes (mad thereby reduced spatial comparability). Furthermore, satellite systems with a comparable backlog as long as possible were necessary for possible timeline comparisons, later. In this context Landsat 5/7 provided the highest continuity over the last decades with a sufficient number of usable scenes since 1984. The cost efficiency of Landsat 5/7 was also a factor since multiple scenes would in the future need to be acquired for potential monitoring. Finally, as noted earlier, band-spectra needed to be sensible for vegetation/lichen reflection and Käykhö & Pellika (1994) found SPOT-XS data less suitable for mapping lichen heath communities due to lacking information from the mid-infrared (MIR) part of the spectrum.

Higher resolution satellite data for lichen biomass assessment possibly would have been favorable for testing and further developments of the method, however. Nevertheless, possible accuracy gains again seem likely to have been limited through the same factors as discussed for land cover classification earlier (see chapter 3.2): Limited precision of available ground control points (RMS: 1 – 7 m), DEM with resolution of 25 m (which is a serious limitation within the mountainous terrain of Hardangervidda), average root mean squares (RMS) of location error of training points limited to 5 m (ranging from 2 – 15 m) and average RMS of GPS radio collars between 4 – 15 m. Altogether it is thus possible to conclude that a 30x30 sqm Landsat resolution is sufficient for the hypothesis tested in this thesis, albeit higher resolution images clearly hold potential for further research and model developments.

The selected Landsat TM5/7 image for the estimation of lichen biomass assessment is shown belo (see Map 4-1):



Map 4-1: Selected images: Landsat TM5 199-18 Aug 09th 2003[73] – overview

The selected image (Landsat TM5 acquired on Aug 9th 2003; path/row: 199/18) is completely cloud free. Resampling was done using cubic convolution[74]. Orthorectification and topographic correction were carried out analog to the land cover procedure (see chapter 3.2).

Prediction model

Previous attempts to measure lichen biomass based on remotely sensed data have used biomass sub-classes (e.g. worn vs. prime quality ranges) derived from single indices like NDVI and NDLI rather than continuous prediction values (Nordberg 1998; Nordberg & Allard 2002). In contrast to this, this thesis aimed for a continuous prediction of lichen volume using a multivariate prediction model in order to enhance overall accuracy and stability. The prediction of lichen volume focuses on ridges dominated by lichen heath communities as identified within land cover classification earlier (see chapter 3.3).

A preliminary examination of possible correlations between lichen biomass estimates and different indexes derived from the L5 image reviled most promising results using Landsat

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[73] NASA Landsat Program 2003

[74] Cubic convolution was preferred to nearest neighbor resampling due to predominate importance of spatial accuracy for the use of normalized differenced indices rather than reflectance values of single bands (see also Reese *et al.* 2003).

bands 2, 4 and 5 (see chapter 4.3). As a prediction model for lichen volume a Lichen Volume Estimator (LVE) was developed using a two-dimensional Gaussian function with NDLI = (TM5 - TM2) / (TM5 + TM2) (Normalized Difference Lichen Index, Nordberg 1998) and NDMI = (TM4 - TM5) / (TM4 + TM5) (Normalized Difference Moisture Index, Wilson & Sader 2002) as factors. NDMI contrasts the near-infrared band 4, which is sensitive to the reflectance of leaf chlorophyll content, to the mid-infrared band 5 - which is sensitive to the absorbance of leaf moisture (Wilson & Sader 2002). Rees, Tutubalina & Golubeva (2004) showed that lichens of the species groups *Cladonia*, *Cetraria* and *Flavocetraria* are well detected in the mid-infrared band 5 (TM), and Neta *et al.* (2010) support this also for wet samples of the same species. Preliminary data investigation suggested better results using two-dimensional Gaussian curve estimates rather than two single linear regression models. This was probably due to a higher robustness towards extreme values and misclassified pixels. Likewise, results were significantly better using Gaussian curve estimates as compared to linear regression. The final regression model to predict the observed lichen volume, i.e. the Lichen Volume Estimator (LVE), is:

$$LVE(NDLI, NDMI) = a \cdot \exp^{-0.5 \cdot \left(\left(\frac{NDLI - NDLI_{mean}}{b} \right)^2 + \left(\frac{NDMI - NDMI_{mean}}{c} \right)^2 \right)}, \quad (4\text{-}1)$$

where $NDLI_{mean}$ and $NDMI_{mean}$ are the mean NDLI and NDMI, respectively, and a, b and c are the normal distribution parameters to be parameterized. Model building and parameter estimation was done using SigmaPlot (SPSS 2000). Due to limited sample size, the model was validated using a tenfold cross-validation procedure (Boyce *et al.* 2002).

4.3 Results

Prediction model for lichen biomass

In this study correlations between lichen biomass and two single predictor variables yielded best results:

(i) A modest and negative correlation was found between NDLI and lichen volume with the strongest sensitivity at intermediate values but poorer predictability for both, very low and high lichen volumes (see Figure 4-4).

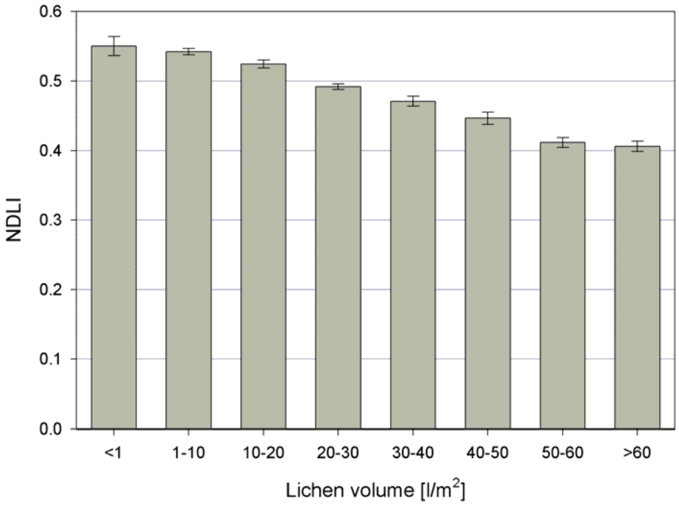

Figure 4-4: Average NDLI values by lichen volume class of sample points (+/- Std. Err.)

(ii) A strong and positive correlation was found between lichen volume and NDMI with a steady increase between 10 and 60 liters of lichen volume per square meter. While separation between lower lichen volumes seemed slightly better for NDMI than for NDLI, again increases in lichen volume beyond 60 liters per square meter showed little or no effect (see Figure 4-5).

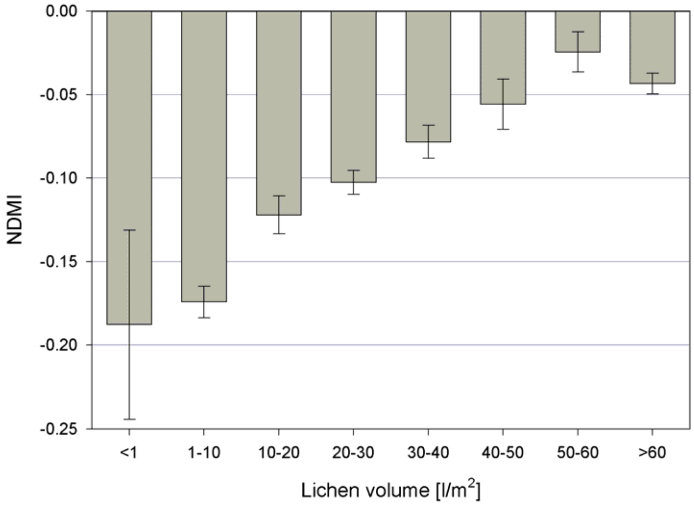

Figure 4-5: Average NDMI values by lichen volume class of sample points (+/- Std. Err.)

The results of the proposed two-dimensional Gaussian regression model to predict lichen volume using NDLI and NDMI as factors were overall promising (see Table 4-1):

Analysis of Variance:

	DF	SS	MS	F	P
Regression	4	45966	11492	120.56	<0.0001
Residual	197	18777	95		
Total	201	64744	322		

	Coefficient	Std. Error	t	P
$NDLI_{mean}$	0.3633	0.0268	13.56	<0.0001
$NDMI_{mean}$	0.0169	0.0029	6.11	<0.0001
a	59.41	4.5511	13.05	<0.0001
b	0.1180	0.0169	6.90	<0.0001
c	0.1834	0.0304	6.04	<0.0001

Table 4-1: Lichen volume model – overview on results of fitted model

The fitted model (n=202) was highly significant with a satisfactory adjusted R-square of 0.704. All estimated parameters were highly significant and no severe violations of regression assumptions (normal distribution of residuals, constant variance between residuals, absence of autocorrelation, no full collinearity between predictors) were detected. For model assumptions see e.g. Neter *et al.* (1996). The curve estimate of the lichen volume model is depicted in Figure 4-6:

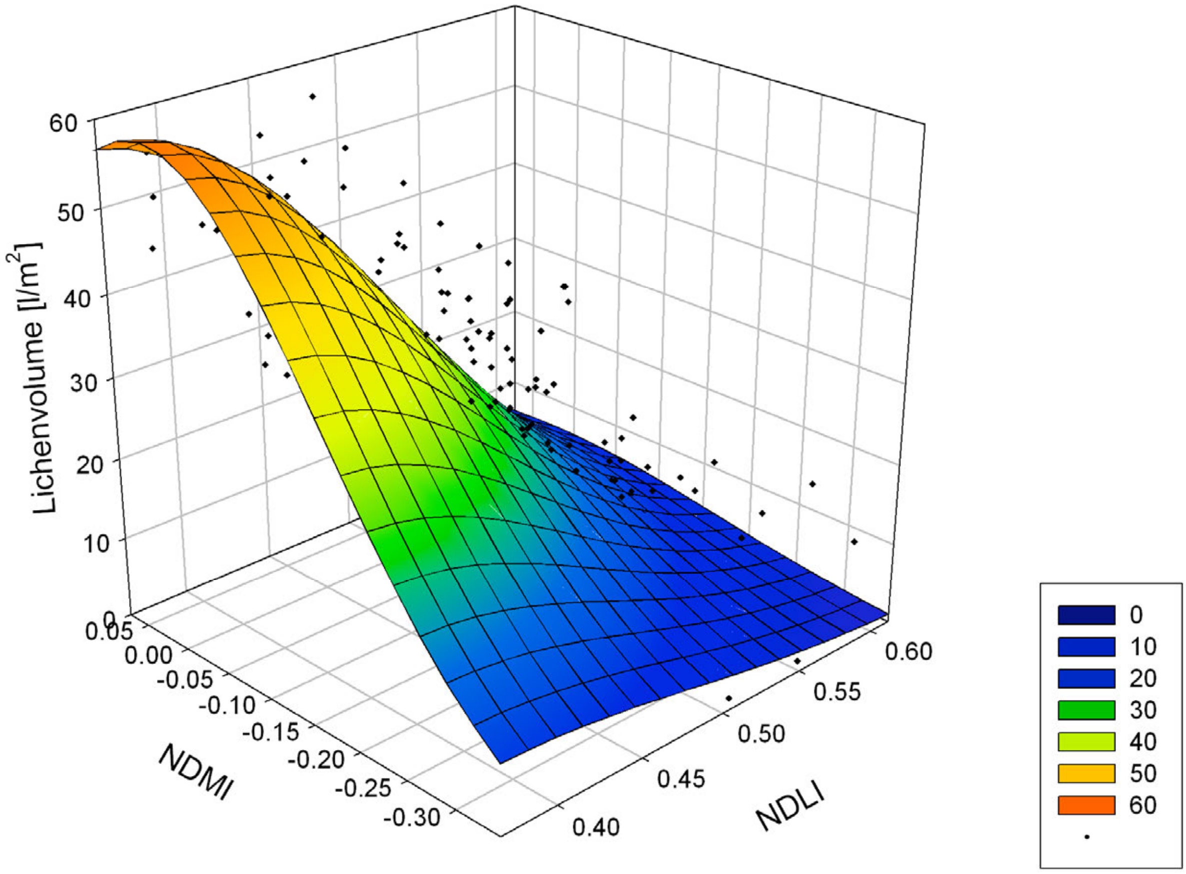

Figure 4-6: Lichen volume model – data points and estimated regression curve of fitted model

Higher lichen volume is predicted both, when NDLI values decrease and/or NDMI values increase. Predicted values for lichen volume reach their maximum at app. 60 liters/sqm (equaling mats of app. 6 cm if the whole area was covered by lichens) at NDLI values of 0.4 and NDMI values of 0.05. The predicted sensitivity to changes in factors was highest for intermediate NDLI/NDMI values and decreased both, with higher and lower values of the two factors.

Cross validation

Due to the limited sample size, a tenfold cross validation of the model was used for accuracy assessment (Boyce *et al.* 2002). The overall results from the different cross validation groups are given in Figure 4-7:

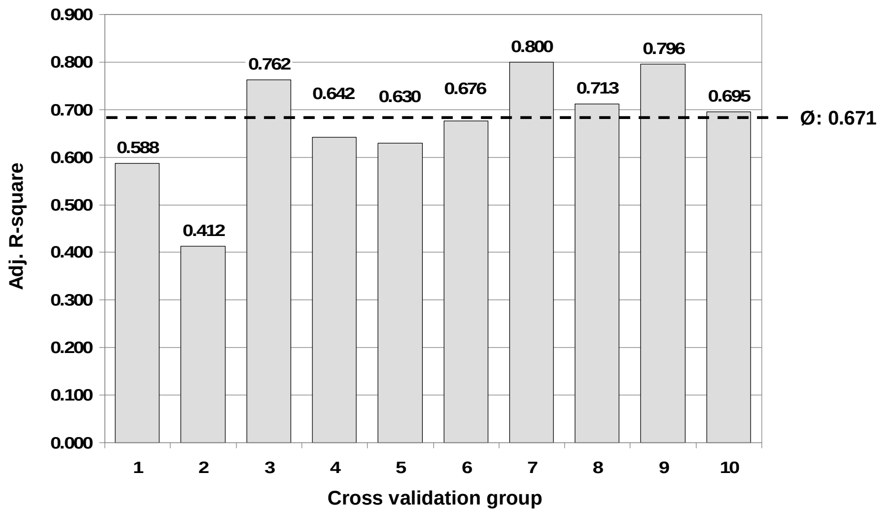

Figure 4-7: Lichen volume model: adj. R-squares by cross validation groups

While the initial model showed slightly better results (adjusted R-square of 0.704), the average value derived from the cross validation groups was still satisfying (average adjusted R-square of 0.671 with a standard deviation of 0.115). All ten models were highly significant overall and all estimated model parameters remained significant through the cross validation procedure; coefficient estimates were stable between groups (compare Table 4-2).

Cross val. sub-group	Adjusted R-square	Coefficients				
		$NDLI_{mean}$	$NDMI_{mean}$	a	b	c
0	0.588	0.343	0.031	62.47	0.133	0.207
1	0.412	0.355	0.021	59.63	0.126	0.197
2	0.762	0.367	0.018	58.70	0.116	0.192
3	0.642	0.374	0.008	58.45	0.111	0.175
4	0.630	0.372	0.011	58.75	0.113	0.169
5	0.676	0.375	0.017	59.35	0.110	0.175
6	0.800	0.363	0.033	61.71	0.116	0.194
7	0.713	0.363	0.018	59.04	0.119	0.172
8	0.796	0.341	0.009	61.55	0.129	0.188
9	0.695	0.363	0.013	57.78	0.116	0.179
Average	**0.671**	**0.362**	**0.018**	**59.74**	**0.119**	**0.185**
Std. dev.	**0.115**	**0.012**	**0.008**	**1.59**	**0.008**	**0.012**

Table 4-2: Lichen volume model: estimated coefficients and adj. R-squares by cross validation groups

Further examination of the 10 different models did not indicate any severe violations of assumptions for the regression models: The linearity test for distribution of residuals was passed within nine of the ten cross validation groups. Although band 5 is used in both, NDLI and NDMI respectively, the correlation between the two indices was still considered modest[75], collinearity was thus rejected. Analysis of residuals indicated constant variances between subgroups, autocorrelation could thus be rejected.

Distribution of lichen volume in Hardangervidda 2003

The spatial distribution of lichen volume (see Map 4-2) predicted form the regression model depicts distinct differences within the study area. Within the central parts of Hardangervidda significantly lower lichen volumes were predicted as compared to the outer parts. High lichen volumes were found in the east (up to 60 liters per square meter), while in the western parts significantly lower values were found (average lichen volumes reaching less than one liter per square meter). Isolated habitat islands in the north east of Hardangervidda showed the highest lichen volumes.

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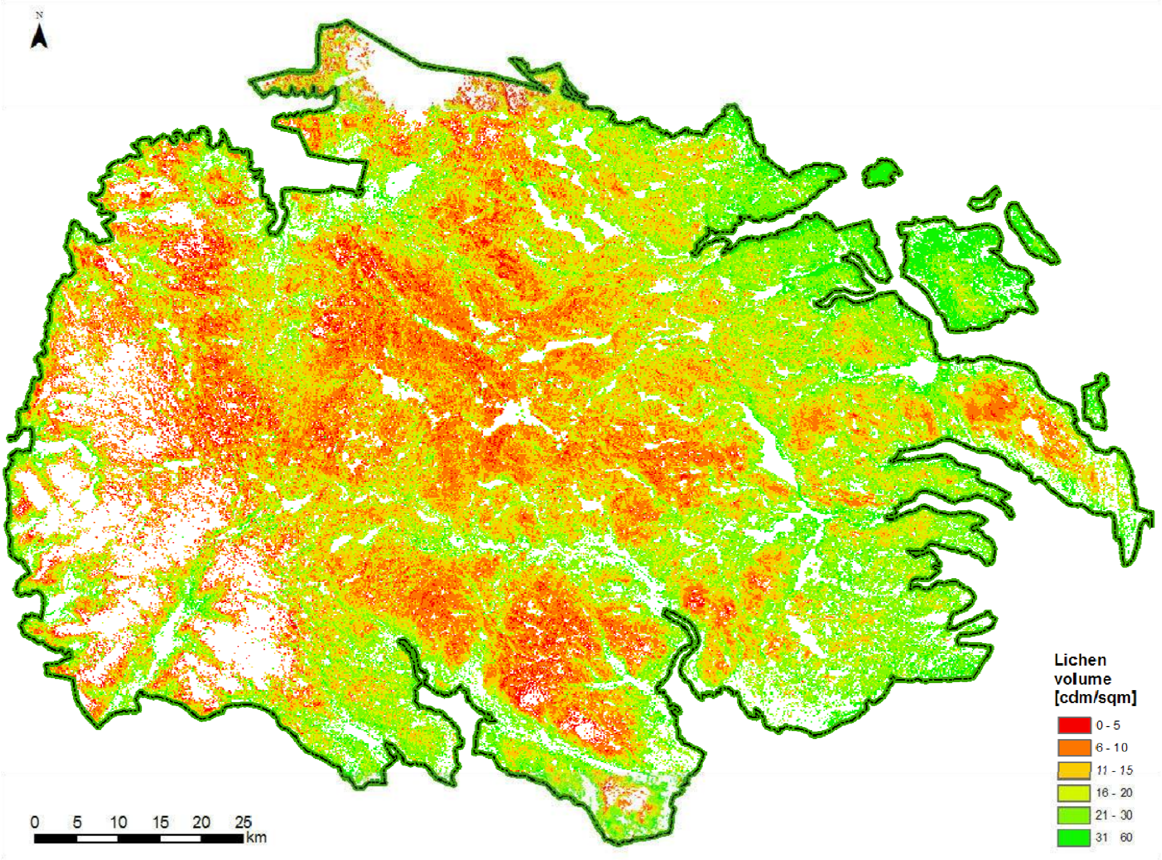
[75] Pearson's 2-tailed correlation index -0.58



Map 4-2: Distribution of lichen volume in Hardangervidda 2003[76]

Visual inspection suggests a possible relation between increased lichen volumes and cumulated human disturbance. As spatial differences in lichen volumes also suggest correlations with altitude and longitude, further investigation is needed to separate the influence of human disturbance on grazing pressure from those two natural gradients.

4.4 Discussion

Model results of multivariate prediction model for lichen volume

In this chapter a method for continuous estimation of lichen volume within ridges based on NDLI and NDMI as predictors derived from Landsat imagery was presented. The results achieved for the above model were promising (R-square of 0.671 using cross validation). Comparative tests using NDLI/NDMI as a single predictors within a logistic regression model indicated significantly lower accuracies (NDLI: 0.613; NDMI: 0.372).

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[76] Note that the gridsize of the image has been resampled from 30 m to 225 m grid in order to enhance visibility as only 26% of the total land cover was classified as ridges for which lichen volume was estimated (compare chapter 3.3). Grid values were obtained treating non ridge pixels as no data.

Since the model used to predict lichen volume utilizes a correlation between NDLI/NDMI and lichen volume valid within land cover classes dominated by lichen heath, the prediction results can be misleading, if the model is applied to pixels belonging to different classes. For such a case an enhanced stability of the combined predictor approach is assumed: While both, NDLI and NDMI, correctly suggest an absence of lichens for snowbed vegetation and mires a model based an NDLI only was found to falsely predict high lichen volumes for land cover dominated by rocks (which can easily be misclassified as lichen ridges when covered by epiphytic lichens). On the other hand, single predictor models based on NDMI would correctly indicate low lichen volumes in such a case but failed for leeside vegetation (where NDLI showed correct behavior). In contrast, the proposed combined model showed plausible results for both, rocks and leeside pixels.

Results in this study indicate an upper limit of app. five centimeters in lichen height beyond which NDLI and NDMI reacted insensitive to further increases. This seems plausible, as lichen mats should yield a theoretical thickness threshold beyond which further increases in height do not affect their reflection characteristics. This threshold seems tolerable since lichen thicknesses of more than five centimeters are rather scarce, at least within the study area.

Distribution of lichen volume within study area in 2003

The average lichen volume within ridges dominated by lichen heath community in Hardangervidda 2003 was predicted from the regression model to be app. 15.4 liters per square meter. The spatial differences in lichen volume as described in chapter 4.3 are assumed to result from two factors: the natural spatial differences in potential lichen volumes (caused by elevation, climate, soil, etc.) and the spatial differences in reindeer grazing pressure (caused by natural habitat features and human disturbance).

Potential lichen volume within ridges dominated by lichen heath communities in Norway is known to be dependent on altitude and longitude (influencing both, precipitation and temperature) as natural factors (Gaare & Skogland 1980). As lichens are mostly independent of soil and ground water (Gaare & Skogland 1980) dryer, more continental climates favor their competitiveness in relation to other vegetation. In Norway those climatic conditions beneficial to lichens are generally increasing with eastern longitude. As a result, lichen volume depicts a profound west-east gradient. Although lichens proof to be fairly resilient towards extreme temperatures (determining length of vegetation period) and wind exposure, both factors are limiting their potential biomass (Longton 1988). As wind exposure and temperatures correlate with altitude potential lichen volumes are likely to do so as well.

As indicated by earlier studies (Vistnes & Nellemann 2008), grazing pressure can be largely affected by human disturbance. Lichen biomass values as estimated from LVE are therefore likely to also reflect spatial differences in reindeer grazing pressure. In order to further test the impact of natural and human related factors the data should be analyzed for spatial correlations of lichen volume with longitude, altitude and human disturbance. A simple multiple linear regression model with altitude, longitude and cumulated human disturbance as independent factors should be used to test their relative impact on lichen volume.

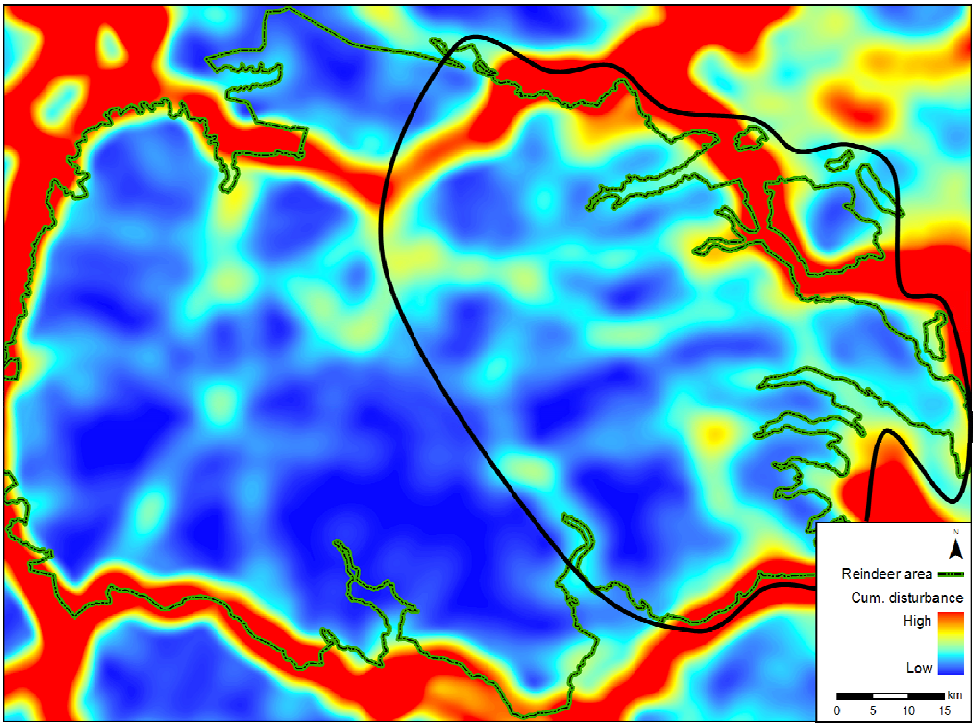
Winter pastures still seem to be a limiting factor for reindeer in Hardangervidda

Comparative studies within Norwegian reindeer areas indicate the Hardangervidda system to hold relatively few areas suitable as winter pastures. With an estimated proportion of app. 15 percent of the total area consisting of suitable winter pastures, Hardangervidda still holds considerably less lichens as compared to areas like Forollhogna, Rondane or Knutshø demonstrating values between 35 and 45 percent (Jordhøy *et al.* 1996).

Winter pastures therefore still seem to be one of the limiting factors for reindeer in Hardangervidda and a further reduction of these pastures could pose a potential threat for the long-term survival of wild reindeer in the study area. In this context both, an increase in human winter activity within the eastern areas of Hardangervidda and a reduced availability of lichens caused by climate change (higher stochastic risk for icing/altered precipitations, e.g. Turunen *et al.* 2009; Stien *et al.* 2010; Aanes *et al.* 2002; Weladji & Holand 2006; Weladji *et al.* 2002; Arctic Climate Impact Assessment 2004; Roald *et al.* 2003), should be closely monitored and their effect on reindeer (winter) pastures further evaluated.

Implication for reindeer management

Spatial analysis of the cumulated human disturbance levels showed higher values for eastern Hardangervidda (see Map 4-3). With these areas being the most important winter pastures for reindeer, on the one hand, and Hardangervidda – as shown earlier – being characterized as relatively short on winter pastures, on the other hand, the importance of land use management (especially within eastern Hardangervidda) becomes apparent for the long-term conservation of reindeer. A better alignment between the recreational use of Hardangervidda by humans with reindeer habitat requirements is discussed in the following:



Map 4-3: Estimated winter pastures in Hardangervidda vs. density of cumulative human disturbance[77]

As winter pastures can still be regarded as one of the limiting factors for the development of the reindeer population, a general shift of human activity from the eastern to western parts of Hardangervidda during winter seems beneficial. The implications for reindeer should be further analyzed and the feasibility of such a shift should be assessed. Any further fragmentations of the reindeer winter habitats should be avoided. Land use and reindeer management should incorporate a monitoring scheme of lichen winter pastures to evaluate earlier changes in land use and plan future developments.

With the proposed approach of this dissertation a promising start for a satellite-based assessment of lichen volume including later change detection could be made. As noted earlier, it is suggested that the findings of this study should be compared using high-resolution satellite imagery. Furthermore, lichen sample points should be selected in the field for monitoring in order to allow for a better absolute calibration between images[78]. Depending on the results an ongoing lichen monitoring scheme for the long-term conservation of wild reindeer in Hardangervidda should be considered.

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[77] See chapter 2.4

[78] For an evaluation of environmental monitoring strategies see e.g. Rönnbäck *et al.* (2003).

Conclusion

The use of a non-linear model to predict the lichen volume within ridge vegetation dominated by lichen heath communities allows utilizing more specific predictor variables, as the correlation requirements can be restricted to lichen volume only. Using a two-dimensional prediction model for lichen volume with NDLI and NDMI as independent variables, leads to both, better model results and increased prediction stability for mixed pixels (and falsely classified pixels within land cover classification), which is especially relevant for the limited resolution of Landsat TM data. The results of the lichen volume prediction model were satisfactory with regard to significance (overall and single factors), R-squares and the stability of model parameters (as confirmed by cross validation).

Nevertheless, weaknesses and possible improvements became apparent: The applicability of the chosen model is limited to ridges dominated by lichen heath communities and therefore assumes an existing vegetation map with a reasonable accuracy. Further, the binned subsampling design used to account for over sampling of training points associated with low lichen volumes lead to considerable data loss reducing model efficiency and forced to select cross validation for accuracy assessment rather than a split in testing and training data. Analogue to the land cover classification, the satellite-based assessment of lichen biomass using Landsat TM should be tested against high-resolution data. The sample data required for model building proved to be time consuming due to the work intensive recording scheme for lichen coverage and height. Finally, while c-correction significantly reduced terrain induced reflectance effects, it was currently limited by the 25 m spatial resolution of the DEM available for the study area.

5 Habitat selection models

5.1 Introduction

A better understanding of reindeer habitat use is needed

With a current population of app. 8,000 animals during summer Hardangervidda holds the largest remaining wild reindeer population in Europe (see chapter 1.1). After a high-density period with over 35,000 animals in the late seventies leading to severe degradation of winter grazing areas (see chapter 4) population numbers have been reduced to about 4,500 animals at the beginning of the twentieth century. Following recovery of lichen pastures and the long-term management objective to stabilize the population at app. 10,000 animals (Skogland 1993; Strand *et al.* 2004) numbers have increased again to app. 8,000 animals in 2006. Even though large carnivores are slowly returning in some of the more eastern parts of Norway (Brøseth, Tovmo & Odden 2010; Brøseth, Tovmo & Andersen 2010; Tobiassen *et al.* 2011; Webakken *et al.* 2010) predation only plays a minor role for the Hardangervidda population, which is almost entirely managed by hunting quotas (Skogland 1990a; Strand et al. 2004; Strand, O., Andersen, R. & Jordhøy, P. 2006; Solberg *et al.* 2010).

The future conservation of the Hardangervidda reindeer population and reindeer in general faces serious challenges. With wild reindeer being vulnerable to disturbance (see chapter 1.1) the ongoing process of piecemeal infrastructure development is a serious concern to the conservation of wild reindeer (Vistnes & Nellemann 2008; Wolfe, Griffith & Wolfe 2000). This since cumulated human disturbance can cause alterations in habitat use causing a suboptimal utilization of grazing resources and a reduced carrying capacity as possible consequences. In addition, piecemeal infrastructure development can increase habitat fragmentation. Traditional seasonal habitats can be disconnected and populations can become more vulnerable in extreme weather events like icing of pastures during winter (Skogland 1978; Kohler & Aanes 2004; Chan *et al.* 2005; Hansen, Aanes & Sæther 2010; Stien *et al.* 2010). Furthermore, the genetic diversity within increasingly isolated populations can be reduced (Fahrig 1997, 2003). Finally, the negative consequences of habitat fragmentation and alterations in habitat use are likely to be amplified through climate change, both through shifts in vegetation and alterations in snow conditions (increased snow depth/ surface icing), further threatening the long term viability of remnant populations (e.g. Turunen *et al.* 2009; Stien *et al.* 2010; Aanes *et al.* 2002; Weladji & Holand 2006; Weladji *et al.* 2002; Heggberget, Gaare & Ball 2002; Arctic Climate Impact Assessment 2004; Roald *et al.* 2003).

In this context a better understanding of reindeer habitat use is crucial for their long-term conservation. Management of reindeer populations and habitats, including impact assessment of existing infrastructure as well as planning future developments, depends on detailed quantitative knowledge of the relative importance of the single factors influencing reindeer habitats.

Furthermore, a better understanding of the seasonal dynamics in habitat use can provide valuable insights for a better alignment of reindeer habitat requirements with recreational use of Hardangervidda by humans. Such knowledge may also support more effective and efficient planning as well as implementation of mitigation measures (e.g. environmental tunnels and overcrossings), aiming to reconnect fragmented habitats (see also Strand, Bevanger & Falldorf 2005 and Bevanger, Falldorf & Strand 2005)[79]. This could promote not only an increase in genetic diversity by favoring exchange between populations but also revive traditional migration corridors allowing for a better utilization of resource with respect to seasonal and location differences. In addition to the more practical benefits discussed above, a better understanding of reindeer habitat use may also yield valuable theoretical knowledge applicable in different contexts both, with respect to species and habitats.

Resource selection is dependent on scale

As introduced in chapters 1.3 and 2.2, resource selection of herbivores has been widely recognized to follow different spatial scales (Wiens 1973; Johnson 1980; Peterson & Parker 1998). Within their concept of hierarchical foraging in grazing ecology Senft *et al.* (1987) divided herbivore foraging response patterns into three different spatial scales (regional, landscape and patch level): At the regional scale animals select between seasonal areas or home ranges on the basis of forage availability, predation, geomorphology, availability of water, regional climate and physical barriers (Senft *et al.* 1987). For reindeer spatial decisions at a regional level are most evident through annual movements between calving grounds, summer and winter habitats (Skogland 1989). Habitat selection by herbivores at the landscape level is defined as selection for larger patches, feeding sites or plant communities attractive to animals. Selection may further be influenced by small-scale differences in water supply, topography, weather and likelihood of predator encounters (e.g. Senft *et al.* 1987; Bailey *et al.* 1996). Movement on the landscape level is generally triggered by a trade off between forage depletion at one feeding site vs. expectations on intake opportunities at alternative sites

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[79] A review on mitigation techniques to maintain wildlife corridors can e.g. be found in Holschuh & Otter (2000). Iuell *et al.* (2003) discuss possible conflicts and solutions for wildlife and traffic from a European perspective. For an overview on road ecology see e.g. Foremann *et al.* (2003).

(Baumont *et al.* 2000). At the patch level herbivores select for feeding stations, plants and plant parts (Senft *et al.* 1987).

Following hierarchal selection theory large-scale selection by animals should primarily be driven by the availability of the most limiting factors, while less important factors should only be visible on smaller scales (Rettie & Messier 2000; Dussault *et al.* 2005). In more recent years it has been common to study resource selection by animals at several spatial scales (amongst others Apps *et al.* 2004; Johnson *et al.* 2004).

Using different temporal scales, the resource selection of animals can be studied in relation to temporal cyclic patterns (Wiens 1989; Boyce 2006). Specific selection processes may only be valid for certain periods in time, after which they attenuate or change (Allen & Hoekstra 1992). Such time dependencies are most frequently analyzed using three different temporal scales (seasonal, periodic and daytime level): At the seasonal scale, the selection processes of animals is usually studied within basic periods like summer or winter, while at the periodic level more fine scaled sub-annual periods are used. At the daytime level characteristic selection patterns can be detected using a 24-hour perspective.

Spatial and temporal scales thus are naturally linked and often overlap, especially at larger scales (landscape level and seasonal level). However, focusing on temporal aspects within one spatial level, can often lead to a better understanding of the overall selection processes.

Two main model types to estimate RSF depending on assumptions on availability: Logistic regression (LR) vs. discrete choice models (DCM)

Quantitative approaches to reindeer habitat use have to deal with three fundamental questions: What are the relevant factors influencing spatial behavior? What is the relative importance of those factors within the selection process? And: How can the functional response of reindeer to those factors be described? To answer these questions statistical models generally compare the qualities of spatially explicit independent factors (e.g. elevation, land cover, ruggedness) between selected and available spatial entities (points, concentric circles, steps). Selected spatial entities (most often points) are usually sampled using direct or indirect observations methods. Direct observation methods typically include aerial surveys, transect counts or photography of marked animals (e.g. Hjermann 2000) as well as telemetry data using radio tracking (Rhodes *et al.* 2005) or satellite systems based on ARGOS (e.g. Durner *et al.* 2004, 2009) or GPS (e.g. Nielsen *et al.* 2002; Fortin *et al.* 2005; Skarin *et al.* 2008). Track or faecal pellet-group counts (e.g. Rhodes *et al.* 2005, 2006; Skarin 2006; Collins & Urness 1981) are examples for indirect observation methods.

Depending on their assumptions on availability[80] , two different statistical model types to estimate resource selection functions (RSF) have been developed and successfully tested in praxis: On the one hand, logistic regression models (LR) generally define available habitat independent of given individual locations (Manly *et al.* 2002). In these models sampling of available habitat is generally based on a random selection of points drawn from either the entire study area or seasonal habitats which can – for example – be knowledge based or defined by minimum convex polygons (MCP) (Samuel & Fuller 1994).

On the other hand, discrete choice models (DCM) are a particular case of RSF, that follows a time specific definition of availability where a specific selection decision made at a particular location is compared to alternative options depending on that location only (Manly *et al.* 2002). Within DCMs sampling of available spatial entities is typically based on random draws within an availability radius (AR) defined by a theoretical threshold or empirically based for example using the 95% interval of the given distribution of step length (Arthur *et al.* 1996). Instead of using a discrete AR Hjermann (2000) suggests a continuous availability function (CAF). Similar Rhodes *et al.* (2005) used a negative exponential model (NE). More recently Fortin *et al.* (2005) used the given distributions of both step length and turning angle within a stochastic model to select available steps within a DCM formulated as a step selection function (SSF).

Based on sample data of selected and available spatial entities, habitat selection can be analyzed either on the population level using pooled data or alternatively using individual-based models (Manly *et al.* 2002). In addition, individual differences between animals can be analyzed within single models using mixed-effects models (Neter *et al.* 1996; Hosmer & Lemeshow 2000; Skrondal & Rabe-Hesketh 2004).

Two spatial domains to define variables: point-based vs. step-based calculation

Habitat selection models normally deal with two spatial domains for independent variables: (i) point-based and (ii) step-based spatial approaches to data.

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[80] For an evaluation of resource selection methods with different definitions of availability see McClean *et al.* (1998).

(i) Usually habitat selection is tested by comparing the differences between point-based spatial properties of selected and available locations such as land cover, elevation, slope, etc. (e.g. Nielsen *et al.* 2002; Durner *et al.* 2004; Johnson, Seip & Boyce 2004). The higher the spatial resolution of the underlying data (e.g. high-resolution DEM) the more fine scaled sampled points can be described and compared within the model. While this seems strictly beneficial in the first place, fine scaled point-based information can be misleading due to two reasons: First, the corresponding GPS accuracy can be a limiting factor. The higher the average root mean squares (RMS) of location, the more likely it is to end up with false data values when using (too) fine scale data. Secondly – due to their random sampling using fixed time intervals – the available GPS positions do not only represent used locations like grazing sites, resting places, etc. but also include positions selected in a wider sense for example when traveling between two feeding sites. When those locations would be used to compare selected and available positions results might be less significant as the selection of those points might not have been caused primarily by their own small-scale spatial properties but rather by the properties of positions attended earlier or later along the selected movement path. While the first problem only seems relevant for low GPS accuracies the second is more fundamental. Authors mainly have either been using average values for spatial properties within a specific radius around sample points or – more sophisticated – distance weighted averages.

(ii) More recently, Fortin *et al.* (2005) proposed the use of step selection functions (SSF). Within these the spatial properties of selected and available steps (lines) are compared in contrast to comparing point-based features like in the more traditional resource selection functions (RSF) (Manly *et al.* 2002). Following this approach, spatial properties like ruggedness of the terrain can be modeled more accurate as they can be described along the traveled path rather than sampled at a randomly selected point along that path or using a point-based distance weighted average within a concentric radius neglecting directionality of movement. Factors like the influence of wind direction on movement/habitat selection can only be addressed comparing selected and available steps as they are directly bound to movement directions and are not applicable for point-based methods. On the other hand, step-based descriptions of factor properties can be limited by sampling intervals as their inherent assumption of a linear connection between two consecutive GPS positions becomes less plausible. Using five-hour intervals Fortin *et al.* (2005) found promising results using SSF for analyzing elk movements in Yellowstone national park. They discuss a positive effect of spatial autocorrelation of factor data making the violation of linearity assumption less severe. In addition, SSF can be more sensitive to the applied sampling scheme for available steps as the resulting mean step length can bias results for factors like distances to roads or trails (Fortin *et al.* 2005).

Autocorrelation of data

Spatial autocorrelation of telemetry data (especially when using short sampling intervals) can be a potential statistical problem for habitat selection models because the assumption of independence of most standard statistical testing procedures is likely to be violated (Legendre 1993; Legendre & Legendre 1998). Following Legendre (1993), spatial autocorrelation can be defined as the property of random variables at pairs of locations a certain distance apart to be more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations. In such cases the value of a random variable (e.g. elevation) at any one locality can be partly predicted from neighboring values. As a consequence the values are not statistically independent from one another and new observations do not each bring with them one full degree of freedom as assumed in classical statistical testing. In case of positive autocorrelation this can lead to test statistics being declared positive too often and thus inducing a potential bias (Lennon 2000). Various methods have been developed to deal with spatial autocorrelation in habitat selection models:

A more traditional way of dealing with spatial autocorrelation has been to sub sample the data and thereby reduce the sampling frequency to longer intervals (e.g. Swihart & Slade 1985). While this can reduce the spatial dependence of data significantly, these methods not only limit habitat selection models to larger spatial scales but can also lead to a severe loss of data making them less efficient (McNay & Bunnel 1994).

More recently, sandwich variance estimators have been used to calculate robust standard errors (amongst others Nielsen *et al.* 2002; Fortin *et al.* 2005). These estimators account for spatial autocorrelation through inflation of standard errors and associated significance intervals without affecting coefficient estimates (White 1982; Newey & West 1987; Pendergast *et al.* 1996). Gillies *et al.* (2006) note, however, that within the presence of an unbalanced sampling design between individuals, variance inflators only provide a partial solution to non-independence, as coefficients will be biased toward the most sampled individuals (Follmann & Lambert 1989).

To account for both, spatial autocorrelation among sample points and unbalanced samples between individuals, mixed-effects models have been used in resource selection studies (Aebischer, Robertson, & Kenward 1993; Gillies *et al.* 2006). Moreover, mixed effects models allow for testing of differences in selection among individuals with respect to both, the magnitude and/or form of functional response (Gillies *et al.* 2006; Bennington & Thayne 1994). Due to computational constraints, however, the implementation of mixed-effects models incorporating both, random intercepts and coefficients, is still limited to smaller datasets (see e.g. May 2007).

Movement patterns can influence habitat selection and are often not addressed

Habitat selection of animals follows the selection/avoidance of multiple external factors like vegetation type, topography, snow conditions and predators at different temporal and spatial scales (e.g. Senft *et al* 1987; Wiens 1989; Boyce 2006). On the other hand, it can also be influenced by “internal” factors affecting movement patterns (hereafter called “internal drivers of movements”) like directionality and activity level which can be independent of external factors. For example, the selection probability for two patches of a particular vegetation type from a given location can simply be different due to their position in relation to the animal’s previous movement direction, if the movement patterns of a species exhibit a tendency towards directional movement.

In habitat selection studies using availability radii to define available locations, internal movement parameters are often ignored. Given a persistence in movement direction and a negative exponential distribution of step length common for many animals, this inevitably leads to biased sampling of available positions (oversampling of longer steps, oversampling of locations in the direction of prior GPS-position of an animal). While this seems tolerable for point-based models depending on the research question, it can be problematic for step-based models as resulting step lengths are often biased (Fortin *et al.* 2005).

A feasible way to deal with this problem is to account for movement patterns within the sampling process of available spatial entities. For example, Fortin *et al.* (2005) used the given distributions of step lengths and turning angles to select available steps for modeling habitat selection of elk in Yellowstone national park applying a DCM. As a result, used and available samples showed equal distributions of both parameters. Selection could therefore be regarded as quasi independent of movement patterns.

Objectives

Against the above background four sets of objectives are followed within this chapter:

i. The first aim is to identify the significant factors influencing habitat selection by season and spatial scale. Their impact and relative importance should be estimated. Based on these estimates, seasonal habitat preference maps for Hardangervidda should be calculated (given the current level of human disturbance). The underlying research questions of this set of objectives are: How do reindeer use their habitats? By which factors can resource selection of reindeer be explained? Which resources are used, which are unused and why? What is the impact of temporal and spatial scale?

ii. The second aim is to better understand the impact of human disturbance on reindeer habitat use by season and spatial scale. To achieve this, potential seasonal habitats should be identified, by simulating the degree of human disturbance. These potential seasonal habitats should than be compared to the habitats preference maps, which were calculated under the current level of human disturbance. Conclusions of this simulation should be drawn for land use and reindeer management plans. By this set of objectives the following questions should be answered: What are the potential habitats for wild reindeer in Hardangervidda with respect to season? Do they differ from used habitats and if so, why? What is the spatial distribution of the used/potential habitats and how can they be characterized? What is the impact of human disturbance on reindeer habitat use in Hardangervidda? How does the grazing pressure differ spatially within the actual and potential reindeer habitats? What are the implications and possible recommendations for reindeer and land use management?

iii. The third aim is to assess the possible impact of altered snow covers in Hardangervidda (as predicted by climate change) on reindeer's predicted habitat preference during winter. Again, this should be achieved by simulating different snow depth situations for the study area within the estimated models. It is asked: What is the impact of altered snow distributions on habitat preference for reindeer during winter? What are the possible consequences for reindeer and which implication can be derived for management?

iv. Finally, the fourth aim of this chapter is to answer to what extent the applied empirical models can help to describe and explain the habitat use of wild reindeer in Hardangervidda. It is asked: What can be learned from comparing the selected model types? How robust are the models? What is the impact of alternative definitions of availability from a modeling perspective? What are their inherent strengths and weaknesses and what knowledge can be derived for other reindeer areas and species?

5.2 Methods

Modeling the habitat selection of reindeer in Hardangervidda followed a four-step approach:

a. Selection and pre-processing of explanatory factors: Potential variables for model building were selected and tested. Variables included topography, land cover, lichen biomass, weather data, snow depth and human disturbance.

b. Model definition and estimation of parameters: Within the second step six different models were defined (two spatial scales within three different seasons). An overview on these models and their objectives is given in Figure 5-1. Parameters were estimated and tested using robust methods accounting for spatial autocorrelation.

	Summer	Winter	Calving
Large scale (LR)	**Objective**: modeling reindeer's large-scale (regional) habitat selection during summer **Independent variables**: land cover, lichen volume, elevation, slope, energy cost of movement, solar radiation, distance to roads, trails, tourist cabins and private cabins, snow depth, wind direction	**Objective**: modeling reindeer's large-scale (regional) habitat selection during winter **Independent variables**: land cover, lichen volume, elevation, slope, energy cost of movement, solar radiation, distance to roads, trails, tourist cabins and private cabins, snow depth, wind direction	**Objective**: modeling reindeer's large-scale (regional) habitat selection during calving **Independent variables**: land cover, lichen volume, elevation, slope, energy cost of movement, solar radiation, distance to roads, trails, tourist cabins and private cabins, snow depth, wind direction
Small scale (DCM)	**Objective**: modeling reindeer's small-scale (landscape) habitat selection during summer **Independent variables**: land cover, lichen volume, elevation, slope, energy cost of movement, solar radiation, distance to roads, trails, tourist cabins and private cabins, snow depth, wind direction	**Objective**: modeling reindeer's small-scale (landscape) habitat selection during winter **Independent variables**: land cover, lichen volume, elevation, slope, energy cost of movement, solar radiation, distance to roads, trails, tourist cabins and private cabins, snow depth, wind direction	**Objective**: modeling reindeer's small-scale (landscape) habitat selection during calving **Independent variables**: land cover, lichen volume, elevation, slope, energy cost of movement, solar radiation, distance to roads, trails, tourist cabins and private cabins, snow depth, wind direction

Figure 5-1: Overview on models used to estimate habitat selection – objectives

c. Preference maps: As a third step, habitat preference maps were calculated by season, utilizing the season specific large-scale model estimates.

d. Simulations: Finally, potential habitats were derived by simulating different snow depth levels and intensities of human disturbance.

Selection and pre-processing of explanatory factors

The independent variables for the above models were selected from six different groups: land cover, lichen volume, terrain related variables (elevation, slope, energy cost of locomotion, solar radiation), disturbance related factors (distance to roads, trails, tourist and private cabins), snow depth and wind direction (see Table 5-1):

	Independent variable	Definition and spatial domain	Spatial scale	Functional response	Interaction terms	Data source
	LANDCOVER	Landcover type of sample points (GPS positions/unused points) as classified from landcover map	30*30m^2	Linear	Daytime	Landsat TM and ancillary data
	LICHENVOLUME	Lichen volume of sample points in liters per square meter using a running average (5*5 roving window) on LV map	30*30m^2	Non linear	-	Landsat TM and ancillary data
Terrain	ELEVATION	M.a.s.l. of sample points	25*25m^2	Non linear	Temperature, wind speed	DEM, met.no
	SLOPE	Slope of sample points in degrees	25*25m^2	Non linear	-	DEM
	ENERGYCOST	Cost of movement for sample steps measured as standard deviation of elevation along linear path between positions	25*25m^2	Linear	-	DEM
	RADIATION	Average intensity of solar radiation calculated from DEM (exposition/slope) and solar position (45/225deg)	25*25m^2	Linear	Daytime	DEM
Disturbance	DROAD	Distance from sample points to nearest road in meters using Euclidean distance	Linear distance	Linear	-	N50
	DTRAIL	Distance from sample points to nearest marked tourist trail (summer/winter) in meters using Euclidean distance	Linear distance	Linear	-	N50, DNT
	DCABIN^{tourist}	Distance from sample points to nearest tourist cabin in meters using Euclidean distance	Linear distance	Linear	-	N50
	DCABIN^{private}	Distance from sample points to nearest private cabin in meters using Euclidean distance	Linear distance	Linear	-	N50
	SNOWDEPTH	Average snow depth of sample points in mm	1*1km^2	Non linear	-	NVE
	MOVEWIND	Movement direction of sample steps in relation to wind direction measured from 0 to 180deg (with/against the wind)	Linear distance	Linear	Daytime	met.no, GPS

Table 5-1: Definition of independent variables used in habitat selection models

In the following the definition of the single independent variables as well as their assumed impact on reindeer habitat selection will be described:

Land cover classification and its importance for spatial behavior of reindeer have been discussed in detail within chapter 3. The eight land cover classes WATER, SNOW, RIDGE, LEESIDE, SNOWBED, MIRE, FOREST and ROCK were used as dichotomous variables with daytime as interaction term, as reindeer's functional response towards different land cover classes was assumed to be dependent on daytime. Spatial resolution for land cover followed Landsat resolution (30x30 sqm).

Both, the definition and importance of lichen volume for reindeer, have been referred to in chapter 4. Average lichen volumes for selected and available points (LICHENVOLUME) were calculated using a 5x5 roving window within ArcGIS (ESRI 2005). Lichen volume was assumed to be selected for by reindeer, especially in winter.

Four terrain related variables have been selected: ELEVATION, SLOPE, energy cost of locomotion (ENERGYCOST) and solar radiation (RADIATION). All factors were derived from 25x25 sqm DEM (Statens Kartverk 2006) using ArcGIS (ESRI 2005). ELEVATION [m a.s.l.] was used with both, temperature and wind speed, as interaction term, as reindeer's selection for elevation was assumed to be dependent on both factors. SLOPE for selected and available positions was defined as the gradient in degrees.

Energy cost of movement is known to influence habitat selection of large herbivores (Pyke 1984; Fancy & White 1987; Ganskopp, Cruz & Johnson 2000; Parker, Robbins & Hanley 1984). This is especially relevant for reindeer living in alpine terrain with a harsh climate and characterized by scarce food resources. As a consequence, energy intake and expenditure have to be balanced carefully (Collins & Smith 1989; McEwan & Whitehead 1970; Loe *et al.* 2007). Standard deviation of elevation along selected and available steps was used as an indicator for reindeer's average energy costs per distance unit (ENERGYCOST). High standard deviations indicate high variation in elevation along steps (high energy cost of locomotion per distance unit) while low values reflect little variation in elevation (low energy cost per distance unit for selected/available step)[81]. Standard deviations of elevation along steps were calculated using Line Raster Intersection Statistics within Hawth's Analysis Tools for ArcGIS (Beyer 2004) for selected/available steps. Therefore, steps were first divided into segments of equal elevation using 25x25 sqm DEM grid cells. The resulting elevation distributions weighted by segment length are later used to calculate standard deviations for individual steps. A more detailed measure for energy cost of locomotion additionally based on snow conditions (Parker, Robbins & Hanley 1984)[82] was tried but later dropped due to its high correlation with snow depth, which was needed as a single independent factor to test for its importance for feeding site selection.

The intensity of solar radiation of sites was expected to be relevant for habitat selection by reindeer both, during summer and winter. This since reindeer are assumed to select patches with high solar radiation, especially during cool and windy winter conditions. In contrast, reindeer are known to avoid those patches during warmer summer days due to increased in-

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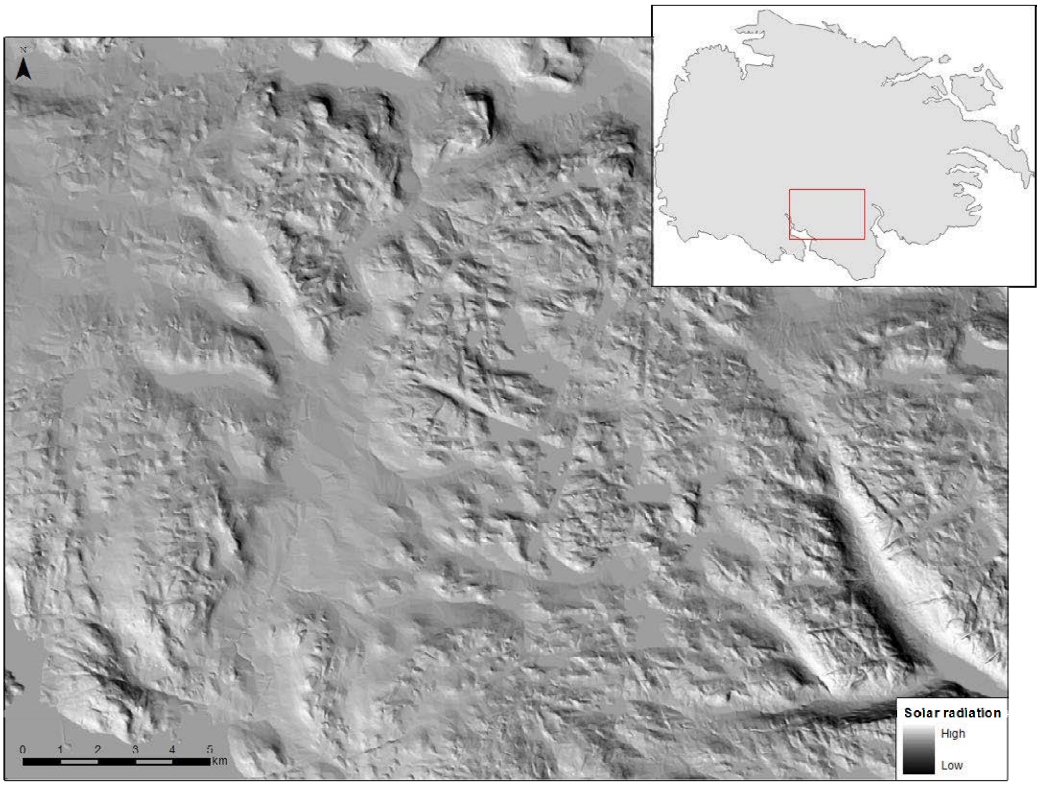
[81] For an alternative ruggedness index see also Riley, DeGloria & Elliot (1999) and Nellemann & Fry (1995).

[82] The influence of snow depth on winter movement patterns is well known and has also been described for other ungulates (e.g. Sweeney & Sweeney 1984).

sect harassment (Hagemoen & Reimers 2002)[83]. The received solar radiation of a site is dependent on its slope and exposition relative to the specific solar position (Kumar, Skidmore & Knowles 1997; Dubayah & Rich 1995).

A sun elevation of 45 deg and an azimuth angle of 225 deg (SW exposition) were chosen to calculate the average intensity of solar radiation for Hardangerviddа (RADIATION) using Hillshade procedure within ArcGIS Spatial Analyst extension (ESRI 2005) on a 25x25 sqm DEM (see Map 5-1 for example). RADIATION was used with daytime as interaction term to account for the assumed dependence of reindeer's functional response to solar radiation on this factor.



Map 5-1: Differences in solar radiation patterns between patches – illustrative example southern Hardangervidda

The sensitivity of reindeer to human disturbance has been shown by numerous studies (Vistnes & Nellemann 2008; Wolfe, Griffith & Wolfe 2000). Within the models the distances to nearest roads (DROAD), marked summer trails (DTRAIL), tourist cabins ($DCABIN^{TOURIST}$) and private cabins ($DCABIN^{PRIVATE}$) were used as major stationary sources of human disturbance to test for their relevance on seasonal habitat selection by reindeer. Linear Euclidean distances in meters to the nearest disturbance feature was calculated per category for selected

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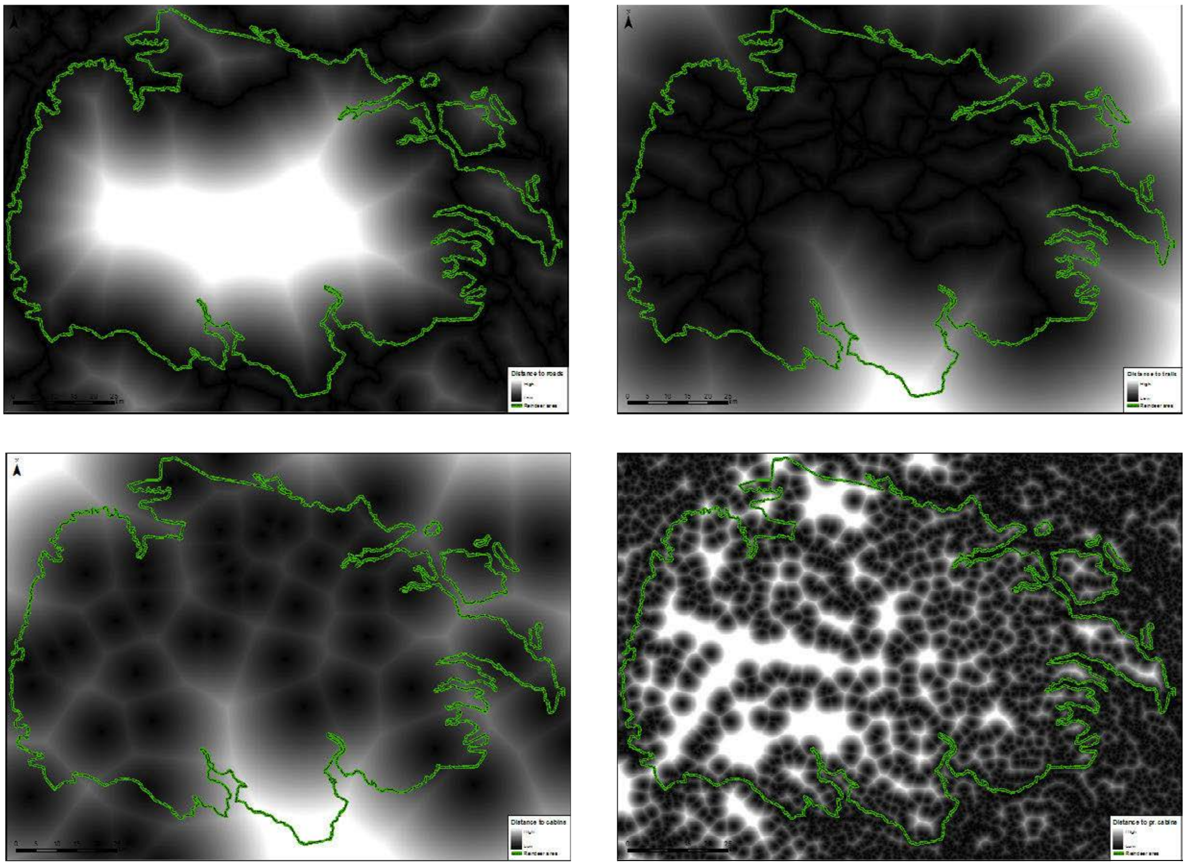
[83] Note that herd formation has also commonly been discussed as a strategy among reindeer to reduce insect harassment during summer (see e.g. Helle & Aspi 1983).

and available points using ArcGIS (ESRI 2005) (see Map 5-2 for illustration). Weighting of summer trails by frequency of use based on census data provided by Den Norske Touristforening (DNT) (unpublished) did not lead to significant improvements in model results. This is expected to be caused by unsolved weighting and calibration problems (extrapolating disturbance values into space). Probably for the same reasons, preliminary testing revealed no significant model improvements through using the cumulated human disturbance map (see Map 2-1) instead of single factors. Both, disturbance by snow scooter driving and cross country skiers during spring/winter, proved to be difficult to test as used trails differ between years and frequency of disturbance is rather limited due to legal restrictions for snow scooter permits and strong clustering of (overall moderate) cross country skiing activities within the Easter holidays.



Map 5-2: Overview on distance to roads / trails / tourist cabin / private cabins in Hardangervidda

Snow conditions are known to be of predominant importance for reindeer habitat selection during winter (Turunen *et al.* 2009; Stien *et al.* 2010; Aanes *et al.* 2002; Heggberget, Gaare & Ball 2002; Weladji & Holand 2006; Weladji *et al.* 2002; Tucker *et al.* 1991). While being able to smell and dig up lichens under considerable snow cover, cratering is limited to maximum snow depths of app. 50 - 60 cm (Skogland 1978)[84]. Furthermore, surface icing can be a severe limiting factor for winter feeding sites (Skogland 1978; Kohler & Aanes 2004; Chan *et al.* 2005; Hansen, Aanes & Sæther 2010; Stien *et al.* 2010). Models of snow depth (SD) and liquid water content (LWC), provided by Norges vassdrags- og energidirektoratet (NVE), were used as parameters to describe snow conditions. To test for their influence on reindeer habitat selection, snapshots of SD- and LWC-values taken at the mid-dates of each of the 13 identified sub-annual periods (see chapter 2.2) of the individual years between 2001 and 2006 were used (see Figure 5-2 for illustration of mean snow depth values within Hardangervidda during the study period). The year-specific SD and LWC values were later linked to the selected and available points based on spatial location and dates using ArcGIS (ESRI 2005). Due to the limited number of weather stations within the mountainous terrain of Hardangervidda, grid size for both parameters was rather coarse (1x1 sqkm) and standard errors of estimates were above the Norwegian average (see chapter 2.4). Distribution of snow depths in Hardangervidda shows both, a distinct annual cyclic pattern and a profound east-west gradient. Average snow covers are highest during Pre-CALVING period in early May within the western areas of Hardangervidda reaching values up to six meters. While snow cover starts to melt down in the eastern parts from CALVING to EARLY SUMMER (late May until June), considerable amounts of snow can be found in the western areas for the best parts of the summer. Lowest values are found from LATE SUMMER to AUTUMN period before persistent snow covers are forming starting from EARLY WINTER (beginning of November).

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[84] Note, however, that the critical limits for cratering reported in the literature vary widely (see Pruitt 1959; Bergerud 1974c; LaPerriere & Lent 1977; Skogland 1978; Helle 1984; Thing 1984; Adamczewski *et al.* 1988; Brown & Theberge 1990).

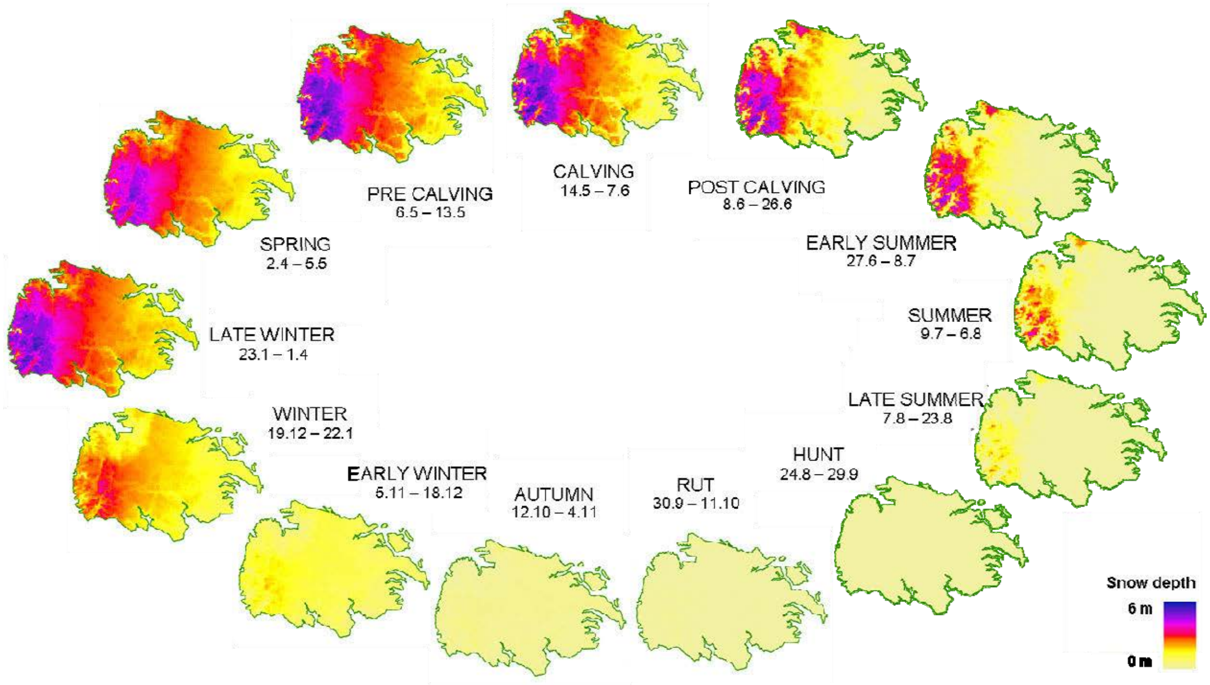

Figure 5-2: Spatial distributions of mean snow depth in Hardangervidda 2001 – 2006 by season[85]

Model results showed no significant improvements using LWC, hence this data was later dropped and only snow depth (SNOWDEPTH) was kept. Reasons for this might be the coarse grid size and the insufficient suitability of LWC as an average density parameter to describe surface condition. Limited data availability proved prohibitive for an accurate description of surface condition both, with respect to temporal and spatial resolution in this context.

Reindeer movements are known to be influenced by wind direction and to serve as an important anti predator strategy (e.g. Colman, Jacobsen & Reimers 2001; Reimers *et al.* 2006; Baskin & Skogland 1997). Reindeer have been suggested to prefer moving against the wind in search of food resources and to avoid predators and insects (e.g. White *et al.* 1981). To test for the relative importance of wind direction for habitat selection the movement direction relative to wind direction was calculated (MOVEWIND) as a step-based parameter for selected and available steps using the below equation:

$$\mathit{MOVEWIND} = \left| \left| \mathit{BEARING} - \mathit{WR} \right| - 180 \right|, \qquad (5\text{-}1)$$

where BEARING is the step bearing and WR is the estimated wind direction during the step. This was done using the data from the nearest of six available weather station within Hardangervidda area (Finsevatn, Geilo-Geilostølen, Midlæger, Møsstrand II, Vågsli, Dagali II) for

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[85] Data available online (URL http://www.senorge.no/). For methods and data description see Engeset, Sorteberg & Udnœs (2000) and Stranden (2010).

each of the (selected and available). Data was provided by the Norwegian meteorological institute (met.no). The calculation of the linear Euclidean distances between the single steps and the weather stations was done using ArcGIS (ESRI 2005). The wind directions of the nearest weather stations (three annual daily recordings at 6/12/18 GMT) were later joined to the steps based on location and daytime. A value of zero indicates movements as directly with the wind while a movement directly against the wind would be depicted by a value of 180. Preliminary results showed a profound influence of wind direction on reindeer's selected movement direction during all seasons (see Figure 5-3).

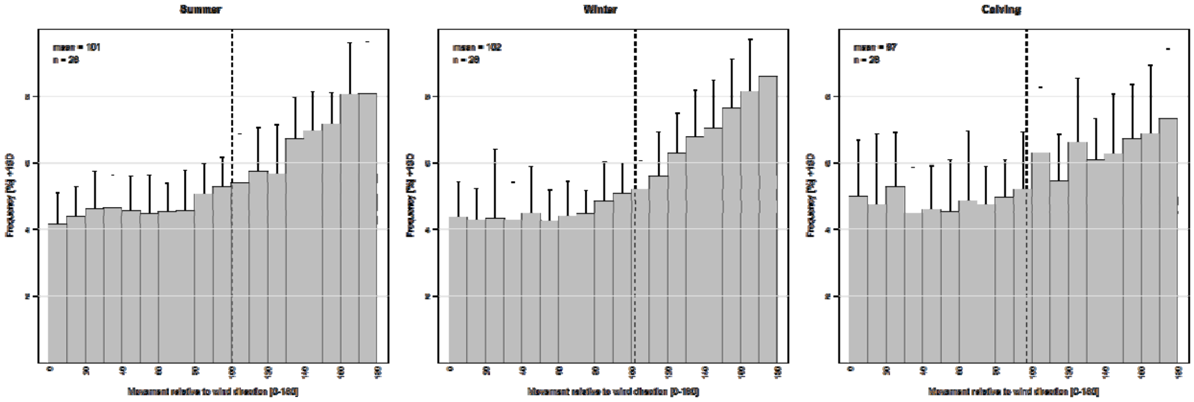

Figure 5-3: Frequency distributions of reindeer movement direction in relation to wind by season

Histogram analysis of MOVEWIND revealed clear tendencies of moving against the wind, most prominent during winter and summer (mean = 102/101), despite possible data inaccuracies caused by both, location and temporal differences between steps and recording of wind direction. Correlation became even stronger, when shorter steps, indicating resting or ruminating times, and movements in low wind speeds sensitive to measurement errors were excluded from the analysis.

Habitat selection models were build for three temporal (Summer, Winter, Calving) and two spatial scales (large scale, small scale)

Habitat selection of reindeer in Hardangervidda was studied at different seasonal and temporal scales. Resource selection was compared to available resources for three temporal scales using four different model types, depending on spatial scale and the treatment of movement patterns.

The empirical analysis of reindeer's movement patterns indicated three major sub annual periods (“summer”, “winter” and “calving”), demonstrating distinct differences in habitat selection (compare chapter 2). Model comparisons of these periods were used to detect differences in resource selection at varying temporal scales (seasonal level). Data was therefore divided into three seasons. The first season, Calving (May 14th – Jun. 7th), meanly characterized by female reindeer giving birth to calves and a subsequent resting period of the neonates, encompassed 6,692 selected locations. The second season, Summer (Jun. 27th – Aug. 6th), included 11,389 selected locations (EARLY SUMMER, SUMMER). The third season, Winter (Nov. 5th – Apr. 11th), accounted for 36,587 selected locations (EARLY WINTER, WINTER, LATE WINTER). To test for short-term temporal scales daytime was used as an interaction term for selected external factors (land cover, solar radiation, movement in relation to wind direction).

In order to compare habitat selection at different spatial scales, data was analyzed at a large and small-scale (corresponding to regional and landscape level, respectively (Wiens 1973)). For large-scale analysis resource selection functions (RSF) were estimated using logistic regression models (LR) comparing the "used" telemetry locations with "unused" locations, which were randomly sampled (Manly *et al.* 2002). To facilitate the detection of large-scale selection differences, availability was defined as all areas within Hardangervidda, which have traditionally been used by reindeer. Boundaries are constituted by the conifer tree line (app. 900 m) at the eastern, western and most parts of the southern edges. Transportation infrastructure (railroad/roads) confined the available area at the northern and some of the southern edges of Hardangervidda. To allow for the utilization of step-based external factors, selected steps were paired with an equal number of available steps using random sampling within the available area.

For small-scale selection analysis a discrete choice model (DCM) approach was chosen using a proportional hazards model for parameter estimation (Manly *et al.* 2002). Each of the selected steps was therefore paired with ten available steps, which were randomly sampled using the same origin as starting points.

Habitat selection models were build as "external models" models controlling for movement patterns

Large- and small-scale habitat selection models were built as “external” models. Internal drivers of movements were "eliminated" by using a sampling scheme for the available spatial entities, which allowed for the same step lengths and turning angle distributions as demonstrated by the used spatial entities. To achieve that, random sampling of available steps was based on independent random draws of the season specific step length and turning angle distributions of reindeer (see chapter 5.3: Results, Distributions of step length and turning angles).

Step length is thereby defined as the linear Euclidean distance in meters between two consecutive steps. Turning angle depicts the change in movement direction (Bearing) between two consecutive steps in degrees. Positive degrees are defined as right turns (0<x<180), negative as left turns (-180<x<0) and values of 0 (180) indicate no (complete) change in movement direction.

For the large-scale models starting points of available steps were randomly placed within Hardangervidda. In addition, each starting point was assigned a random previous movement direction. From these starting points steps were calculated to endpoints, which were created using vectors derived from independent random draws from the seasonal distributions of step lengths and turning angles. Following this sampling scheme, the selected and available steps showed identical distributions of step length and turning angle. Therefore, independence of reindeer habitat selection from these two movement parameters was assumed.

For the small-scale models each of the selected steps was paired with ten available steps. Selected and available steps shared the same starting point (and previous movement direction). Analogue to the large-scale models, endpoints were derived using independent random draws of the seasonal distributions of step lengths and turning angles. Again, the resulting distributions of the two parameters were equal as compared to the selected steps and hence considered independent.

Sampling was programmed in R release 2.3.1 (R Development Core Team 2006). Random selection of large-scale starting points was carried out using the Random Point Generator within Hawth’s Analysis Tools for ArcGIS (Beyer 2004).

Model definition and estimation of parameters

Given the two spatial (large- vs. small-scale) and three temporal scales (summer, winter and calving) described above, a total of six different models was used, in order to analyze reindeer habitat selection (compare Figure 5-1). Model types and availability definitions/sampling schemes for each of the six models are summarized in Figure 5-4.

	Summer	Winter	Calving
Large scale (LR)	**Model type**: Logistic regression model calculated as binominal logit glm model within R using robust Newey/West-estimator to correct for spatial autocorrelation **Availability and sampling scheme**: random selection of steps within Hardangervidda (random starting points, end points defined through random draws from summer distributions of step lengths and turning angles)	**Model type**: Logistic regression model calculated as binominal logit glm model within R using robust Newey/West-estimator to correct for spatial autocorrelation **Availability and sampling scheme**: random selection of steps within Hardangervidda (random starting points, end points defined through random draws from winter distributions of step lengths and turning angles)	**Model type**: Logistic regression model calculated as binominal logit glm model within R using robust Newey/West-estimator to correct for spatial autocorrelation **Availability and sampling scheme**: random selection of steps within Hardangervidda (random starting points, end points defined through random draws from calving distributions of step lengths and turning angles)
Small scale (DCM)	**Model type**: DCM estimated as an adapted stratified proportional hazards model using coxph within R with paired selected/available steps and autocorrelation clusters as strata **Availability and sampling scheme**: random selection of 10 (available) steps per selected step (identical starting points, end points defined through random draws from summer distributions of step lengths and turning angles)	**Model type**: DCM estimated as an adapted stratified proportional hazards model using coxph within R with paired selected/available steps and autocorrelation clusters as strata **Availability and sampling scheme**: random selection of 10 (available) steps per selected step (identical starting points, end points defined through random draws from winter distributions of step lengths and turning angles)	**Model type**: DCM estimated as an adapted stratified proportional hazards model using coxph within R with paired selected/available steps and autocorrelation clusters as strata **Availability and sampling scheme**: random selection of 10 (available) steps per selected step (identical starting points, end points defined through random draws from calving distributions of step lengths and turning angles)

Figure 5-4: Overview on models used to estimate habitat selection - model types and definition of availability/sampling scheme

Following Fortin *et al.* (2005), the large-scale selection models were defined as step selection functions (SSF), estimated from observed and random steps. SSF were chosen to allow for testing of both, point and step-based independent variables. Based on resource selection functions (RSF; Manly *et al.* 2002), SSF take the structure:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + ... + \beta_n x_n), \qquad (5\text{-}2)$$

with β_i as the selection coefficients based on the external factors x_i. Here w(x) is the SSF score with higher scores indicating higher odds for a step being chosen by an animal. Logistic regression was used to estimate coefficients of the explanatory variables (compare Table 5-1) in all three models (calving, summer and winter).

To account for spatial autocorrelation the Newey-West (Newey & West 1987) estimator of variance was used within a binominal logit generalized linear model (GLM[86]; McCullagh & Nelder 1989) for estimation of standard errors and associated significance levels. To determine the spatial autocorrelation structure within the selection data, autocorrelation and partial autocorrelation functions were used on deviance residuals, derived from initial individual-level models, not accounting for spatial autocorrelation (naïve models). Depending on individual and model type, evidence for spatial autocorrelation was found for locations recorded

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[86] For GLM models see also Breslow & Clayton (1993).

within 8 to 20 distance lags (1 to 2.5 days). As reindeer were collared within different herds, observations between individuals were assumed to be independent. Based on autocorrelation results from naïve models, a truncation lag of 20 observations for Newey-West variance estimation was used. Parameter estimation was carried out in R release 2.3.1 (R Development Core Team 2006) using binominal logit glm with NeweyWest variance estimator.

The small-scale selection models were again defined as SSF based on equation 5-3, but followed a case-control design, where each selected step (“case”) was matched with 10 available steps (“controls”). Parameters were therefore estimated using conditional logistic regression with individual reindeer and pairs of observed/random steps as strata (Hosmer & Lemeshow 2000).

Following Fortin *et al.* (2005) robust sandwich estimates of variance (Lin & Wei 1989; Wei *et al.* 1989) were used to account for spatial autocorrelation within conditional logistic regression. This approach assumes observations to be independent between clusters, while observations within clusters can be correlated (Wei *et al.* 1989; Hardin & Hible 2003). Again, deviance analysis of residuals from individual-level naïve models using autocorrelation and partial autocorrelation functions revealed, that autocorrelation was not significant after 20 lags for all reindeer and model types. As noted earlier, observations between individuals were assumed to be independent. Selected steps were therefore divided into independent clusters using a truncation lag of 20 observations.

Parameter estimation of conditional logistic regression models was carried out using an adapted stratified proportional hazards model (Klein & Möschberger 2003), using the coxph function within R release 2.3.1 package “survival” (R Development Core Team 2006) with paired selected/available steps and autocorrelation clusters as strata (for mathematical details see Fortin *et al.* 2005).

Both, large and small-scale models, were defined at the population level, pooling selection data of individual reindeer (n = 28). Variation analysis of coefficients from initial models estimated on individual-level did not indicate significant differences. Furthermore, variability between individuals was found to be low using mixed effects logistic regression with random intercepts for individuals (Hosmer & Lemeshow 2000; Pinheiro & Bates 2000) implemented within R release 2.3.1 package “lme4” (R Development Core Team 2006; Bates & Maechler 2010).

Model selection

To reduce the number of explanatory variables parsimonious model building strategies (Burnham & Anderson 2002) were employed using Akaike’s information criterion (AIC, Akaike 1974). Variables leading to an increase in AIC, using a leave-one-out approach for single models, were dropped from corresponding models. To assess the overall fit of the most parsimonious models Pearson’s χ^2 goodness-of-fit test with associated p values was used (Hosmer & Lemeshow 2000).

Each coefficient within the final models was also tested weather it significantly differed from zero using t-tests (Manly *et al.* 2002). This was done by dividing the estimated coefficient by their robust standard errors (z-values) and then comparing the absolute z-values to a normal distribution.

Absolute log-likelihoods (and AIC as a derivate) are dependent on model type and sample size (Burnham & Anderson 2002). In this study models were both different in parameter estimation (large-scale models based on binominal logit GLMs vs. small-scale models using adapted stratified proportional hazards models) and sample size (differences in season length; model definition with/without application of case-control design). Accounting for those differences Nagelkerke’s R-square (Nagelkerke 1991) was used to compare model fits between seasons and model types.

Logistic regression is sensitive to collinearities among the explanatory variables (Hosmer & Lemeshow 2000). The selected explanatory variables within the models were therefore checked for collinearity by calculating all pairwise Spearman’s rank correlation coefficients. Pairs of variables were considered highly correlated within models, when their absolute correlation coefficient exceeded a threshold of > 0.6 (compare Booth *et al.* 1994). High correlations occurred only between different sources of human disturbance (most frequently between distance to tourist cabins and trails, respectively). In such cases only the variable yielding the lower AIC value was kept.

Preference maps and simulation

A primary objective of this work was to develop tools that would predict where reindeer may occur with respect to seasons. To do that, seasonal preference maps were derived from the SSF scores of all single pixels within Hardangervidda using a 30x30 sqm grid. SSF scores were calculated from the estimated coefficients of the large-scale models (excluding movement in relation to wind direction with daytime as interaction terms). To exclude temporal differences in factor values within seasons, average values for temperature and wind speed were used when included as interaction terms. For snow depth mean seasonal values were used, calculated over all years of the study period (2001 to 2006).

Preference maps use current factor levels of significant factors to predict seasonal occurrence of reindeer. As one focus of the study was to assess the impact of human disturbance on habitat use by reindeer, the derived preference maps were compared to potential habitats assuming non-disturbance. To do that, simulation maps were calculated, in which the effects of human disturbance were excluded from SSF scores.

In addition to human disturbance, alterations in snow conditions, potentially caused by future global climate change, are topical to the future conservation of wild reindeer, not only in Hardangervidda (see chapter 1.1). Both, increased snow falls and probabilities for surface icing, could potentially reduce forage availability, not only in the western and central parts of Hardangervidda but also in the eastern winter pastures, (currently) dominated by lichen communities. To examine the impact of snow conditions on habitat selection during winter, two different snow depth scenarios (lower bound and upper bound scenario) were simulated, based on historical data recorded between 2001 and 2006. In contrast to the preference maps, which were based on mean seasonal snow depth values within study period (2001 to 2006), lower (upper) bound scenario uses lowest (highest) average snow depth values within the above years.

5.3 Results

Distributions of step length and turning angles

Analysis of step lengths and turning angles from GPS data revealed specific distributions of both parameters. Results are shown in Figure 5-5 and Figure 5-6.

Histogram analysis of step length over all seasons revealed a negative exponential distribution (mean = 879 m for 3h intervals) with low standard deviation between individuals (n = 28). Turning angles over all seasons showed a normal distribution centered on zero with low standard deviation between individuals (n = 28) indicating a persistence tendency in movement direction between consecutive steps.

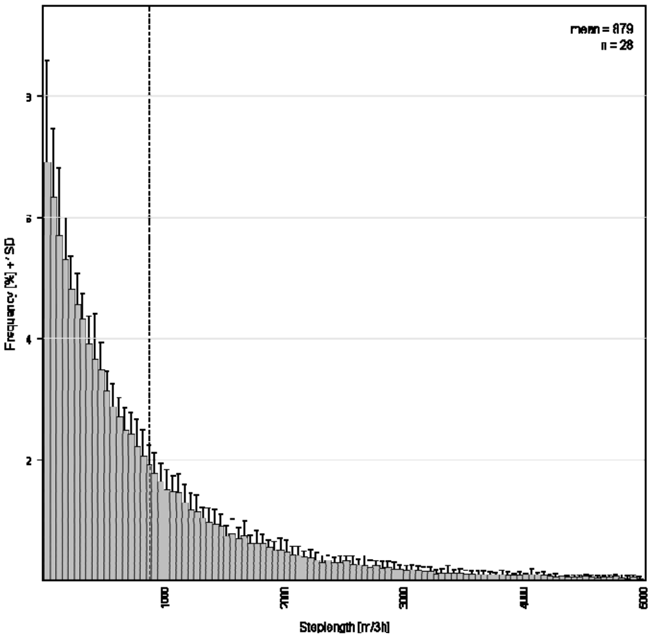

Figure 5-5: Frequency distribution of step length for GPS-data over all individuals and seasons

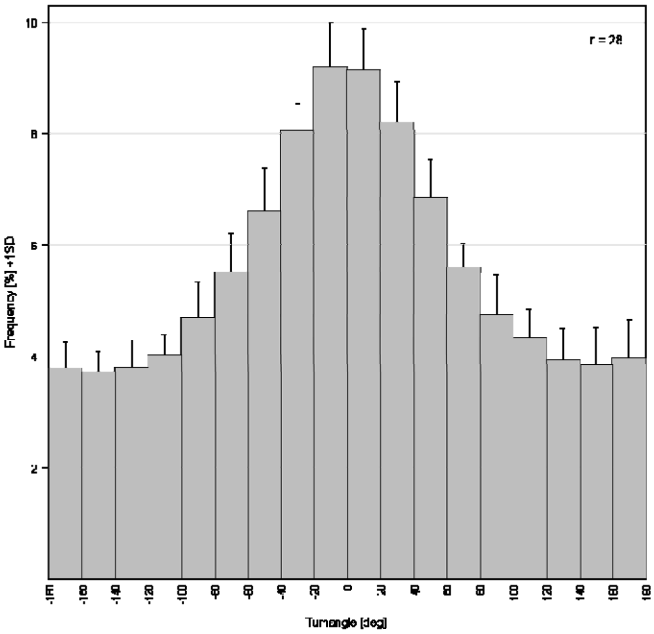

Figure 5-6: Frequency distribution of turning angles for GPS-data over all individuals and seasons

Distribution of step length was significantly influenced by season (see Figure 5-7) and daytime (see Figure 5-8). Step length revealed the highest average values for the summer periods (2-5) and significantly lower values for the winter seasons (6-10) (compare also chapter 2.3). Daily activity pattern showed increased movements between 6 and 15 hours GMT.

The distribution of turning angles depicted moderate, but significant differences between the sub-annual periods (highest directionality of movements during winter) (see Figure 5-9). Daytime showed little effect on reindeer's directionality of movement (see Figure 5-10).

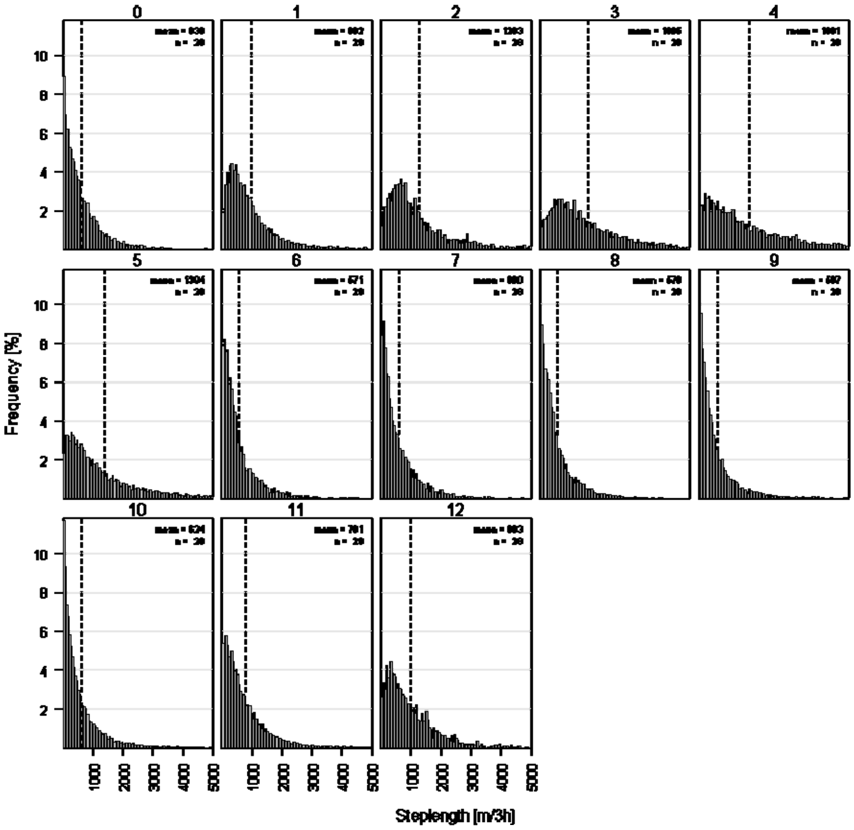

Figure 5-7: Frequency distribution of step length for GPS-data over all individuals by season

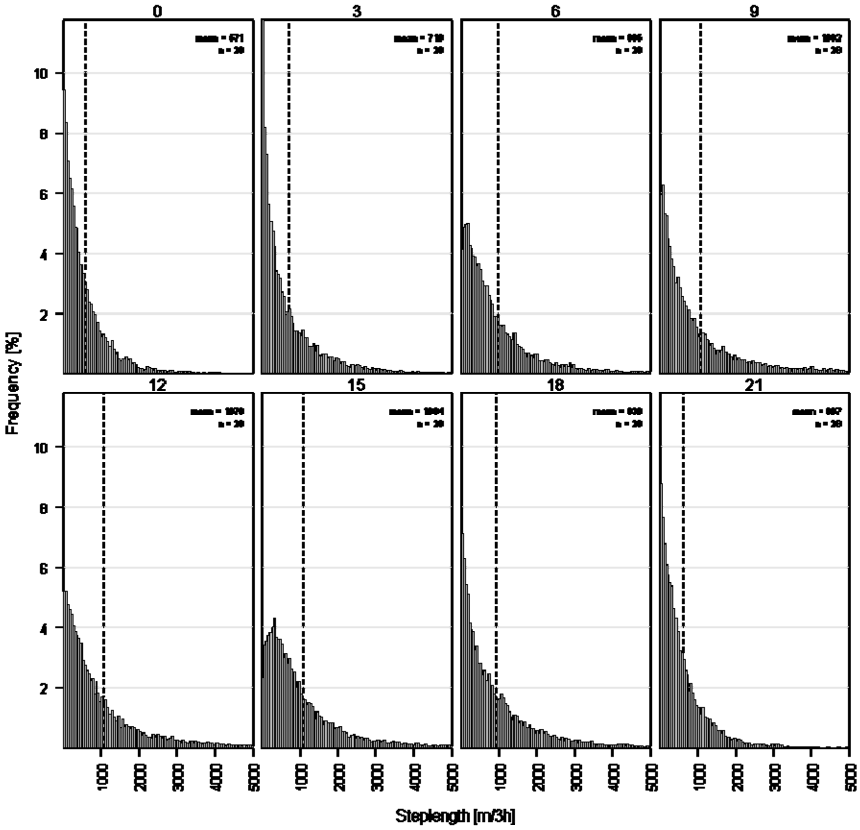

Figure 5-8: Frequency distribution of step length for GPS-data over all individuals and seasons by daytime

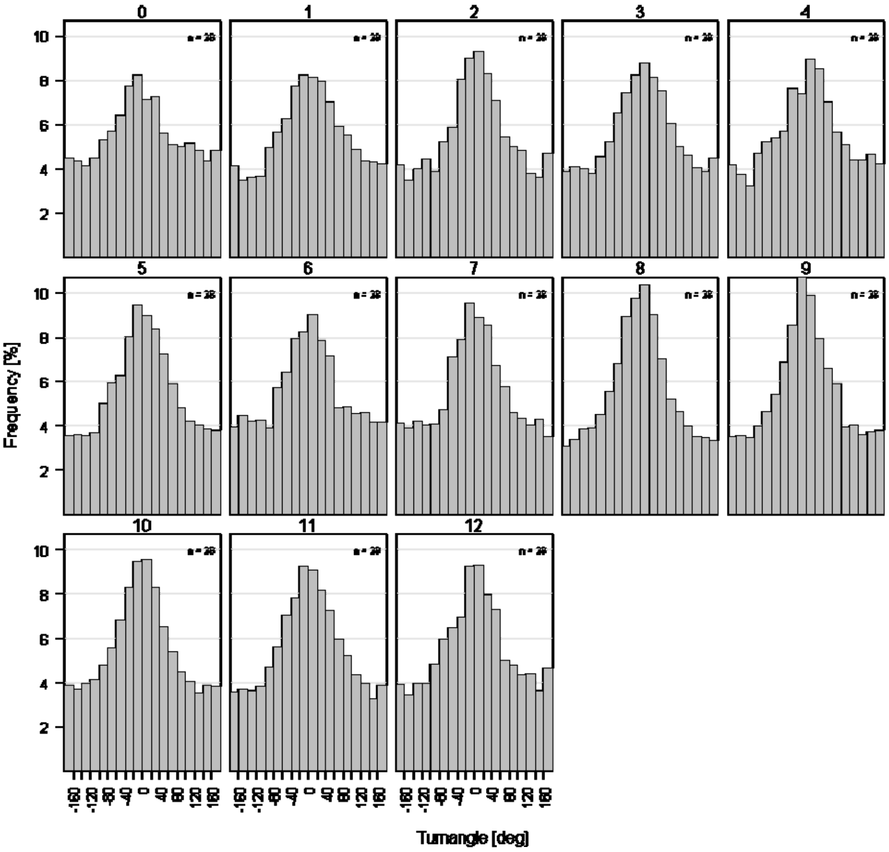

Figure 5-9: Frequency distribution of turning angles for GPS-data over all individuals by season

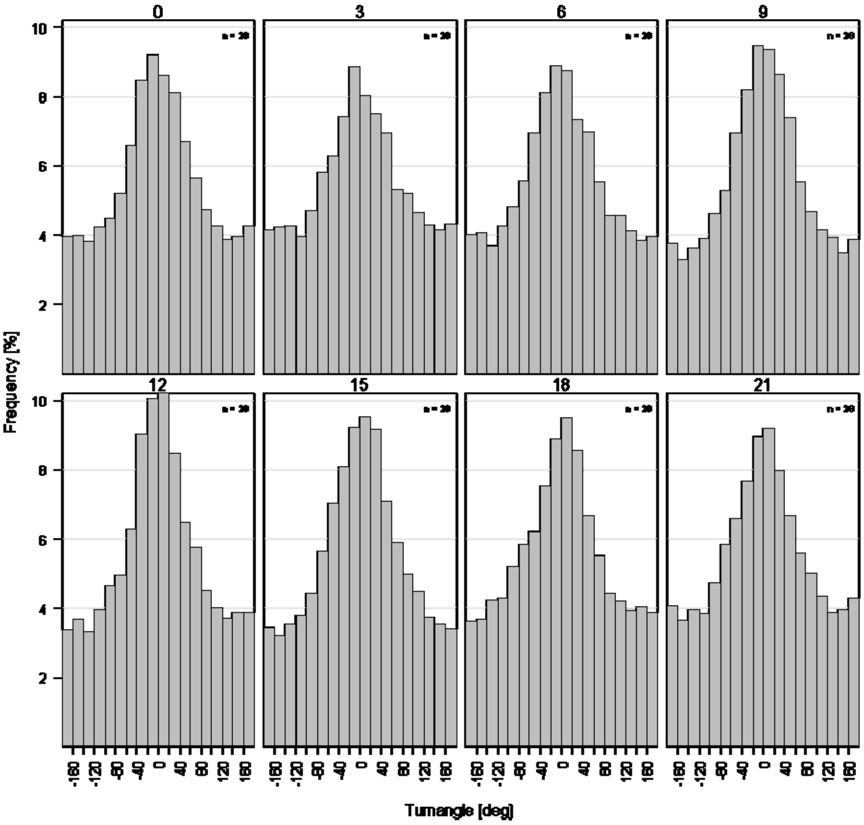

Figure 5-10: Frequency distribution of turning angles for GPS-data over all individuals and season by daytime

Overall model results

All six models tested highly significant, but Nagelkerke's R-square revealed significant differences between model types and seasons (see Figure 5-11):

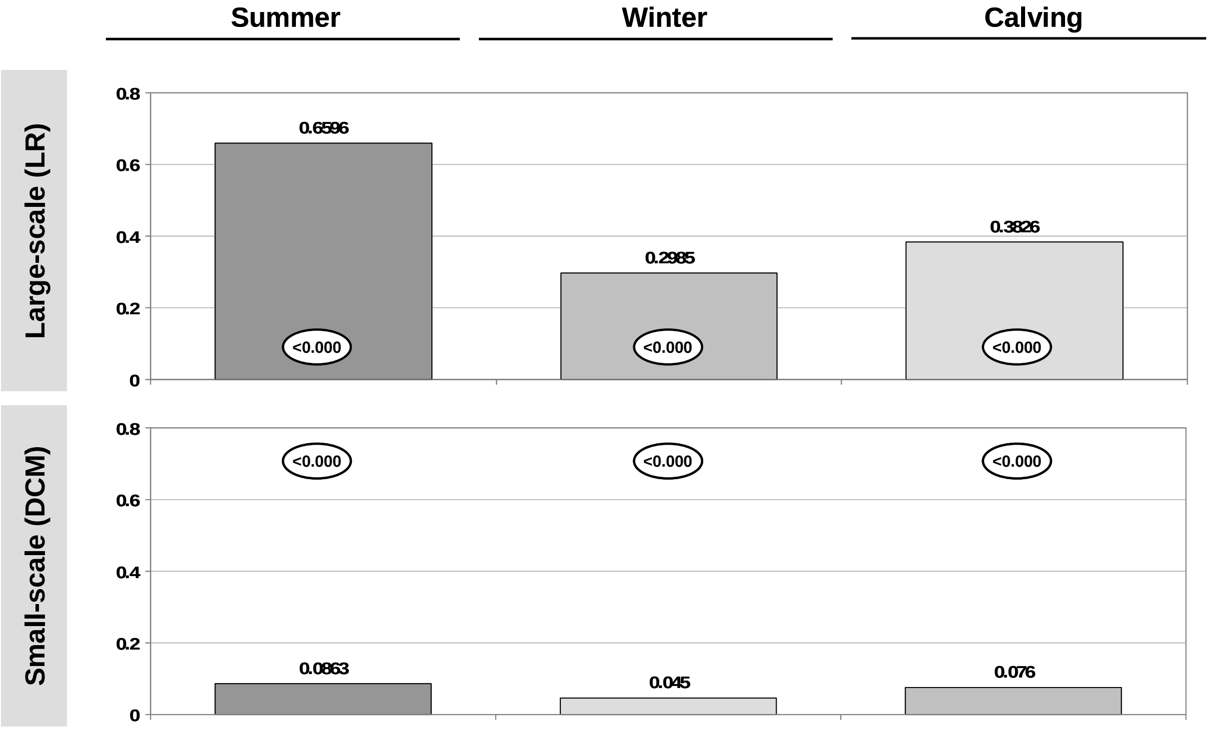

Figure 5-11: Model summary (Nagelkerke's R-square and Chi-squares) – overview by model type

Results from large-scale models (LR) were overall satisfactory. Within this group the summer model could explain a significantly higher proportion of variance (Nagelkerke's R-square from 0.6596) as compared to calving (0.3826) and winter (0.2985).

The small-scale models (DCM) explained significantly less of the total variance between selected and available spatial entities as compared to large-scale models, but ranking between seasons stayed constant. Again, the summer model could explain the largest proportion of the overall variance (0.0863), followed by calving (0.076) and winter (0.045).

Model selection

Summaries for the six individual models are shown in Table 5-2, including gain in AIC for all single independent variables:

		SUMMER		WINTER		CALVING	
		LR	DCM	LR	DCM	LR	DCM
Summary	LogLik^{zero}	-15781	-27310	-50702	-87730	-9275	-16047
	LogLik^{full}	-8010	-25371	-41434	-84504	-7013	-15045
	CHI^2	15542	3878	18538	6452	4525	2004
	Df	25	19	25	18	24	17
	Probability	0.000	0.000	0.000	0.000	0.000	0.000
	Pseudo-R$^2_{Nagelkerke}$	0.6596	0.0863	0.2985	0.0450	0.3826	0.0760
	AIC	16072	50781	82919	169047	14075	30125
	n	22767	125279	73148	402446	13381	73612
Landcover	SNOW * daytime	2	-19***	-159***	-12***	-12**	-28***
	WATER * daytime	-179***	-421***	-218***	-401***	-129***	-217***
	RIDGE * daytime	-5**	-70***	-104***	-124***	-50***	-27***
	LEESIDE * daytime	0	-30***	-12***	-16***	-31***	-5**
	SNOWBED * daytime	-8**	-4*	-106***	-122***	-25***	-71***
	BOG * daytime	-32***	-22***	-15***	-48***	1	-17***
	FOREST * daytime	-36***	-35***	-126***	-85***	-14**	-12***
	ROCK * daytime	-30***	-85***	-157***	-54***	-8**	-37***
Lichen	LICHENVOLUME	-534***	-76***	-1,224***	-44***	-414***	-30***
	LICHENVOLUME^2	-613***	-49***	-1,203***	-27***	-609***	-21***
Terrain	ELEVATION	-187***	-54***	-195***	-30***	-8´	-101***
	ELEVATION^2	-133***	-37***	-63***	-11***	0	
	ELEVATION * tempreture	-40**		-71**		-31*	
	ELEVATION^2 * tempreture	-43**		-68**		-29*	
	ELEVATION * windspeed	-115***		-195***		-41**	
	ELEVATION^2 * windspeed	-110***		-200***		-40**	
	SLOPE	-330***	-77***	-614***	-5*	-482***	-2
	SLOPE^2	-144***	-17***	-625***	-112***	-335***	-7*
	ENERGYCOST	-230***	-434***	-303***	-257***	-99***	-146***
	RADIATION * daytime	-306***	-92***	-759***	-852***	-315***	-415***
Disturbance	DROAD	-1,680***	-62***	-719***			
	DTRIAL	-4,321***	-30***				
	DCABIN^{tourist}			-49´			
	DCABIN^{private}	-20*					
Snow	SNOWDEPTH					-823***	-48***
	SNOWDEPTH^2			-3,436***	-51***	-520***	
Wind	MOVEWIND * daytime	-408***	-972***	-892***	-1,536***	-133***	-151***

Note: signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 ''' 0.1 ' ' 1

Table 5-2: Model summary – gain in AIC for covariates by model type and season

All tested models were overall highly significant as indicated by results from chi-square tests (17 – 25 df). Absolute AIC (LogLik) was used for model selection but not comparable between models due to differences in sample size; Nagelkerke’s pseudo R-square was used instead and ranged from 0.045 to 0.6596.

LANDCOVER lead to significant improvements of AIC-values for almost all model types and seasons. A significant interaction with daytime was detectable. Single insignificant interaction terms were not excluded since the overall interaction terms between land cover type and daytime proved to be significant. LICHENVOLUME tested significant for all model types and seasons.

ELEVATION gained significant improvements of AIC values for all models and seasons, mostly visible as a non-linear effects. Significant interaction terms were detected with temperature and elevation for the large-scale selection models. SLOPE showed non-linear effects, significantly improving all model types. ENERGYCOST (of movement) as well as (solar) RADIATION with daytime as interaction term were tested significant within all model types.

DROAD and DTRAIL (Distance to roads/trails) proved significant for all summer models. $\text{DCABIN}^{\text{PRIVATE}}$ (distance to private cabins) significantly improved the large-scale summer selection model. For the large-scale winter model both, DROAD and $\text{DCABIN}^{\text{TOURIST}}$ (distance to tourist cabins), tested significantly. Habitat selection during calving (large- and small-scale) as well as during small-scale winter selection was not significantly affected by disturbance related variables (as measured by AIC).

SNOWDEPTH yielded significant improvements for the winter and calving models, mostly visible as non-linear effects. MOVEWIND (movement direction in relation to wind) interacted with daytime tested significant for all model types and seasons.

Relative contribution of factor groups

The relative contribution of the factor groups to the explained variance depended on model type and season. To assess their contribution, changes in Nagelkerke’s R-square was calculated using forward and backward selection procedures, alternatively: Within backward selection the contribution of each factor group was estimated as loss of r-squares when the within group factors and interaction terms were dropped from the fully defined models. In opposite, within forward selection, the contribution of factor groups was estimated as gain in r-squares when the within group factors and interaction terms were entered to the models.

While the relative contributions remained more or less stable, the absolute contributions to the explained model variance were found to significantly differ depending on the method used[87] with the forward entering method yielding considerably higher values than the backward dropping method (compare Table 5-3). It was therefore decided to use the average values of the forward and backward methods as estimates for the absolute changes in Nagelkerke’s pseudo r-squares as indicators for the relative contribution of the factor groups to the overall explained model variance.

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[87] Even though external factors have been checked for collinearity and were excluded from models when Spearman’s correlation index exceeded a threshold of 0.5, the remaining collinearity between factors is likely to account for some of the above differences.

		SUMMER			WINTER			CALVING		
		Backward	Forward	Average	Backward	Forward	Average	Backward	Forward	Average
Large-scale (LR)	Land cover	1.07	16.10	8.59	2.04	9.97	6.01	3.65	10.97	7.31
	Lichen	1.85	16.00	8.93	1.79	9.84	5.82	5.51	13.60	9.56
	Terrain	5.19	30.66	17.93	5.53	13.26	9.40	6.68	13.72	10.20
	Disturbance	18.29	53.79	36.04	1.04	6.37	3.71	0.00	0.00	0.00
	Snow depth	0.00	0.00	0.00	4.98	7.22	6.10	7.87	15.14	11.51
	Wind	1.22	1.08	1.15	1.27	1.68	1.48	0.97	0.47	0.72
Small-scale (DCM)	Land cover	1.72	3.33	2.53	0.94	1.53	1.24	2.80	4.15	3.48
	Lichen	0.21	0.52	0.37	0.03	0.25	0.14	0.14	0.39	0.27
	Terrain	3.08	4.35	3.72	1.95	2.39	2.17	2.81	3.69	3.25
	Disturbance	0.18	0.08	0.13	0.00	0.00	0.00	0.00	0.00	0.00
	Snow depth	0.00	0.00	0.00	0.04	0.01	0.02	0.18	0.01	0.09
	Wind	2.14	1.74	1.94	1.07	0.87	0.97	0.57	0.51	0.54

Table 5-3: Relative contribution of factor groups to explained model variance by model type and season: changes in Nagelkerke's R-square in percentage-points from forward/backward selection and average

In the large-scale habitat selection models (LR) land cover had a significant impact on the explained overall variance of the single models (6.0% to 8.6% average change in Nagelkerke's R-square from forward/backward selection). Summer yielded the highest values (8.6%), whereas winter benefitted least from land cover information (6.0%). Lichen volume showed similar contributions as land cover in the large-scale models (5.8% to 9.6%). The contribution in winter (5.8%) was slightly lower than in summer (8.9%) and calving (9.6%). The terrain related factors contributed highly to the explained overall variance of the large-scale selection models (9.4% to 17.9%). The effect of terrain was found most important for summer (17.9%); winter and calving depicted lower values (9.4% and 10.2%). The disturbance related factors were the most important single contributors to the explained overall model variance during summer (36,0%). In contrast, disturbance only gave a minor contribution in the winter models (3.7%) and was not significant during the calving period (0,0%). Snow depth contributed significantly to the explained overall model variance for winter (6.1%) and even more so for calving (11.5%). The contribution of wind direction was modest for all seasons and model types (0.7% to 1.5%). It was of minor importance during calving (0.7%) as compared to summer (1.2%) and winter (1.5%).

Within the small-scale habitat selection models (DCM), land cover made a modest contribution to the explained model variance. The values for the winter season proved to be lower (1,2%) compared to summer (2.5%) and calving models (3.5%). Lichen volume only contributed minor in all seasons (0.1% to 0.4%). The terrain related factors within the small-scale models contributed significantly within all models (2.6% to 3.7%). No clear pattern was visible between seasons. Disturbance in the small-scale models had very little impact within the summer models (0.1%). For both, calving and winter, no significant contribution was found. The relative contribution of snow depth was also limited (<0.1% for winter and calving). The contribution of wind direction to the explained model variance was modest within the models (0.5% to 1.9%), with highest values for summer (1.9%).

When comparing the absolute factor group contributions within the models, the small-scale selection models gained significantly lower proportions to the explained overall variance for all factors and seasons: Land cover and terrain showed a significant loss (6.0% to 8.6% vs. 1.2% to 3.5% for land cover; 9.4% to 17.9% vs. 2.2% to 3.7% for terrain). Lichen volume and snow depth became almost irrelevant within the small-scale selection models (0.1% to 0.4% for lichen volume and <0.1% for snow depth) while of significant importance for the large-scale models (5.8% to 8.9% for lichen volume and 6.1% to 11.5% for snow depth). Human disturbance within the small-scale summer model demonstrated very little remaining explanatory power (0,1%) while being the most important factor for large-scale selection model (36,0%). Relative movement to wind direction depicted constant but little contribution to the explained model variance for the large- and small-scale models (0.7 to 1.5 vs. 0.5 to 1.9).

Reindeer’s functional response to single factors

Reindeer’s functional response towards the single factors was based on the estimated coefficients and beta values for the covariates. Summaries are given in Table 5-4 and Table 5-5.

		SUMMER		WINTER		CALVING	
		LR	DCM	LR	DCM	LR	DCM
Landcover	SNOW * daytime	0.06249	0.00249***	-3.25261***	1.38564***	-2.22379**	2.46097***
	WATER * daytime	1.59786***	1.49856***	-0.62943***	0.60935***	-1.41085***	1.48888***
	RIDGE * daytime	0.13071**	0.15770***	0.27918***	0.17518***	0.47455***	0.25595***
	LEESIDE * daytime	0.08360	0.02341***	0.06599***	0.03581***	0.39520***	0.12554**
	SNOWBED * daytime	0.18345**	0.04160*	-0.31467***	0.22555***	-0.27740***	0.48055***
	BOG * daytime	0.58686***	0.26554***	-0.11941***	0.15852***	-0.07554	0.09054***
	FOREST * daytime	1.13751***	0.77896***	-0.68019***	0.47437***	-0.48802**	0.28980***
	ROCK * daytime	0.00292***	0.01786***	-0.50499***	0.18176***	-0.27150**	0.41503***
Lichen	LICHENVOLUME	0.33609***	0.16489***	0.12422***	0.07063***	0.27743***	0.17048***
	LICHENVOLUME^{2}	0.01096***	0.00418***	-0.00271***	0.00131***	-0.01034***	0.00458***
Terrain	ELEVATION	0.05323***	0.03793***	0.01502***	0.01908***	0.00486´	0.00447***
	ELEVATION^{2}	0.01997***	0.01222***	-0.00364***	0.00488***	-0.00098	
	ELEVATION * tempreture	0.00059**		-0.00015**		0.00037*	
	ELEVATION^{2} * tempreture	0.00047**		0.00012**		-0.00028*	
	ELEVATION * windspeed	0.00180***		0.00052***		0.00073**	
	ELEVATION^{2} * windspeed	0.00136***		-0.00042***		-0.00057**	
	SLOPE	0.23079***	0.07962***	0.11844***	0.01448*	0.23179***	0.02133
	SLOPE^{2}	0.05165***	0.01246***	-0.04186***	0.01929***	-0.06080***	0.00970*
	ENERGYCOST	0.16971***	0.13551***	-0.09776***	0.06514***	-0.11464***	0.08586***
	RADIATION * daytime	0.00104***	0.00177***	0.00724***	0.00754***	0.01347***	0.01207***
Disturbance	DROAD	0.11759***	0.06099***	0.03024***			
	DTRIAL	0.18606***	0.04501***				
	DCABIN$^{\text{tourist}}$			0.01196´			
	DCABIN$^{\text{private}}$	0.08277*					
Snow	SNOWDEPTH					2.07077***	0.59120***
	SNOWDEPTH^{2}			-0.20018***	0.20452***	-0.30347***	
Wind	MOVEWIND * daytime	0.00481***	0.00400***	0.00466***	0.00427***	0.00273***	0.00265***

Note: signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 ''' 0.1 ' ' 1

Table 5-4: Model summary – estimated coefficients for covariates by model type and season

		SUMMER		WINTER		CALVING	
		LR	DCM	LR	DCM	LR	DCM
Landcover	SNOW * daytime	1.06449	0.99751***	0.03867***	0.25016***	0.10820**	0.08535***
	WATER * daytime	0.20233***	0.22345***	0.53290***	0.54371***	0.24394***	0.22563***
	RIDGE * daytime	1.13963**	1.17082***	1.32204***	1.19146***	1.60728***	1.29168***
	LEESIDE * daytime	0.91980	0.97686***	1.06821***	0.96483***	1.48467***	1.13377**
	SNOWBED * daytime	1.20136**	1.04248*	0.73003***	0.79807***	0.75775***	0.61844***
	BOG * daytime	0.55607***	0.76679***	0.88744***	0.85340***	0.92724	0.91344***
	FOREST * daytime	0.32062***	0.45889***	0.50652***	0.62228***	0.61384**	0.74841***
	ROCK * daytime	0.99709***	0.98230***	0.60351***	0.83380***	0.76224**	0.66032***
Lichen	LICHENVOLUME	1.39946***	1.17926***	1.13227***	1.07318***	1.31974***	1.18587***
	LICHENVOLUME^{2}	0.98910***	0.99583***	0.99729***	0.99869***	0.98971***	0.99543***
Terrain	ELEVATION	1.05467***	1.03866***	1.01513***	1.01927***	1.00487´	1.00448***
	ELEVATION^{2}	0.98023***	0.98785***	0.99636***	0.99513***	0.99902	
	ELEVATION * tempreture	0.99941**		0.99985**		1.00037*	
	ELEVATION^{2} * tempreture	1.00047**		1.00012**		0.99972*	
	ELEVATION * windspeed	1.00180***		1.00052***		1.00073**	
	ELEVATION^{2} * windspeed	0.99864***		0.99958***		0.99943**	
	SLOPE	1.25959***	1.08288***	1.12574***	1.01459*	1.26085***	1.02156
	SLOPE^{2}	0.94966***	0.98762***	0.95901***	0.98090***	0.94101***	0.99035*
	ENERGYCOST	0.84391***	0.87327***	0.90686***	0.93693***	0.89169***	0.91772***
	RADIATION * daytime	0.99896***	0.99823***	1.00727***	1.00757***	1.01356***	1.01215***
Disturbance	DROAD	1.12478***	1.06289***	1.03070***			
	DTRIAL	1.20449***	1.04604***				
	DCABIN$^{\text{tourist}}$			1.01203´			
	DCABIN$^{\text{private}}$	1.08629*					
Snow	SNOWDEPTH					7.93092***	0.55366***
	SNOWDEPTH^{2}			0.81858***	0.81504***	0.73825***	
Wind	MOVEWIND * daytime	1.00482***	1.00401***	1.00467***	1.00427***	1.00273***	1.00266***

Note: signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 ''' 0.1 ' ' 1

Table 5-5: Model summary – estimated betas for covariates by model type and season

Based on the above results reindeer's functional response to the single independent factors with and without interaction terms is described in detail.

Land cover

Reindeer’s relative selection probabilities between the single land cover classes with daytime as interaction term revealed significant differences between seasons (see Figure 5-12).

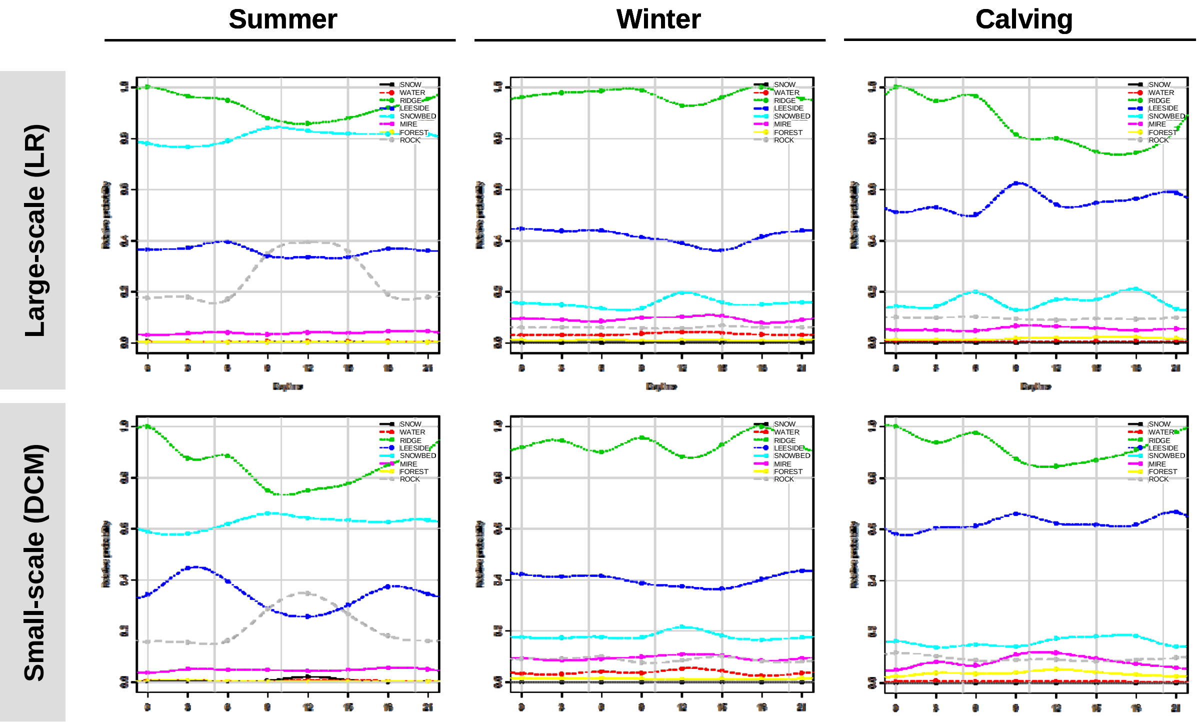


Figure 5-12: Relative selection probabilities for land cover classes: interaction with daytime by model type and season

Within the large-scale habitat selection models, RIDGE depicted the highest selection probability relative to other land cover classes during all seasons and similar interaction patterns with daytime were visible. The relative selection probabilities for RIDGE were lowest during midday (more pronounced within the calving and summer models). LEESIDE vegetation showed the second highest selection probability (next to RIDGE vegetation) during WINTER and CALVING, but SNOWBED vegetation revealed the second highest relative probabilities during summer (with slightly higher values during midday). ROCK also showed highly increased relative probabilities within the summer model and, like for SNOWBED vegetation, probabilities increased during midday. Relative selection probabilities for other land cover classes were relatively low.

Within the small-scale selection models, overall similar relative probability patterns between seasons were found as within the large-scale models described above. Still both, relative probabilities for SNOWBED vegetation and ROCK, were significantly higher during summer and demonstrated the same interaction profiles with daytime (increase during midday), but LEESIDE interaction with daytime was more visible (two peaks during 3 and 18 hours GMT).

A season by season comparison between the large and small-scale models revealed similar relative selection probabilities, overall. Within the summer models higher daytime interactions for RIDGE and LEESIDE was visible in the small-scale model and SNOWBED vegetation had a slightly lower relative selection probability. For both, winter and calving, no significant differences were found between the differing spatial scales.

Relative selection probabilities between the land cover classes as described above are dependent on class distribution. Reindeer's functional response to the single land cover classes (selection or avoidance) independent of class distribution is depicted in Figure 5-13 based on the estimated beta values.

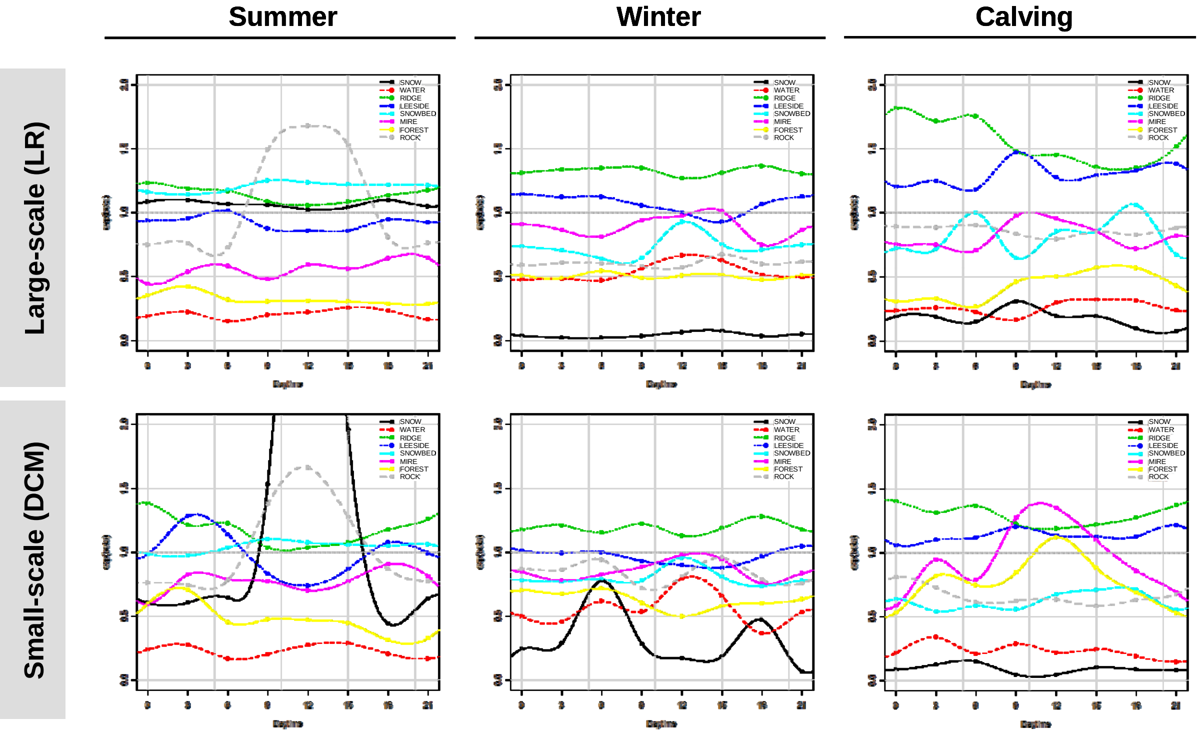


Figure 5-13: Functional response to land cover classes – interaction with daytime by model type and season

Within the large-scale models, RIDGE was selected during all seasons (exp(beta)>1) but significantly more so during the calving and winter period. A modest to strong interaction with daytime was visible for RIDGE vegetation with lower (but still positive) selection during midday. (Strong) avoidance of (SNOW) ROCK was visible for calving and winter but positive selection during summer with a strong interaction with daytime for rocky terrain (highest selection during midday). Reindeer demonstrated active selection for SNOWBED vegetation during summer, while avoidance for winter and calving was revealed. WATER and FOREST were avoided within all seasons, but significantly less during winter. No clear selection pattern was visible for MIRE within the large-scale models.

Season comparison within the small-scale selection models yielded similar results (than within the large scale models), but the differences were partially more pronounced: RIDGE demonstrated highest selection for winter and calving; for summer reindeer's functional response to RIDGE showed clearer interaction with daytime (lower selection during midday). As in the large-scale models, ROCK was avoided during winter and calving. The same trend was visible for summer during night but – as in the large-scale models – for daytime a strong selection of the land cover class ROCK was found. Similarly, SNOWBED vegetation was selected for during summer and avoided during winter and calving. While SNOW showed a similar selection profile as within the large-scale models (avoidance during winter and calving, selection during summer), within the small-scale selection models a much stronger interaction with daytime was visible during summer (strong selection for these habitat patches during midday). Both, WATER and FOREST, were avoided during all seasons.

Comparison of model types within seasons revealed similar results, though some differences occurred: For summer the small-scale model predicted a significantly clearer interaction with daytime for both, LEESIDE (peaks at 3/18 hours GMT) and SNOW (strong peak at 12 hours GMT). During winter only small differences in selection patterns were found between the small- and large-scale models and interaction with daytime was far less important as compared to the summer models: while SNOW demonstrated strong avoidance in both model types, stronger interaction with daytime was visible within the small-scale model. Also for calving similar selection patterns between model types prevailed, but selection for RIDGE and LEESIDE vegetation was not as predominant for the small-scale model than as for large-scale model even though interaction with daytime was similar.

Lichen volume

Results revealed clear differences in reindeer's selection patterns for lichen volume between seasons and spatial scales, but the functional response to lichen volume was non-linear (2nd order) in all models (see Figure 5-14).

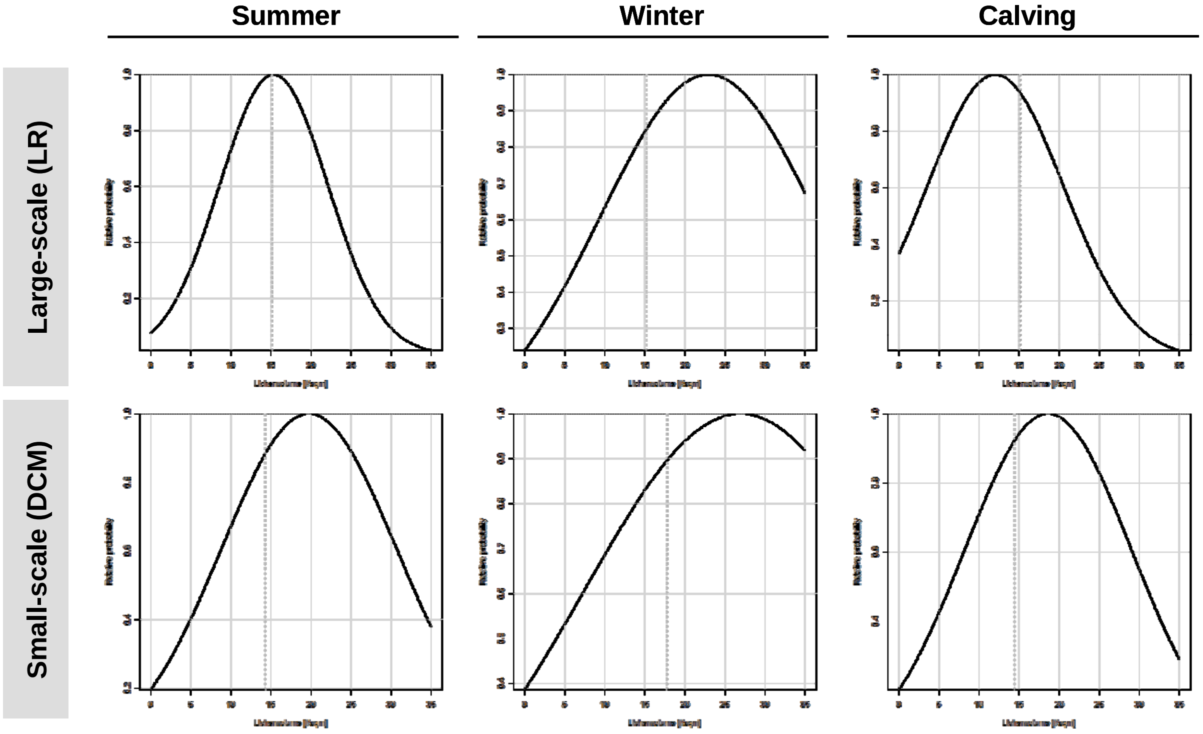


Figure 5-14: Relative selection probability for lichen volume by model type and season

Within the large-scale models reindeer selected for areas characterized by significantly higher lichen volumes during winter (~23 liters/sqm). While during summer the selected optimal lichen volume fell more in line with the average lichen volume of the available habitat (~15 liters/sqm), a negative selection for lichen volume was visible during calving (~12 liters/sqm) in a large-scale perspective.

During all seasons higher selection optima for lichen volume were found within the small-scale models. While on a larger scale no clear selection tendency towards high lichen volume was visible during summer, reindeer actively selected for patches with higher lichen volumes on a smaller scale (15 liters/sqm vs. 19 liters/sqm). During winter reindeer demonstrated both, large- and small-scale selection for well above average lichen volumes. Note, however, that the relative selection probability drops beyond lichen volumes of ~23 liters/sqm in the large-scale model, whereas the selection optimum in the small-scale model almost fell together with the maximum values for lichen volume available in winter. Finally, a comparison of spatial scales within the calving models indicated large-scale area selection characterized by below average lichen volume values (~12 liters/sqm), while reindeer selected for above average lichen volumes (~19 liters/sqm) within the large-scale area chosen.

Elevation

Reindeer's functional response to elevation was non-linear (2nd order) within all models. In a large-scale perspective, a significant interaction was found with both, temperature and wind speed, during all seasons, while in the small-scale selection models no significant interaction with those two parameters could be detected. In the following, results will first be described with temperature as interaction term (see Figure 5-15), later with wind speed (see Figure 5-16).

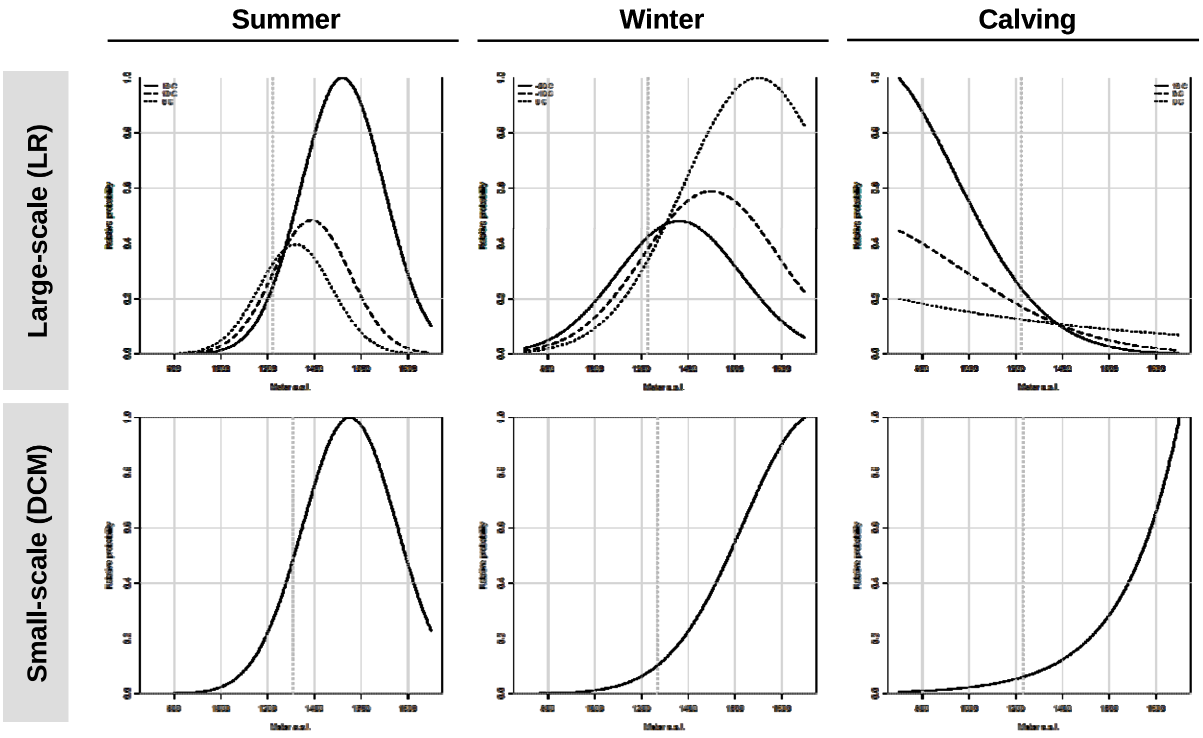


Figure 5-15: Relative selection probability for elevation – interaction with temperature by model type and season

In the large-scale models the selection for optimal elevation incorporated a significant interaction term with temperature for all seasons. Higher areas were selected as temperatures increased. During summer and winter higher relative selection probabilities were found for well above average elevations. During the calving period findings were opposite (low elevation).

In the small-scale selection models interaction with temperature proved non significant. All small-scale models revealed selection for well above average elevations. The highest relative optima were found during calving (lowest, but still above average during summer).

Comparing small vs. large-scale habitat selection in summer revealed non-linear selection for high elevations for both model types with optimum values well above average values of the available habitat. Interaction with temperature was only visible for large-scale models with selection for higher areas in warmer weather (and higher relative factor importance in such a case). Models for the winter season indicated large and small-scale (non-linear) selection for higher elevations, with small-scale selection almost for the highest areas available. On a large scale, animals selected for higher elevations, when the temperature was higher (elevation with higher relative importance when warmer). In opposite, during calving a (non-linear) large-scale selection was found for below average elevations (again the relative factor importance was higher for warmer temperatures). On a small-scale reindeer selected for high areas during both, winter and calving (higher during calving).

Results for elevation with wind speed as interaction term are presented in Figure 5-16:

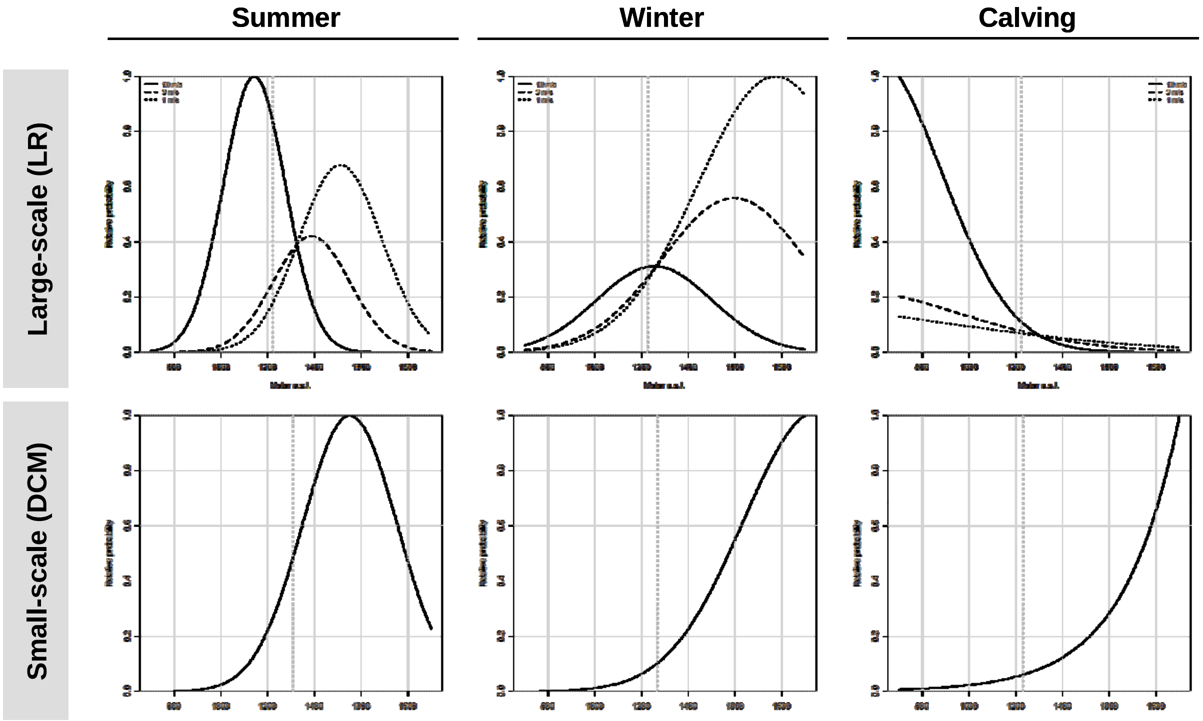


Figure 5-16: Relative selection probability for elevation – interaction with wind speed by model type and season

In the large-scale habitat selection models reindeer showed similar functional responses to elevation with wind speed as interaction term, as they did to elevation with temperature: non-linear selection patterns during all seasons, large-scale selection for higher areas at lower wind speeds and selection of above average elevations during summer and winter (below average during the calving period).

In a small-scale perspective, again, an interaction with wind speed was not significant during all three seasons. Analogue to the findings for temperature as interaction term, animals generally selected above average areas (highest during the calving period, lowest, but still above average, during summer).

Slope

Reindeer’s selection for slope differed significantly between seasons and, even more so, between large- and small-scale models (see Figure 5-17).

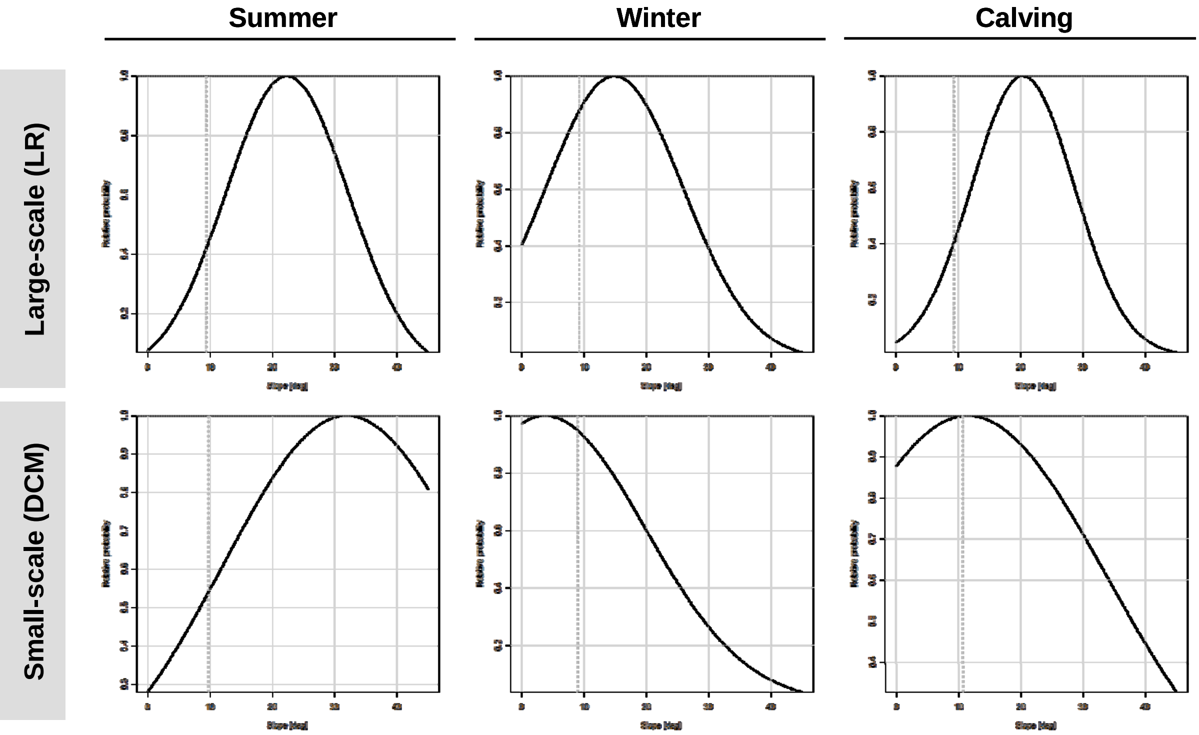


Figure 5-17: Relative selection probability for slope by model type and season

At a large-scale reindeer showed a non-linear selection for well steeper than average slopes for all seasons (compared to average slope of available habitat). The highest selection optima were predicted for summer (~22 deg) and calving (~20 deg); selection in winter was significantly lower (~16 deg), but still above the average value of the available habitat (~10 deg).

Non-linear functional responses were also apparent in the small-scale selection models for all seasons. Summer was characterized by a strong selection for high slopes with a peak at approximately 30 deg, beyond which the relative selection probabilities were declining again. In contrast, reindeer selected for slopes less steep than average during winter (~6 deg). Finally, during calving reindeer selected for average slopes (~10 deg).

In all seasons the functional response to slope differed significantly between spatial scales: During summer both, the large and small-scale selection model, indicated a positive response to slopes, but more profound in the small-scale model (~22 deg vs. ~30 deg). While reindeer during winter selected for steeper slopes at a larger scale (~15 deg), the relative probabilities for small-scale selection already declined at values below the average slopes of the available habitat (~6 deg). Similar selection patterns were found during calving, but slightly shifted towards selection for higher slopes.

Energy cost of movement

Reindeer showed a clear tendency to select for movements characterized by lower energy expenditures (see Figure 5-18).

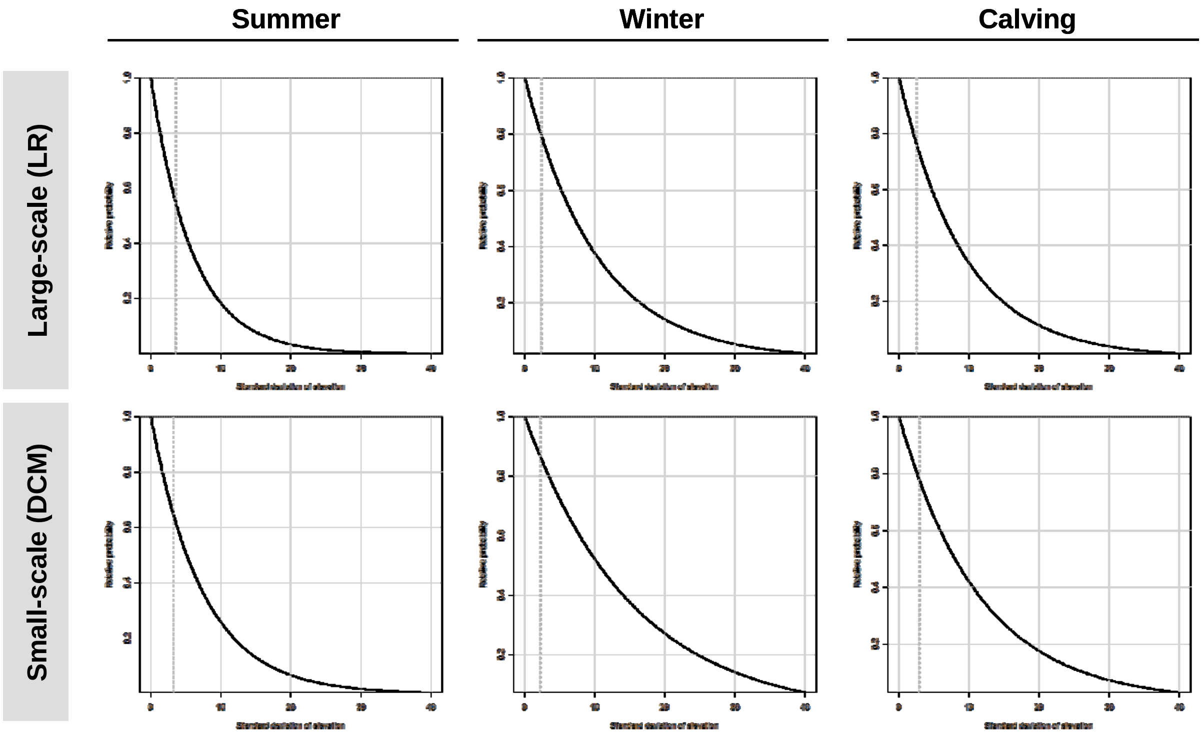


Figure 5-18: Relative selection probability for energy cost of movement by model type and season

Both, at large and small scale, reindeer selected for movements with low energy requirements in all seasons. Relative selection probabilities dropped faster for summer (compared to winter and calving) when average standard deviation of slopes for steps increases. Within season comparisons of spatial scales revealed no significant differences for all three temporal scales und regard.

Solar radiation

Concerning the selection of areas exposed to different quantities of solar radiation, significant differences in selection patterns were found between seasons, but not between spatial scales (see Figure 5-19).

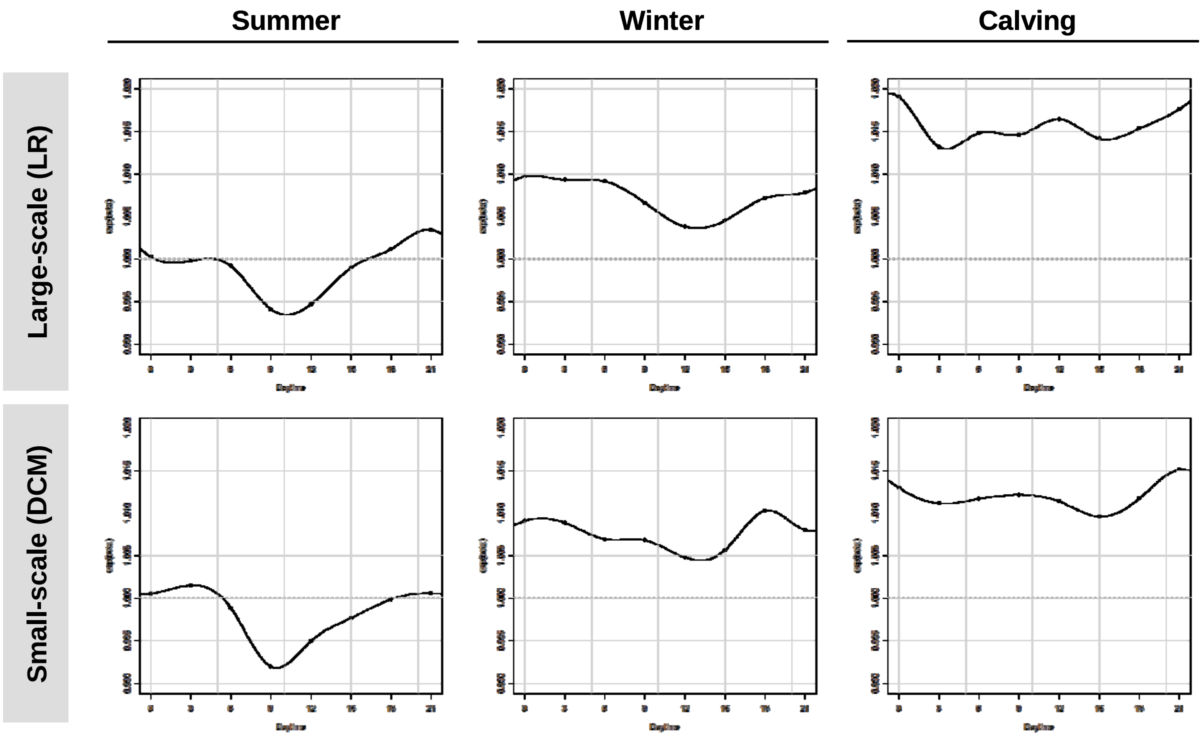


Figure 5-19: Functional response to solar radiation – interaction with daytime by model type and season

In both, large and small-scale models, reindeer’s functional response to solar radiation depended on daytime in all seasons. Profound differences between seasons were visible: As expected, the preference for areas with above average solar radiation (exp(beta)>1) was biggest during the calving period (ranging from 1.013 to 1.020, depending on daytime). Winter still demonstrated considerably positive selection for solar radiation during the entire daily cycle (1.004 to 1.010). In summer the response to solar radiation was split: selection of patches, which received high proportions of solar radiation, was found during late evening/night (1.000 to 1.005), whereas animals avoided such patches during daytime (0.993 to 1.000). During no season significant differences in selection patterns were found between spatial scales.

Distance to roads

Significant avoidance of roads was found during summer (both spatial scales) and within the large-scale winter model (see Figure 5-20). The large-scale model for summer showed the strongest positive correlation between relative selection probabilities and distance to roads (low intercept with steep sloped curve). In the small-scale summer model reindeer’s functional response to distance to roads was still positive (non-linear selection curve), but not as sensitive as in the large-scale model (higher intercept and less steep slope). In the large-scale winter model avoidance of roads was still visible, but significantly less profound as in the summer models.

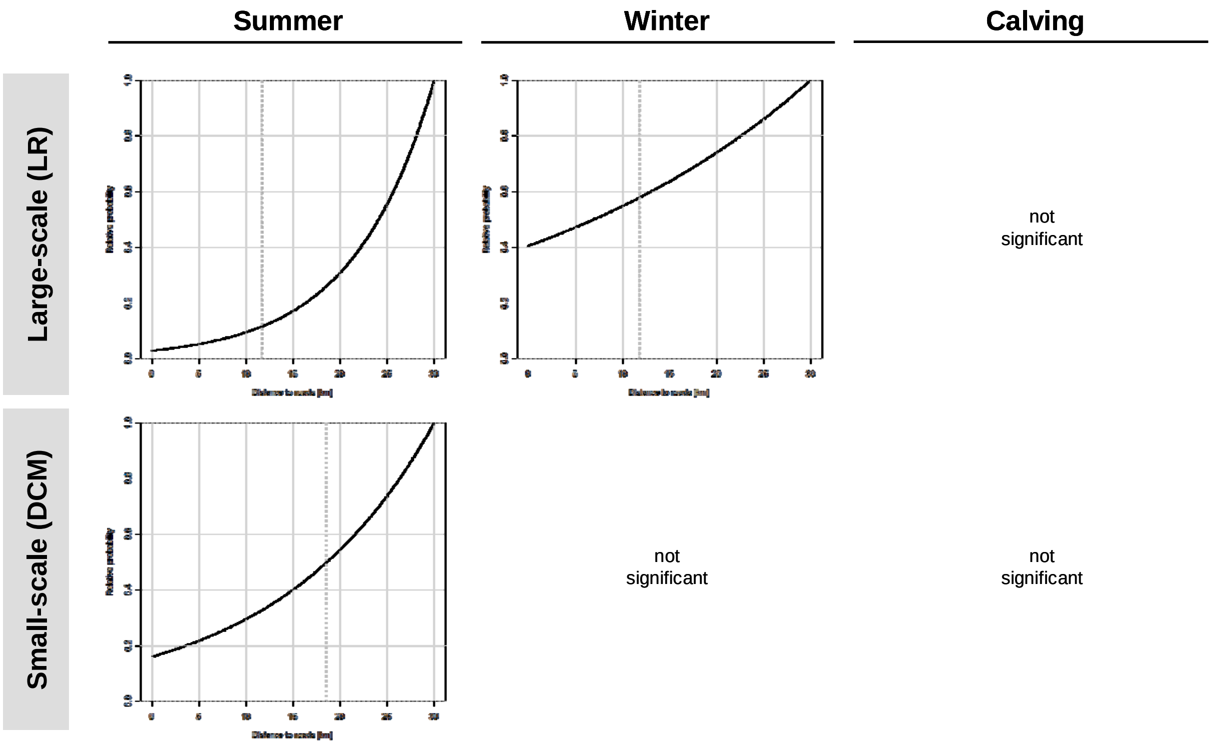


Figure 5-20: Relative selection probability for distance to roads by model type and season

Distance to trails

Tourist trails showed a significant negative impact in the summer models (see Figure 5-21).

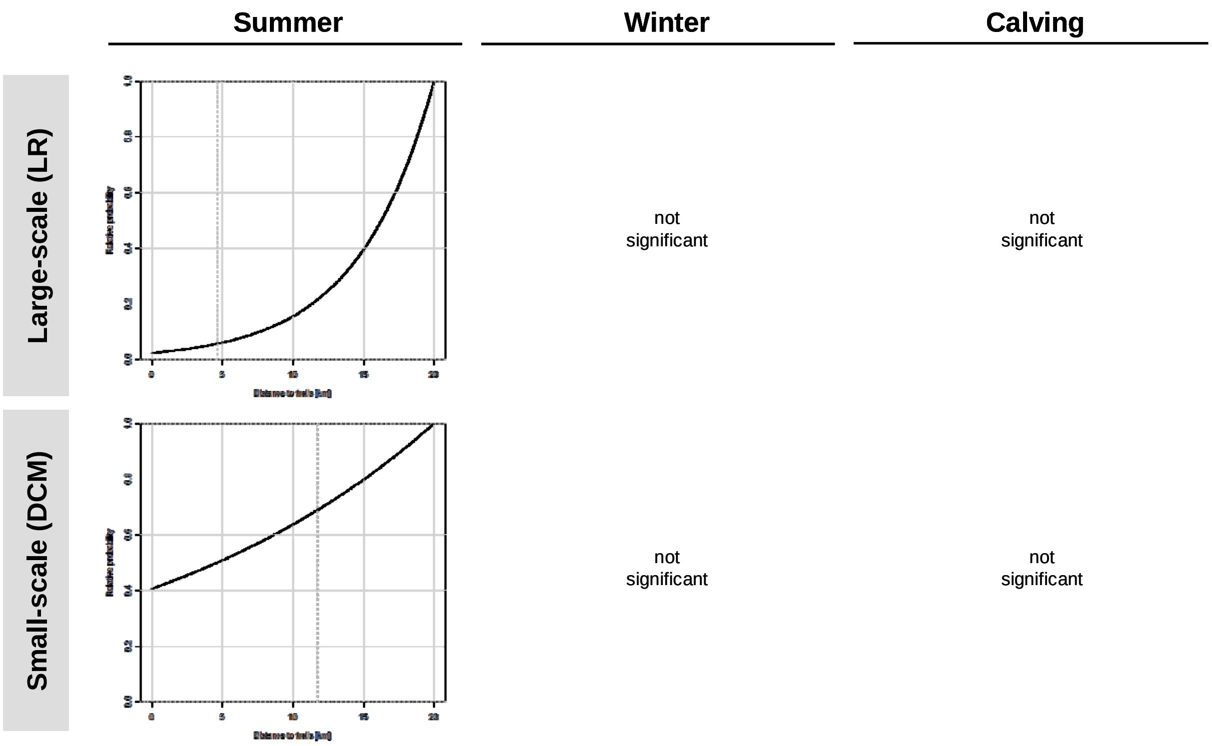


Figure 5-21: Relative selection probability for distance to summer trails by model type and season

Strong avoidance of tourist trails during summer was found in the large-scale habitat selection model (low intercept with steep 2nd order curve). At small scale reindeer still selected patches, which were further away from tourist trails, but the negative influence of such trails was significantly smaller (measured by intercept and slope). For both, the winter and the calving model, no significant impact of tourist trails on reindeer's spatial habitat selection could be detected.

Distance to cabins

A significant impact of private cabins was found within the large-scale summer and winter models, but not in the calving period or any of the small-scale models (see Figure 5-22)

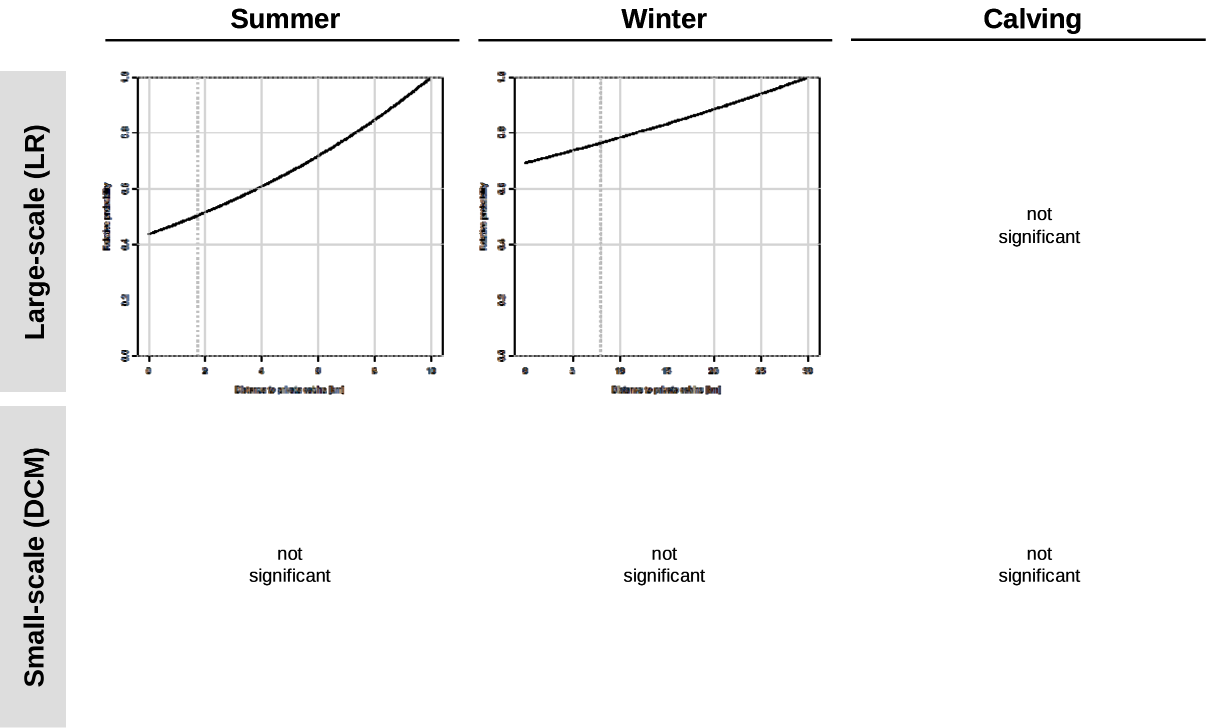


Figure 5-22: Relative selection probability for distance to private cabins by model type and season

A tendency to avoid areas close to private cabins was modest in the large-scale summer model (relatively large intercept and modest slope of 2nd order curve). A still significant, but even weaker trend to avoid areas closer to private cabins was visible in the large-scale winter model.

Snow depth

Snow depth was identified as a significant external factor for habitat selection during winter and calving, both, at larger and smaller scale. All functional responses followed non-linear curves (2nd order) and differed significantly between temporal and spatial scales. During summer snow depth did not affect selection significantly. See Figure 5-23 for an overview:

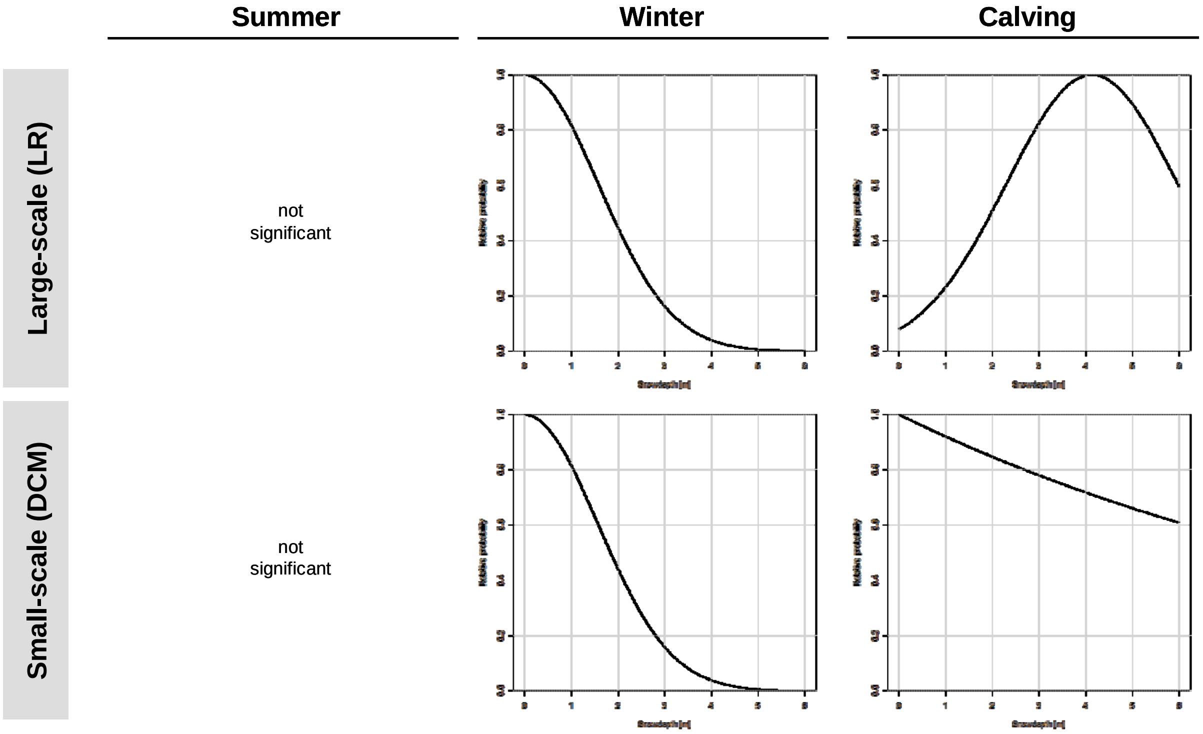


Figure 5-23: Relative selection probability for snow depth by model type and season

Significant differences in large-scale selection patterns for snow depth were found between calving and winter: Selection probabilities during winter increased with lower snow depth (most sensitive between 1 m and 2 m), whereas reindeer aimed to select for a snow depth optimum of app. 4 m during calving.

In contrast, to this, the small-scale models showed reindeer to select for lesser snow depths during both, winter and calving. Nevertheless, sensibility to altered snow depth was significantly lower during calving than during winter.

Within season comparison of spatial scales revealed reindeer to select for lower snow depth in both, small and large-scale models, during winter. The sensitivity was highest at app. 1.5 to 2 m snow depth and the selection probabilities became very low beyond 3 m snow depth. No significant effects of spatial scale were found. During calving, reindeer selected areas with considerable amounts of snow coverage at large-scale, whereas in a small-scale perspective selecting for lower snow depth within those areas.

Wind direction

Reindeer selected for movements against the current wind direction within all spatial and temporal scales (exp(beta)>1). While results were stable between spatial scales significant differences were found depending on season (see Figure 5-24).

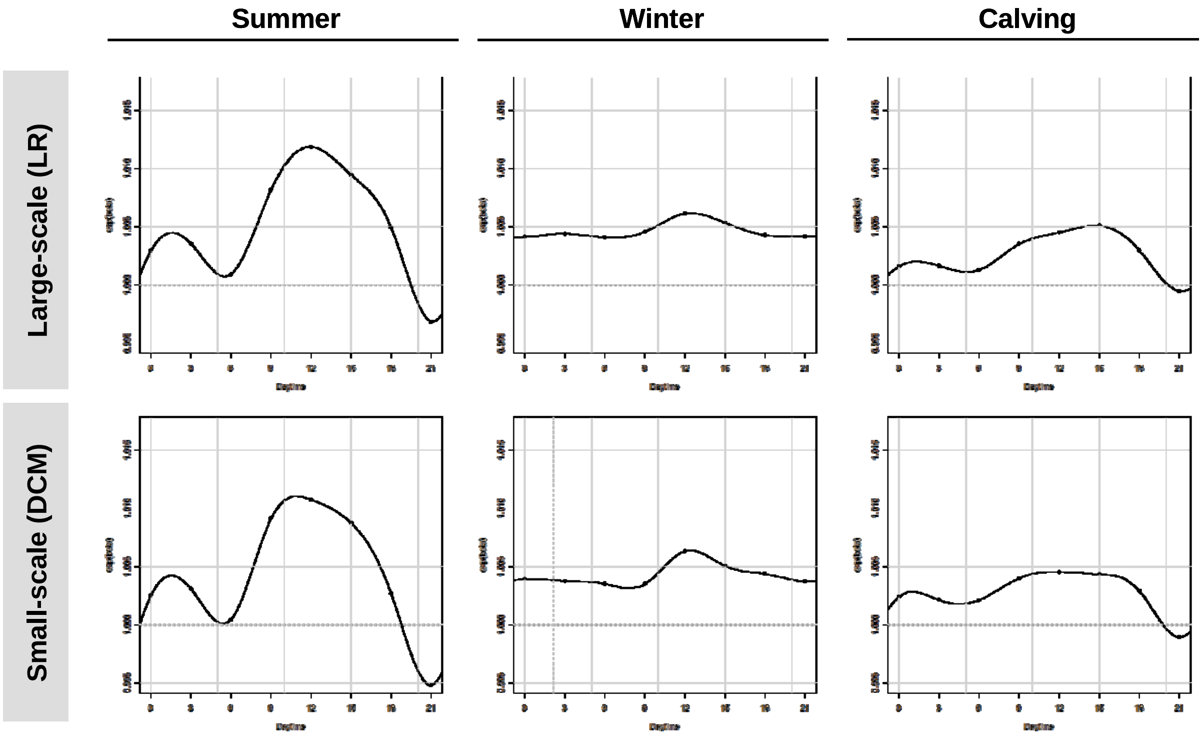
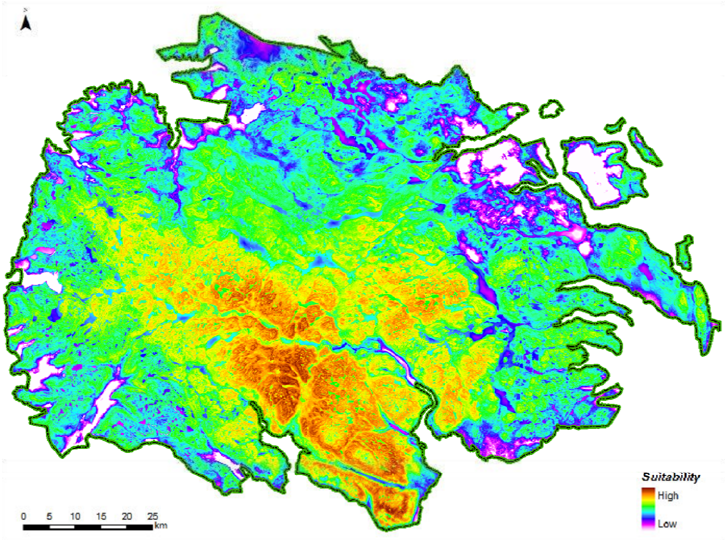


Figure 5-24: Functional response to wind direction – interaction with daytime by model type and season

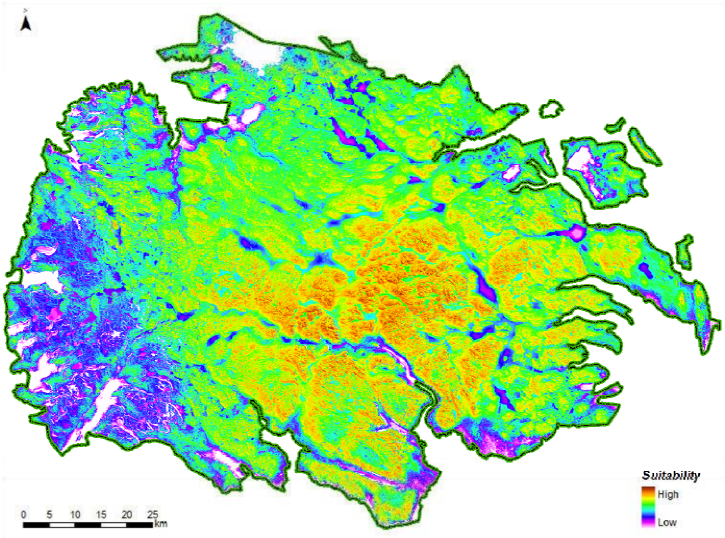
Interaction with daytime was also significant in all cases. Selection peaks for moving against the wind were visible during daytime (all models), but with differences in amplitudes, ranging from very low in winter (exp(beta) from ~1.004 to ~1.007) to marked during summer (~1.000 to ~1.012). At smaller scale the selection for movement related to wind showed similar patterns as detected in the large-scale models. Inter season comparison of spatial scales did not reveal significant differences between spatial scales.

Predicted habitat preference maps for summer, winter and calving

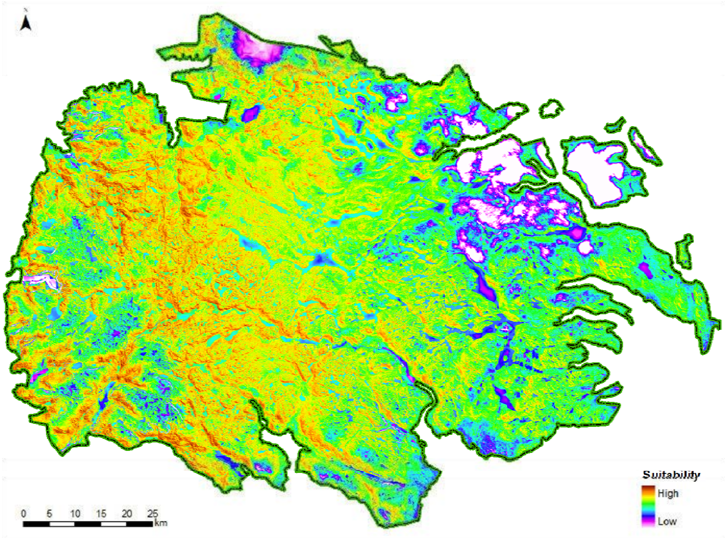
The estimated coefficients for the significant factors from the large-scale models were used to calculate habitat preference maps for summer, winter and calving (compare chapter 5.2). Profound differences in habitat preference were found between the seasons (given the current level of human disturbance and snow conditions). For the spatial differences in the predicted habitat preference compare Map 5-3 (summer), Map 5-4 (winter) and Map 5-5 (calving).



Map 5-3: Predicted large-scale habitat preference (suitability) for current levels of human disturbance – Summer



Map 5-4: Predicted large-scale habitat preference (suitability) for current levels of human disturbance – Winter



Map 5-5: Predicted large-scale habitat preference (suitability) for current levels of human disturbance -Calving

For summer the highest predicted reindeer habitat preferences were clustered within the south-central parts of the study area. Eastern, western and northern areas all showed significantly lower values (see Map 5-3). During winter the most preferred habitats predicted were located within the eastern-central areas of Hardangervidda. Western areas demonstrated low preference values during this season (see Map 5-4). In contrast, the large-scale selection models predicted the preferred calving habitats of reindeer in Hardangervidda to be within the western areas. A clear east-west gradient was visible and distribution of preferred areas was less clustered than in summer (see Map 5-5).

Estimated habitat preferences simulating different levels of human disturbance and snow depth

As described above, the disturbance related factors (distance to roads, trails and cabins) had a significant impact on large-scale habitat selection of reindeer both in the summer and in winter (but more profound during summer). In order to examine the spatial impact of the current level of human disturbance, habitat preference maps were calculated, excluding these factors[88] (compare chapter 5.2). The results of this simulation are presented in Map 5-6:

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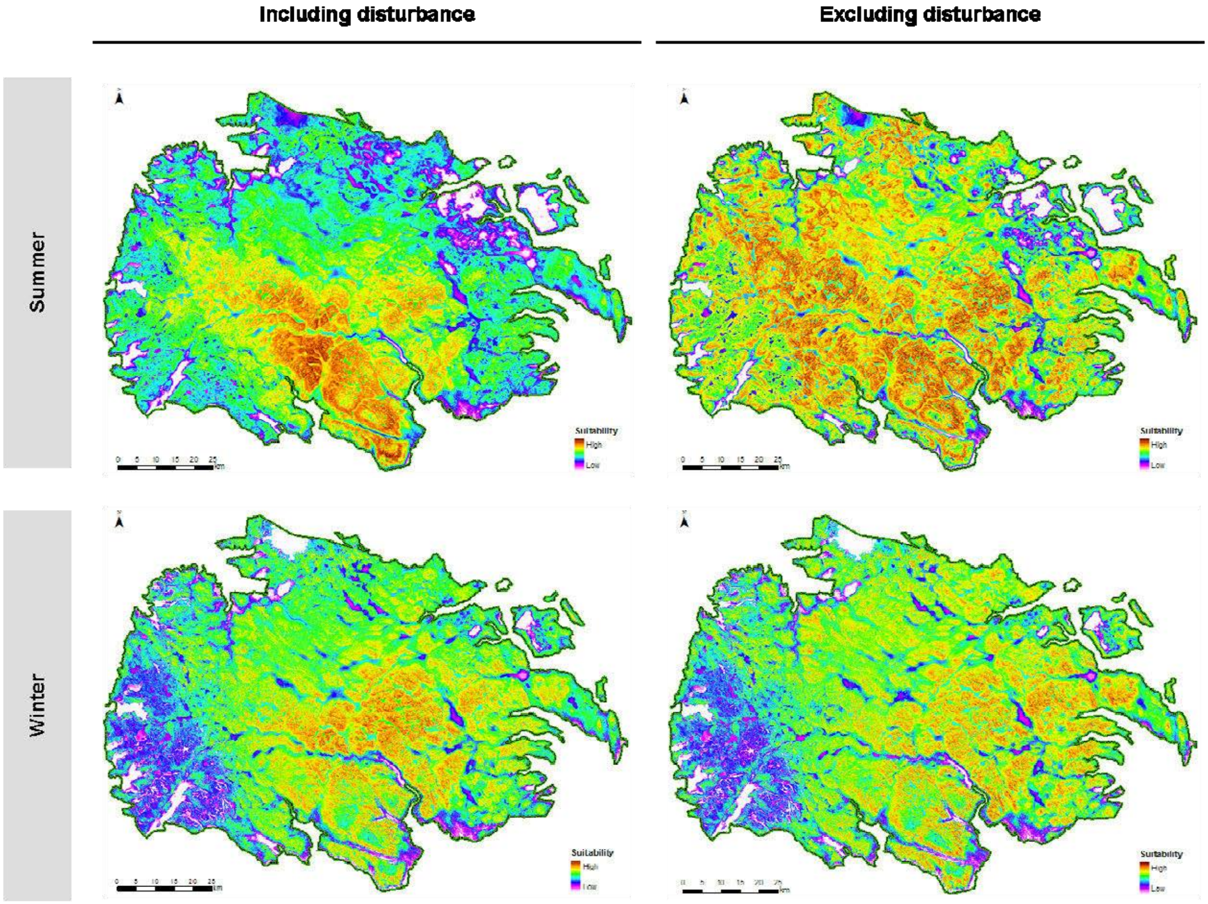
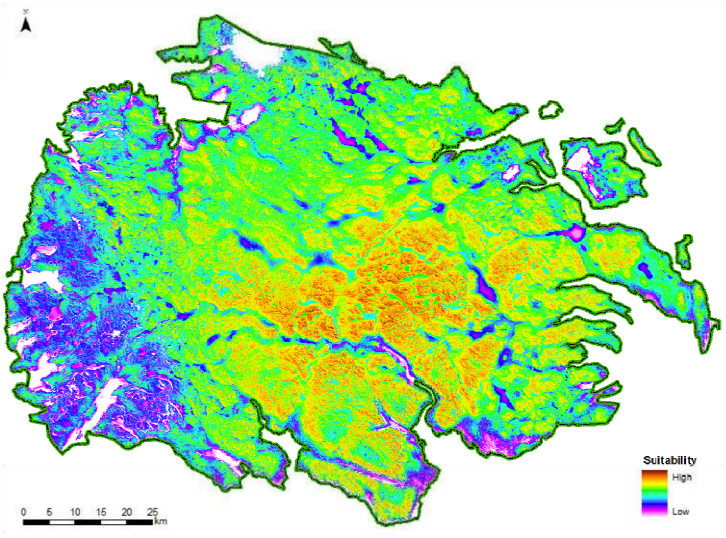
[88] This simulation was done, by assuming a spatially even distribution of all disturbance related factors. Technically this was achieved by using the mean value for each of the single factors for the entire study area instead of the spatially differing real values. The relative contribution of the single disturbance related factors was than calculated by multiplying the means of the factor with the estimated factor coefficient from the large-scale selection models of the corresponding season. All calculations were performed in ArcGIS (ESRI 2005).



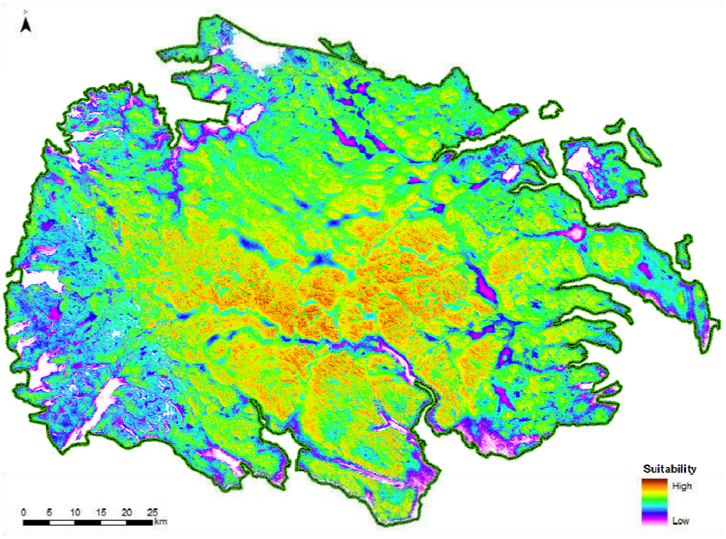
Map 5-6: Estimated large-scale habitat preference (suitability) in summer and winter with/without human disturbance

Hypothetically eliminating the effects of human disturbance reduced the predicted concentration of high value habits during summer significantly (compare Map 5-3: Predicted large-scale habitat preference (suitability) for current levels of human disturbance – Summer). The simulation model predicted high quality summer habitats especially within the western and northern areas of the study area (around Hardangerjøkull), which were not recognized as suitable summer habitats, when the current levels of disturbance related factors were used. Simulating non-disturbance during winter lead to significantly higher preference values for the eastern most areas of Hardangervidda. While this eastbound shift was clearly visible, overall effects were not as profound as for the summer habitats.

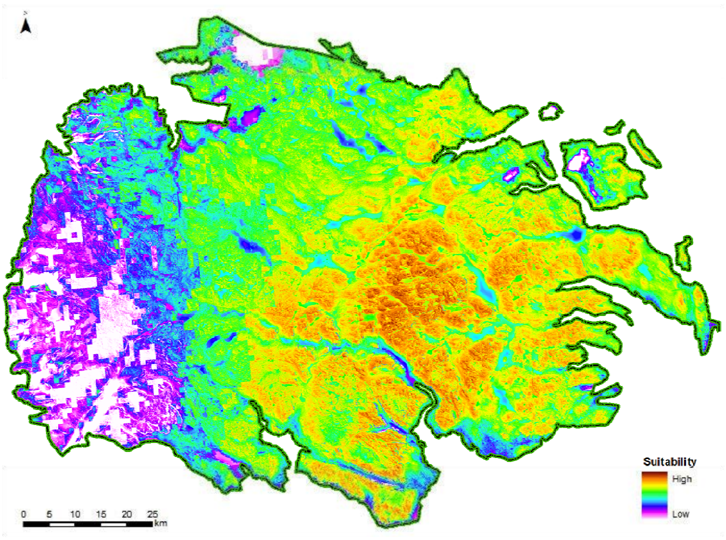
Large-scale habitat selection by reindeer was also shown to be significantly influenced by snow depth during winter (see above). As argued earlier (see chapter 1.1), climate changes are likely to cause alterations in winter precipitation within Hardangervidda (increased snowfalls and surface icing). Against this background the spatial impact of altered snow depths values on reindeer's predicted winter habitat preferences was simulated using lower and upper bound snow depth within the study period as coefficients (instead of mean values) (compare chapter 5.2). Results from this simulation are presented in Map 5-7:



Map 5-7: Estimated large-scale habitat preference (suitability) during winter: average snow depth values 2001 - 2006



Map 5-8: Estimated large-scale habitat preference (suitability) during winter: lower bound snow depth values



Map 5-9: Estimated large-scale habitat preference (suitability) during winter: upper bound snow depth values

As described above, the highest winter habitat preferences of reindeer in Hardangervidda were estimated for the (south-) central to eastern areas, if the average snow depths values from 2001 to 2006 were used for prediction. An east-west gradient of snow depth prevailed but was superimposed by other factors (disturbance/terrain).

When the lower bound values for snow depths from the 2001 to 2006 period were used for model prediction instead, habitat preferences were shifted westwards significantly. Lower preferences for northern areas still prevailed. Finally, a significant eastward shift of predicted high quality winter habitats was visible, when the highest occurring snow depth values between 2001 and 2006 were used for prediction. Even though high habitat preferences were stretching all the way to the eastern outskirts of Hardangervidda, a tendency towards more central areas remained.

5.4 Discussion

Significant differences in explained Model variance

Model results indicated significant differences in the overall explained variance depending on model type and season, with Nagelkerke’s pseudo R-square ranging from 0.045 (small-scale winter model) to 0.660 (large-scale summer model).

Differences in the explained proportions of variance between individual models reflect the varying capabilities of the applied models to separate between selected and available spatial entities (see also Barry & Elith 2006)[89]. The ability of a model to separate between theses two groups of locations is in principle dependent on systematic differences in values of the independent factors. This said, a perfect model should capture all systematic differences existing. In the real word, however, the total model variance needs not necessarily be the result of systematic processes. It may, for example, at the same time, partially be the result of an animal exhibiting random movements.

In order to evaluate the model results presented in chapter 5.3 more systematically, a schematic overview on possible factors contributing to the unexplained overall model variance is given in Figure 5-25. Six factors discussed: (i) data limitations, (ii) available vs. unused spatial entities, (iii) transition vs. selection, (iv) individual behavior, (v) movement patterns and (vi) random components.

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[89] For a comparison of type I error rates for statistical analysis of resource selection see also Bingham & Brennan (2004).

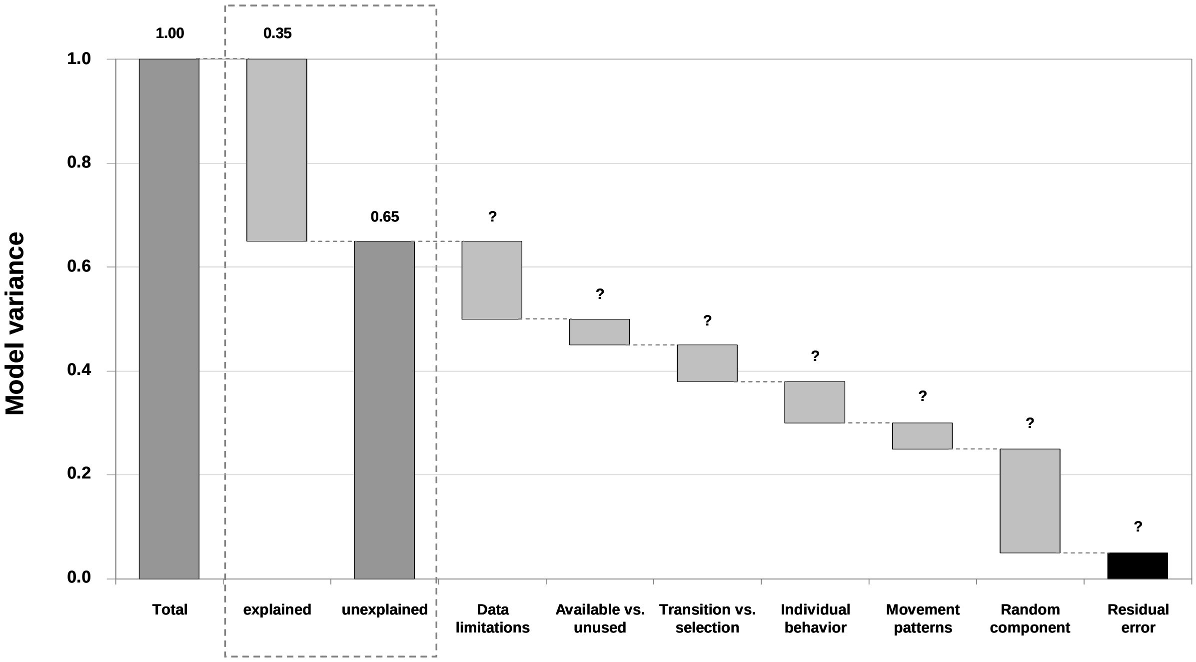

Figure 5-25: Explained vs. unexplained model variance by factors – schematic

(i) Existing systematic differences in values of independent factors between selected and available points can be hidden by incomplete data (limited spatial and/or temporal resolution, unavailability of potential factors).

(ii) Within RSF/SSF selected locations are tested against available rather than unused locations (hence available vs. unused). In consequence, a certain proportion of the available random points could indeed have been used, judged from their feature qualities. As a result, a potential overlap between available and selected locations can be assumed.

(iii) Furthermore, models are lacking behavioral information on selected locations. If a GPS fix is triggered at a location between two selected points of interest, the spatial qualities of this "transition point" are likely to conceal systematic differences between selected and available points to a certain degree.

(iv) If, as in the case of this thesis, resource selection is modeled on population level, potential differences in the functional response to independent factors between individual animals can not be recognized. Even though systematic differences between selected and available spatial entities might exist on individual level, this proportion of the total model variance will be left unexplained.

(v) Within the presented models, the influence of internal drivers of movements on reindeer habitat selection was aimed to be leveled out by controlled for the distributions of step lengths and turning angles. Both parameters were distributed equally within selected and available steps and were hence considered irrelevant. While it was possible to reduce the influence of internal movement parameters significantly by this method, not all relevant movement patterns could be captured (compare chapter 2.3).

(vi) Finally, the location of an animal can to a extant be influenced by a random component (compare chapter 2.1). Especially at smaller scales this component might become more significant.

Within chapter 5.3 two general trends in model differences have been described: Model fits are higher (i) for large-scale than for small-scale models and (ii) for the summer than for the winter/spring models. Against the above background, these trends will be discussed:

(i) The model fit for the small-scale models was considerably lower as compared to the large-scale selection models for all seasons. The discovered differences in the explained variance are assumed to reflect a fundamental shift between the proportions of active selection and random components as well as the relative importance of data limitations (see Figure 5-25). Large-scale models compare selected GPS positions against available locations, sampled within the entire home range. Discrete choice models, on the other hand, are using a case-control design, resulting in a more small-scale comparison between selected and available positions. Given these different assumptions on availability, the lower model fits for the small-scale models are likely to be caused by two effects. First, small-scale selection of locations by reindeer could demonstrate a higher proportion of randomness. Reindeer within a homogeneous landscape (characterized by considerable spatial autocorrelation between its features) can be expected to either select specific locations based on (correlated) random movements or subtle differences in external factors. For both cases the proportion of explained model variance can be expected to be lowered. In the first case, because GPS positions do not follow an active selection based on systematic differences of external factors and, in the second case, because the decisive systematic differences cannot be detected due to limitations in data.

(ii) The higher model fits for summer (as compared to winter and spring) are assumed to be largely caused by a higher relative impact of both, human disturbance and land cover. The summer results indicated human disturbance to be a predominant factor for the large-scale selection, while winter and spring were hardly affected. Land cover – on the other hand – can be interpreted as less important for winter and spring, as existing differences are leveled out, when they are covered by thick snow.

Functional response to land cover classes

The predicted differences in the selection probabilities of single land cover classes between seasons (compare chapter 5.3) seem overall plausible: Ridge vegetation yielded the highest relative selection probabilities (for all spatial and temporal scales). This can be seen as an indicator of reindeer's dependence on lichens as an important forage type, especially during winter (e.g. Klein 1968; Heggberget, Gaare & Ball 2002). This interpretation is underlined by the fact that winter models demonstrated by far the highest absolute difference between RIDGE (as the most probable vegetation type selected) and the second most probable vegetation type (LEESIDE) and is also supported by the selection for areas with high lichen biomass. The significantly increased selection probability for snowbed vegetation within the large and small-scale summer models (second most selected land cover class), strengthens the hypothesis of the high importance of this vegetation type for reindeer during summer as a major contributor of proteins, which are essential for body growth and maintenance (compare e.g. Heggberget, Gaare & Ball 2002; Reimers 1997; Barboza & Parker 2009).

The initial hypothesis of insect harassment during summer (compare e.g. Mörschel & Klein 1997; Anderson & Nilssen 1998; Hagemoen & Reimers 2002; Colman *et al.* 2003; Skarin *et al.* 2004) as a major factor determining reindeer's spatial behavior can be supported by the model results. Both classes, ROCK and SNOW, as potential refugia for reindeer during warm and calm weather conditions in summer (high elevation, wind exposed) were highly selected for by reindeer within the summer models (both spatial scales) and demonstrated a profound interaction with daytime (higher selection probabilities during midday). While ROCK also depicted high relative selection probabilities as it constitutes a significant proportion of land cover within the study area (compare chapter 3.3), selection for SNOW was foremost visible within the beta values, as this class only accounted for a minor proportion of land cover (~1% of study area). An over proportional selection of these land cover classes during midday in summer can also (partially) explain the opposite interaction effects with daytime for most of the other classes (especially RIDGE and LEESIDE).

The relative stability between the large- and small-scale selection models in all seasons can be seen as an indicator for the robustness of the models. Despite the above argumentation for Landsat as a suitable compromise between decisive parameters within this thesis (compare chapter 5.2) a spatial resolution of 30 m can be regarded as a potentially limiting factor within the study area characterized by small-scale mountainous vegetation. Higher resolution data should therefore be tested. An activity-based evaluation of land cover selection is expected to further increase the predictive qualities of land cover within habitat models.

Functional response to lichens

The differences in lichen volume selection between the spatial and temporal scales (see chapter 5.3) supports the increased importance of lichen volume during winter as mentioned in numerous studies (e.g. Klein 1968; Gaare 1968; Gaare & Skogland 1975; Heggberget, Gaare & Ball 2002; Joly, Chapin III & Klein 2010). While during calving and summer a positive impact of high lichen volumes on the selection probabilities is only visible at the smaller scale, the selection in winter seems clearly influenced by the abundance of lichens at the larger scale, also. In contrast to this, during calving and summer, lichen volume does not seem to drive the large-scale habitat selection, as optima do not significantly differ from the average values of the available habitats. At a small-scale the selection for lichen volume by reindeer seems to favor higher lichen volumes as compared to the selection at large-scale (in all seasons). This suggests a higher importance of lichens in a small-scale perspective, in that animals are selecting for lichens as part of their foraging strategy within (larger) areas, which potentially have been selected for other reasons (e.g. absence of human disturbance during summer).

The overall factor importance of lichen volume is expected to be underestimated by the models: First, like for all the land cover classes, the lack in spatial resolution is likely to account for a reduced recognition. Second, and possibly more important, behavioral aspects of reindeer are not accounted for within the models (see also Sutherland 1998). While lichen volume might yield a higher relative factor relevance for foraging, indeed, this might partly be concealed by the selection for non-ridge land cover types triggered by other behavioral needs (e.g. resting/ruminating). Hence, to further increase the explained model variance, modeling approaches incorporating behavioral aspects are expected to be beneficial.

Functional response to terrain related factors

As shown in chapter 5.3, the selection patterns for elevation at a larger scale were all found to depend on both, temperature and wind speed. In all seasons elevation optima were significantly higher within warmer weather and lower wind speeds, especially during summer and winter. For summer this results can be explained as a strategy to avoid insect harassment through selecting higher, wind exposed areas during the most critical weather situations (e.g. Coleman *et al.* 2001, 2003; Weladji *et al.* 2003), while selecting for fresh, protein rich herbs and graminoids, found in lower parts of the terrain, whenever possible (Coleman *et al.* 2001, 2003). During winter, the observed selection patterns are interpreted as an optimization strategy to trade-off between energy intake at higher and lichen rich ridges whenever possible (warmer, calmer weather conditions) and energy expenditure, which is increasing in harsher conditions (low temperatures and high wind speeds). The selection of higher elevations thus seems plausible for both, summer (insect harassment and possibly disturbance) and winter (forage availability). While selection during calving shows similar, yet not as prominent interaction patterns with temperature and wind speed (possibly to be interpreted as energy trade-offs), reindeer here selected for lower elevations during all weather types at a larger scale. However, on a smaller scale, the animals during this period selected for the highest patches in the used large-scale areas. This might be caused by the steep and rugged terrain found in the reindeer calving grounds of Hardangervidda (Skogland 1984a), enabling animals to seek refuge within higher and rocky terrain in a small-scale perspective, while at the same time being able to stay within the vicinity of the early green-up wave starting in the lower parts of the same area. In contrast, the small-scale selection during summer does not significantly differ from the large-scale selection. During winter the selection for the highest available patches could be explained by reindeer's dependence on lichen ridges during this time period (Heggberget, Gaare & Ball 2002; Gaare 1968; Gaare & Skogland 1975). The absence of significant interaction terms in all small-scale models (both, temperature and wind speed) is assumed to be caused by the smaller variation in elevations at this scale.

The large-scale selection for above average slopes (local optima centered on ~20 deg) during all seasons can be interpreted as a preference of reindeer to choose curved terrain possibly for both, foraging and shelter seeking (e.g. during rumination). This tendency is more profound during summer and calving, and is less visible in winter. This is assumed to be caused by the landscape characteristics of the study area (a more undulating terrain in the eastern areas, which are used as winter habitats). As shown in the results, reindeer's selection towards steeper slops during summer was even more profound in a small-scale perspective. This seems in line with the hypothesis of reindeer selecting steeper terrain for insect relieve and the hypothesis that reindeer avoid human disturbance through seeking refuge in higher, less accessible terrain (e.g. Hagemoen & Reimers 2002; Anderson & Nilssen 1998; Skarin *et al.* 2004). The small-scale selection for below average slopes during winter could, on the other hand, very well be explained by reindeer foraging on the flat, upper most surfaces of lichen ridge communities.

As shown in the results, the used index for the energy costs of movement (ENERGYCOST) proved to be significant, and suggested that reindeer prefer steps with low standard deviations of elevation (negative exponential selection functions) in all models. This can indeed be interpreted as a locomotion strategy to minimize energy expenditure (Parker, Robbins & Hanley 1984) and similar results have been described for ungulates by other authors (e.g. Ganskopp, Cruz & Johnson 2000; Leblond, Dussault & Ouellet 2010; Frair *et al.* 2005). Even though the above tendency holds true for all spatial and temporal scales, the results are assumed to partially reflect inherent model imperfections: First, the faster drop of the relative selection probabilities in summer (as compared to winter and calving) is likely to be influenced by systematic differences in average step length during this season (see also chapter 2.3). Even though it can be shown that the standard deviation of elevation is theoretically independent of step length, the underlying straight-line assumption bridging two positions seems less valid, when the average step length increases. Second, a possible movement strategy by reindeer to follow small-scale features within the surrounding terrain, which has been discussed by authors (see e.g. White & Yousef 1978; Johnsson *et al.* 2002), is not captured within the proposed modeling approach. It might, nevertheless, be dependent on season, and therefore contribute to seasonal differences in selection functions.

Reindeer’s selection of patches with differing solar radiation (RADIATION) differed significantly between seasons: Calving is characterized by a strong selection for patches receiving above average solar radiation, almost throughout the entire daily cycle. This corresponds with early plant growth (photosynthesis> 6 deg. C) and seems to underline the hypothesis that there may be thermal effects associated with calving ground selection (e.g. Russell, Kofinas & Griffith 2002; Skogland 1980). Likewise, the positive selection of sun-exposed patches during winter (both in large- and small-scale models) can be regarded as a strategy to minimize energy expenditure during the harsh climate conditions of this period. Patch selection during summer, on the other hand, is much more dependent on daytime with a positive selection of areas with high solar radiation during night, but negative selection during midday. This seems to reflect a strategy to avoid insect harassment during the warmer parts of the daily cycle (e.g. Anderson & Nilssen 1998), but also optimizing for areas with higher solar radiation and thus richer plant communities during night. The similar findings for reindeer’s functional response to solar radiation between all seasons and spatial scales can be seen as an indication for the relative stability these results.

Functional response to human disturbance

The factors related to human disturbance were recognized as the single most important group of covariates in the large-scale summer model and explained a large part of the model variance between the selected and available spatial entities (compare Table 5-3). More precise, the distance to roads and tourist summer trails yielded the highest gains in AIC (see Table 5-2). Reindeer's sensitivity towards disturbance related factors is well known and has been emphasized by numerous authors, mostly assessed as single stimuli (see e.g. Wolfe, Griffith & Wolfe 2000; Reimers 2001; Strand *et al.* 1997; Mahoney & Schaefer 2002; Berntsen *et al.* 1996; Bleich *et al.* 1990; Colman, Jacobsen & Reimers 2001; May *et al.* 2006; Rowland *et al.* 2000 or Côté 1996). This sensitivity seems to be clearly underlined by the large-scale summer model results.

Even though the negative functional response to human disturbance is also visible in the summer models at small scale, the contribution to the explained model variance is dramatically lower (compare both, Table 5-2 and Table 5-3). Three possible explanations for this are discussed:

(i) First, the large-scale habitat selection in summer could be driven by factors that spatially correlate with the absence of human disturbance, such as vegetation, terrain or other. However, the large-scale model results do not give any valid indication on such underlying factors. Furthermore, the exclusion of the disturbance related factors in the summer simulation model suggested significantly more areas as suitable summer habitats (see chapter 5.3).

(ii) Second, natural barriers and/or edge effects (e.g. Ries *et al.* 2004 and Woodroffe & Ginsberg 1998) could account for some of the explanatory power, which was allocated to the human disturbance related factors in the large-scale summer model. This is if these barriers/edge effects spatially correlate with human disturbance. A visual analysis of the population densities during summer[90], indeed, seems to suggest the valley of Kvennedalen to act as a possible natural barrier in that sense (compare Map 5-10).

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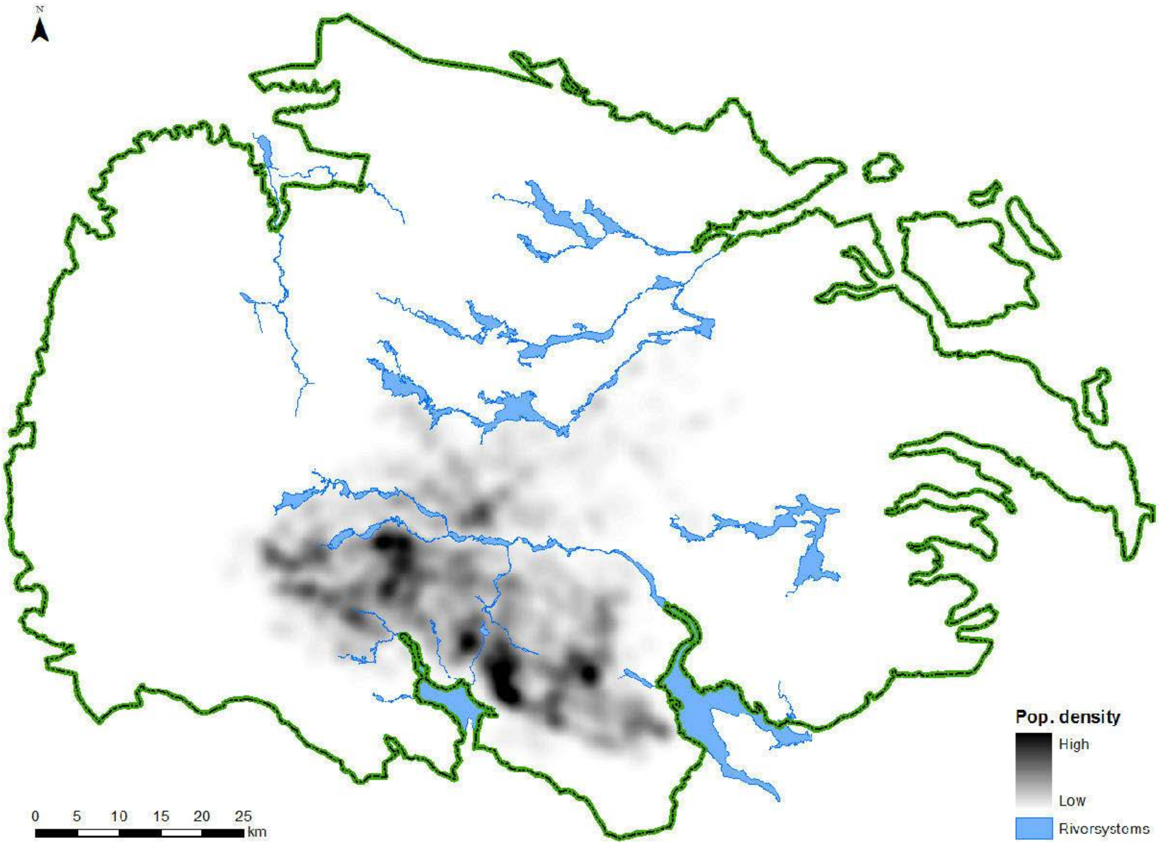
[90] Derived from summer GPS-data using kernel estimates within ArcGIS (ESRI 2005).



Map 5-10: Reindeer population densities during summer in relation to natural barrier systems

(iii) Third, the influence of the human disturbance related factors could be underestimated in the small-scale summer model, as both the selected and available positions are far away from possible sources of human disturbance. In other words: if reindeer already optimized their large-scale selection of summer habitat based on the avoidance of human disturbance (DROAD, DTRAIL), these factors are no longer recognized as important for reindeer's small-scale selection. Both, the second and third explanation, are assumed to partially account for the differences in the relative factor importance between the spatial scales in summer.

While distance to private cabins (DCABIN^{Private}) was still significant in the large-scale summer model (but with a minor relative factor contribution), distance to tourist cabins was not. This seems plausible due to the high correlation of this factor with the tourist summer trails. Since these trails yielded higher single explanatory power, DCABIN^{TOURIST} was not recognized as a significant factor by the summer models.

As for summer, distance to roads was also a significant factor in the large-scale winter model, but with a significantly lower factor contribution. Marked ski trails, however, were not recognized as significant by the winter models, which is probably due to the very low intensity of use[91]. Distance to private cabins was significant also in winter at a larger scale (but with minor importance).

The models recognized no significant factor related to human disturbance for the calving season. This seems plausible, as first the traditional calving grounds within the central and western parts of the study are remote and far from any source of disturbance, and second human utilization of Hardangervidda during the calving period is very low.

Three findings seem most important for reindeer's functional response to human disturbance:

(i) First, disturbance statistically does have a predominant impact on the summer habitat selection of reindeer in Hardangervidda at a smaller scale, but further investigation is recommended. This, since the selection results at small scale differ from large-scale model results, and the impact of natural barrier systems has not been included in the models.

(ii) Second, further research on a better alignment between the human use of Hardangervidda and reindeer habitat requirements is needed. Results of the simulation models leveling out human disturbance related factors (see Map 5-6: Estimated large-scale habitat preference (suitability) in summer and winter with/without human disturbance) suggest to focus recreational use during summer more on the eastern parts of Hardangervidda and on the western parts during winter.

(iii) Third, GPS data suggest an existing barrier effect of Rv7 in the north and Rv55 in the south of Hardangervidda. Only one crossing was registered within the entire study period and for all individuals, even though the simulation models, which controlled for human disturbance, suggested good habitat values, especially north of Rv7, both, during winter (north eastern parts) and summer (south of Hardangerjøkull). As noted earlier, historic migration routes of reindeer included both, the Nordfjella area north of Rv7 and the area of Setesdal-Ryfylke south of Rv55 (see Map 1-7). A reestablishment of these former migration routes is considered helpful for the long-term conservation of wild reindeer in Hardangervidda, since it allows for enlarged genetic diversity (Fahrig 1997, 2003) and reduces the population vulnerability in extreme stochastic weather events (snow and surface icing) (Skogland 1994b; Fryxell, Greever & Sinclair 1988). Further research on the effects of mitigation measures is needed, though.

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[91] Because of its remoteness, recreational skiing in the core areas of Hardangervidda is limited and assumed to be relevant only during the Easter period. Since spatially explicit information on skiing in the study area is scare, further data is needed for a deeper analysis.

Functional response to snow

Snow conditions play an important role in reindeer’s (winter) habitat selection (e.g. Skogland 1978; Fancy & White 1985; Collins & Smith 1991). The results of the large- and small-scale winter models support this: The relative selection probabilities are significantly higher for non or little snow-covered patches, with the highest sensitivity centered on 1 m to 1.5 m, beyond which reindeer are not able to crater for forage (see Pruitt 1959; Bergerud 1974c; LaPerriere & Lent 1977; Skogland 1978; Helle 1984; Thing 1984; Adamczewski *et al.* 1988; Brown & Theberge 1990). But while the relative factor importance in the large-scale model is rather high, the factor contribution to the explained model variance is only minor in the small-scale model (see Table 5-2 and Table 5-3). It can thereby be followed that the selection of the winter areas is a large-scale rather than a small-scale decision.

In contrast to the winter models, during calving the large-scale selection optimum for snow depth is predicted at app. 4 m, while patches with as little as possible snow-cover were selected at a smaller scale. This selection for high snow depth areas on a larger scale can be interpreted as a positive correlation between snow depth and rugged terrain in the western parts of Hardangervidda, where animals also can select for shelter and vicinity to protein rich herb and graminoid stands.

Overall, the factor contribution of the snow condition is assumed to be significantly underestimated, not only in the small-scale, but also in the large-scale models. For this potential underestimation three possible reasons are discussed:

(i) First, available data quality is poor. Both, the current spatial resolution of 1 sqkm and the uncertainty of the underling models, resulting from a limited number of weather stations at the outskirts of the study area (Meteorologisk institutt 2007), clearly represent a serious limitation, especially for the small-scale selection models.

(ii) Second, the temporal resolution of snow depth, as used in selection models, is unsatisfactory, since only average values within the empirical sub seasons could be used (and not real hourly values for the corresponding GPS fixes).

(iii) Third, snow condition as the underlying factor is only partially described by SNOWDEPTH. Information on the surface quality for the study area is currently unavailable, yet important, for many authors stress its relevance for reindeer’s cratering possibility (e.g. Kohler & Aanes 2004; Stien *et al.* 2010; Chan *et al.* 2005; Skogland 1978).

Summing up, data resolution, temporal scale and information on surface quality are assumed to hold a potential for further increasing the explanatory power of snow conditions, especially in the small-scale selection models. In this context, a snow-pack model developed by Kohler & Aanes (2004) to assess the effects of winter snow and ground-icing on a Svalbard reindeer population, which is based on precipitation and temperature as input factors only, could proof beneficial[92]. Also the results from the snow simulation models give a strong indication that alterations in precipitation during winter could seriously affect the availability of winter pastures (see Map 5-7: Estimated large-scale habitat preference (suitability) during winter: average snow depth). Together with a hypothesized increase of surface icing (due to more frequent thawing/freezing-cycles in early winter) the stochastic vulnerability of the Hardangervidda reindeer population could increase significantly. Given that, reindeer's ability to cope with such situations will depend even more on the access to undisturbed winter habitats. More research is clearly needed on this topic.

Functional response to wind direction

A clear tendency of reindeer to move against the direction of the wind was visible at all spatial and temporal scales. One of the possible underlying factors for this observation might be an early perception of predators (Reimers *et al.* 2006; Baskin & Skogland 1997). As a second factor an increased olfactory sensitivity for detecting preferred vegetation species may be a possible contributor to the observed movement strategy, since reindeer's olfactory sensing of forage species has been described by authors (Bergerud & Nolan 1970; LaPerriere, A. J. & Lent, P. C. 1977; Hansen, Aanes & Sæther 2010).

While the interaction with daytime is fairly limited during winter and calving (with only minor peaks in movement tendency against wind direction for midday), the selection peaks in summer are significantly larger, but within the same daytime. Two underlying factors for this finding are discussed:

(i) The first effect is a technical one: Since during midday reindeer tend to move more (higher mean step length during the active part of the day)[93], pseudo movements resulting from resting or ruminating (but still detected by GPS-sensors due to marginal location differences or localization errors) are reduced. As these pseudo movements are associated with random directions, which are independent of the wind direction, the effect of reindeer moving against

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[92] For estimating the spatial distribution of snow in mountainous terrain see also Cline, Bales & Dozier (1998).

[93] Compare Figure 5-8: Frequency distribution of step length for GPS-data over all individuals and seasons by daytime.

the wind becomes more apparent. In other word: the inherent tendency of reindeer to move against the wind is less blurred.

(ii) Second, moving against the wind is also likely to reduce insect harassment, especially during the warmer parts of the day in summer (e.g. Mörschel 1999; White *et al.* 1981).

Altogether MOVEWIND accounts for a significant but limited amount of the overall model variance, constant between the two spatial scales (see Table 5-2 and Table 5-3). Again, data limitations are probably contributing to a potential underestimation of the factor importance:

(i) First, weather stations in Hardangervidda recording wind direction are scare and spatial resolution thus is limited (see chapter 5.2). As wind related parameters are only recorded three times a day the temporal resolution is coarse, also. In consequence, the estimated wind direction at a given GPS position is rather uncertain and changing wind directions during the day or effects of micro climates can not be captured appropriately.

(ii) Second, the potential effects of wind direction on reindeer's movement patterns are again masked by pseudo movements (see above) and within low wind speed situations, where the wind direction might shift or not be noticeable for reindeer.

Large-scale vs. small-scale selection

Different spatial scales as used within this thesis can provide valuable insights for reindeer habitat use or, more generally, habitat use by animals. First, and foremost, such differences in functional response can directly deliver information on relative importance of and functional response towards single factors, such as land cover or terrain. In this regard, it could be shown that hierarchal decisions for spatial behavior of reindeer have to be assumed. This supports results both, from other studies (e.g. Johnson *et al.* 2002; Johnson, Seip & Boyce 2004; Mårell & Edenius 2006) and different species (e.g. Boyce *et al.* 2003; Meyer & Thuiller 2006; Boyce 2006).

Second, differences between spatial scales can be traced back to and/or deliver indications on data insufficiencies or imperfect model definition. SNOWDEPTH, as argued above, is clearly an example for this. Generally it can be stated that small-scale selection models based on discrete choice models clearly suffer more of data quality, as their selected and available spatial entities, in contrast to large-scale selection models based on logistic regression, often only demonstrate little differences in factor values. This problem is even enhanced, when fix rates of GPS positions become more frequent (e.g. 15 min intervals instead of 3h intervals, as used within this approach). Hence, it can be followed that demands concerning data quality pose a serious limitation on small-scale selection models.

Finally, following the theoretical model for contributors to overall model variance (compare Figure 5-25) it seems likely that random components within small-scale selection models do play a significantly larger role as compared to large-scale models. First, reindeer movements at a small-scale might increasingly follow random walk theory (see e.g. Reynolds 2005), which clearly can be rejected for large-scale habitat selection (compare chapter 2.3). Second, as models are based on comparison between selected and available (not unused!) spatial entities, the likelihood of sampling entities as available that indeed could have been selected, simply increases due to spatial autocorrelation. Both random components are expected to decrease the explained model variance.

Density dependence of functional responses

Reindeer's functional response to single factors as discussed above has been the result of models using data sampled at a specific reindeer density. It has been argued that the current reindeer density within Hardangervidda of app. 8,000 animals represents a rather low density when compared to longer timelines (compare chapter 1.3). Against this background it is important to note that reindeer's functional responses to single factors, such as distance to roads, trails or other disturbance related factors, might not be independent of population density (see also McLoughlin 2010; Morris 1987).

Historical data suggests e.g. that reindeer utilized most of the eastern outskirt of the study area during winter within a high-density period (Skogland 1989a, 1990a). Analogue historical evidence of migration between Hardangervidda and Nordfjella/Setesdal-Ryfylke has been presented for a high-density period (Strand *et al.* 2010). On the other hand, human disturbance related factors clearly did increase since high-density periods within Hardangervidda 20 years ago. It can thereby be argued that statements concerning density dependent behavior of reindeer to human disturbance related factors are difficult to derive, since both, the density and level of disturbance, changed within the relevant period. Low-density findings as presented within this thesis should hence be compared to habitat selection profiles at a high-density situation in the future.

Conclusion

The presented assessment of reindeer habitat selection in Hardangervidda comprehensively addressed temporal and spatial scales using six alternative models: Large-scale (LR) vs. small-scale selection (DCM) for three temporal scales (summer, winter, calving). The selection of step and point-based spatial domains for independent variables allowed for increased flexibility in variable selection (e.g. movement related factors like chosen direction relative to wind or standard deviation of terrain covered by chosen step). Complete model definition included six different factor groups (land cover, lichen volume, terrain, disturbance, snow depth and wind direction). Robust sandwich estimators were used to account for spatial autocorrelation where necessary. Estimated model coefficients allowed for later testing of the spatial impact of altered levels of both, human disturbance and winter snow coverage.

While reindeer's functional responses to individual factors can be described and compared rather well between different model types, there is no 'definite' answer to relative importance of factors as well as overall goodness of fit as both are depending on model type; used surrogates (Nagelkerke's pseudo R-square for overall proportion of explained model variance and average change in pseudo R-square resulting from forward/backward-selection of factors to assess their relative importance) therefore remain proxies. The distribution of the unexplained proportion of model variance on possible factors remains unanswered within the applied models; three possible improvements have been identified to account for currently undiscovered variance: First, data limitations, especially for small-scale selection models (snow depth, surface condition, resolution of DEM/derivates, land cover and lichen biomass maps, etc.) have to be reduced. Second, behavior of reindeer should be included in models through field observation/parameter recording. Third, individual differences in functional response to factors should be tested comprehensively through mixed effects models (e.g. Gillies *et al.* 2006; May 2007; Bennington & Thayne 1994), assuming technical feasibility. Currently the large data sizes of models restrict testing of mixed effects models to random effects for intercept and slopes for a single factor only (see also Chen & Kuo 2001); simultaneous assessment of individual responses to all possible independent factors proved to be not feasible. Finally, density dependence of reindeer habitat selection in Hardangervidda calls for later comparison of model findings within a high-density situation.

6 General results and discussion

6.1 Summary of results

Seasonal distributions and movement patterns

28 wild, female reindeer (*Rangifer t. tarandus*) were equipped with global positioning system collars (GPS) in Hardangervidda, Norway, to analyze their seasonal distributions and movement patterns. In order to define relevant seasons empirically, linear regression with floating cutoff-points for net squared displacements (NSQD) were used within correlated random walk (CRW) models. For the identified sub-annual periods, reindeer's spatial distributions and movement patterns were compared. In order to characterize seasonal movement patterns, a four dimensional approach was proposed, incorporating results from CRW models, fractal analysis, size/inter-annual stability of seasonal home ranges and activity level as parameters.

Based on the results of the above movement parameters, it was decided to merge the 13 identified sub-seasonal periods into eight relevant seasons. Among those, summer, winter and calving were separated furthest from another, whilst the remaining seasons (migration, rut, hunt, pre/post calving and early summer) were characterized by more intermediate values.

Movement patterns differed significantly between the identified seasons: Summer periods were characterized by high activity levels in combination with low fractal dimensions and over prediction from CRW, indicating irregular movements and site fidelity. Home ranges during summer were very stable between years and showed a high concentration of reindeer in a relatively small area in south-central Hardangervidda. In contrast to this, movements were found to be regular and directed during winter, indicated by low fractal dimensions and significant under prediction from CRW. Winter home ranges covered large areas of eastern and central Hardangervidda, with a distinct variation between years. Activity levels were significantly lower during winter as compared to during summer. Similar to winter, reindeer showed little activity during calving. But in contrast to winter, here high fractal dimensions together with significant over prediction from CRW models were found, indicating irregular movements and site fidelity. Activity level during calving was significantly lower as compared to summer and the seasonal home ranges showed high levels of inter-year variability.

Regular, directed movements characterized the migration periods (spring and autumn) and here activity levels were limited (as compared to summer). Home ranges during the migration periods were rather large and showed intermediate stability between years. During hunting reindeer used very large areas and showed both, high activity levels and regular movements.

For the rutting season activity levels were found to be low. Movements were rather regular and directed within intermediate size home ranges, which showed little stability between years. Pre\post calving and early summer could be characterized as transition periods between calving and summer/migration, respectively. Here, intermediate values were found for most of the selected movement pattern attributes.

Land cover classification

Land cover composes a core input factor for modeling reindeer habitat selection. To test for selection and avoidance of land cover, eight specific classes were defined and a satellite-based land cover classification was carried out, using Landsat TM imagery. Classification accuracies were compared for three selected parametric (ML) and non-parametric (kNN, decision tree) classifiers, with and without ancillary data. This data (relative elevation and snow cover in early summer) was used to define four relevant subsets (homogeneous sub-areas), for which prior probabilities for classification were adjusted, based on the sub-area specific distributions of training data. Finally, topographical data (slope, elevation, and other) was used as additional data (second order ancillary data) to refine classification results via post-classification rules.

Overall, k-nearest neighbor classification (kNN) showed superior results (total classification accuracy of ~80 percent; kappa value of 0.75) as compared to decision tree (~73 percent; kappa: 0.67) and maximum likelihood classifier (~71 percent; kappa: 0.65). Ancillary data proved to raise classification accuracy significantly for all tested classifiers with an average gain of four to five percentage-points. For the kNN-classifier using ancillary data, the best class accuracies were found for SNOW, WATER and ROCK (average user’s/builder’s accuracies ranging between ~90 to 100 percent). RIDGE, LEESIDE and FOREST all showed average user’s/builder’s accuracies around ~78 percent, while SNOWBED and MIRE experienced lowest accuracies (~67 to 73 percent). While being significantly lower in total, decision tree and maximum likelihood classifiers showed a comparable ranking of classes with respect to average user’s/builder’s accuracies.

Nearly all classes benefited from the use of ancillary data, but significant differences in absolute gains were found between classes. Analysis of confusion matrices for the tested classifiers revealed significantly less confusion between snowbed- and ridge-vegetation, gaining ~9 to 12 (SNOWBED) and ~5 to 8 (RIDGE) percentage points, depending on classifier. In average, also FOREST, ROCK and LEESIDE could gain significantly from ancillary data, while

SNOW and WATER already showed very high class accuracies without the additional data. In contrast to other classes, implementation of ancillary data lead to a slight reduction in average user’s/builder’s accuracy for MIRE.

The predicted distribution of land cover classes from the kNN classifier was found to be overall in line with the assumptions on prior probabilities, derived from other studies. With an estimated distribution of ~26 and ~23 percent RIDGE and LEESIDE were found to be the most frequent land cover classes within the study area. Both, SNOWBED (~17 percent) and ROCK (~11 percent), followed a distinct east-west gradient, while WATER (~9 percent) and MIRE (~7 percent) were equally distributed across Hardangervidda. FOREST accounted for ~5 percent of the terrain, located mostly in the lower areas at the edges of the study area. Hardangerjøkull accounted for the majority of perennial SNOW (~1 percent), while the remaining part of this class was mostly located in the higher western areas.

Estimation of lichen biomass

Lichen ridges are known to hold the most important winter pastures for reindeer. Landsat TM imagery was used to quantify and map lichen biomass in Hardangervidda. A new Lichen Volume Estimator (LVE) was proposed to predict lichen volume from a two-dimensional Gaussian regression model using the Normalized Difference Lichen Index (NDLI) and the Normalized Difference Moisture Index (NDMI) as factors. A 10-fold cross validation procedure indicated a sufficient prediction accuracy for lichen volume within ridge vegetation (adjusted R-square of ~70 percent) and stable estimates of parameters.

Significant differences in the current distribution of lichen volume were found, ranging from less than 5 liters of lichen per square meter in the more western and central areas of Hardangervidda to more than 30 liters per square meter at its eastern borders. Lichen volume seemed to correlate negatively with altitude and positively with eastern longitudes. Especially the exceptional high lichen volumes in the north-eastern parts of Hardangervidda (and within the habitat fragments) as well as the low lichen volumes in the (south)-central areas could be an effect of the spatially differing grazing pressure caused by cumulated human disturbance.

Habitat selection models

Logistic regression and discrete choice models were used to estimate reindeer's large- and small-scale habitat selection in Hardangervidda, Norway, during summer, winter and calving. While all tested models proved highly significant, distinct differences in explained variance, significance of factors, their relative importance and reindeer's functional response to those factors were found, depending on model type and season.

In general, the explained model variance was always higher for large- than for small-scale models. Relative factor importance revealed a predominant impact of human disturbance for large-scale habitat selection during summer. While still significant during large-scale winter selection, small-scale habitat selection was only little affected by human disturbance. Land cover and terrain related factors proved to be of major importance, with higher values during summer and in the large-scale selection models. While lichen volume contributed significantly to the explained variance in the large-scale models, small-scale selection seemed little affected. Snow depth could improve the large-scale winter and calving models substantially, while the small-scale models could not benefit to a larger extent. Movement relative to wind direction could improve the small and large-scale models significantly, but not substantially.

Analysis of reindeer's functional response to land cover type revealed highest relative probabilities for the selection of ridges for all model types and seasons, especially during winter. During summer reindeer selected for snowbed vegetation significantly more as compared to during winter and calving. Small- and large-scale selection of rocks and snow patches were positive during summer and showed a significant interaction with daytime (highest relative probabilities during midday).

deer exhibited non-linear selection functions for lichen volume in all model types and seasons. Their selection optima were highest in winter, especially in a small-scale perspective, where reindeer selected almost for the highest available lichen volumes within their vicinity. While reindeer selected areas with about average lichen volumes during summer and calving on larger scales, they still selected above average lichen volumes on a small-scale level.

Significant responses by reindeer to several terrain related external factors were found: In general, reindeer selected for above average elevations at all spatial scales and during all seasons. At large-scale, significant interaction was found between elevation and temperature as well as wind speed, indicating selection for higher elevation when temperature was high and wind speed low. Towards slopes reindeer showed non-linear responses during all seasons and at all spatial scales, with a general selection for above averages slopes (as compared to available slopes). Selection optima were found to be significantly higher during summer than during winter. This holds especially true for small-scale selection, were during summer reindeer selected for well above average slopes, while they selected for lower than available slopes during winter. Reindeer seemed to prefer staying in steeper than average areas, especially during summer, but they selected for movements with low energy requirements in all model types and during all seasons. Reindeer’s functional response to solar radiation indicated a clear preference for above average values both, during winter and calving. During summer reindeer selected for patches with above average reception of solar radiation only during night; during daytime those patches were avoided.

In the summer models a strong avoidance of human disturbance was found. This, since relative probabilities for selection dropped significantly with declining distances to both, roads and marked tourist trails, with higher sensibility in the large-scale selection model. During large-scale winter selection roads still affected selection probabilities negative, but less severe. No significant negative effects of human disturbance were found during calving.

Reindeer were found to respond negatively to increased snow depths during winter at both spatial scales. Relative probabilities showed the highest sensitivities at app. 1.5-2 m snow depth and reached very low values beyond 3 m. During calving reindeer seemed to select for large-scale areas with above average snow depths, while optimizing for lower values on a smaller scale.

Reindeer selected for relative movement against the wind at all spatial scales and during all seasons. Interaction with daytime indicated increased tendencies to do so during daytime, especially in summer.

Habitat preferences of reindeer in Hardangervidda were calculated based on the estimated large-scale model coefficients. Profound spatial differences were found between seasons: During summer reindeer's preferred habitats were found to be strongly clustered within the south-central part of Hardangervidda. Eastern, western and northern areas showed low predicted preference values, given the current disturbance levels. During winter the predicted habitat preferences were highest within the eastern-central areas of the study area, while the western and northern areas showed significantly lower preference values. Reindeer's predicted calving areas were located in the western parts of Hardangervidda, covering rather large areas and demonstrating a profound east-west gradient.

Simulation results for different levels of disturbance indicated a major influence of this factor during summer. When disturbance was eliminated, significantly more and larger areas were predicted to be preferred, especially in the north and west. When simulating non disturbance during winter, increased preference values were estimated for the most eastern areas as well as for the north-eastern parts of Hardangervidda.

Results from snow depth simulation suggested a significant impact of this factor on reindeers winter habitat selection. Using upper (lower) bound values for snow depth (from the investigation period 2001 to 2006), instead of average values, significantly shifted the distribution of the predicted preferred winter habitat towards more eastern (western) areas.

6.2 General discussion and conclusion

Presented results can contribute to a better understanding of reindeer habitat use

Within this thesis a method was presented for getting a better understanding of reindeers seasonal habitat use within Hardangervidda, Norway, structured within five sets of questions (research interests) as described within the general introduction (see chapter 1.2 Aims of the thesis):

Within chapter 2 (Seasonal distributions and movement patterns) spatial patterns of the current distribution of wild reindeer in the study area were described with respect to seasons. A method has been presented to detect and define annual sub-seasons empirically, based on floating cut-off points within CRW models. Reindeer could be shown to perform migrations between seasonal home ranges and underlying movement patterns were described and quantified using multiple parameters (directionality and regularity of movement, activity level and size/stability of seasonal home range). Significant seasonal differences within movement patterns could be detected and were related to (potential) underlying factors (climate, differences in spatial distribution of resources between seasons, disturbance and social behavior of reindeer).

Based on the results of seasonal distributions and movement patterns, three core seasons (summer, winter, calving) were singled out in chapter 5. Reindeer habitat selection could be described as specific functional responses by reindeer towards six significant factor groups (land cover, lichen volume, terrain, disturbance, snow depth and wind direction). To address the impact of scale, two sets of models were defined (large vs. small-scale selection using LR and DCM respectively). The relative importance of the single factors (including differences within model types) were estimated and discussed in relation to reindeer’s biology. Based on the estimated factor coefficients of the large-scale models, habitat preference maps were calculated for the selected seasons to get a better understanding of which resources are used and which potential resources are unused. Simulation models of both, cumulated human disturbance and snow conditions, were used to illustrate the effect of these two factors. A profound influence of cumulated human disturbance and snow conditions on reindeer's seasonal habitat selection could be shown.

As a prerequisite for model definition within chapter 3 (Land cover classification) a method for land cover classification within a mountainous area was proposed, based on Landsat imagery and ancillary data (DEM and derivates, images from different seasons). Relevant land cover classes for resource selection of wild reindeer within the study area were defined and their spatial distribution was mapped. Methodologically, the kNN classifier could be shown to yield superior results for vegetation classification within the study area as compared to others (ML, decision tree). Ancillary data significantly improved classification accuracy for all tested classifiers and the vast majority of classes.

Information on lichen biomass was essential for a full model definition within resource selection functions. More specific, a lichen biomass map was needed as a basis for modeling habitat selection and for a possible later change detection of grazing pressure within the winter pastures of the study area. This was addressed within chapter 4 (Estimation of lichen biomass): The current status of lichen biomass in Hardangervidda and its spatial distribution could be modeled. Furthermore, the potential relationship between this distribution and the spatial distribution of reindeer within the study area could be worked out.

Methodologically it was discussed, to what extent the applied empirical models (CRW, fractal dimension, LR, DCM, kNN, decision tree, ML, utilization of ancillary data, two-dimensional Gaussian curve estimate for lichen biomass) can help to describe and explain the habitat use of wild reindeer. Their robustness has been reviewed and inherent strengths and weaknesses have been demonstrated, possible improvements were addressed.

Clustered summer distribution likely to be influenced by human disturbance

As shown within chapter 2.3, reindeer distribution during summer is clustered within a remarkably small area within the south-central parts of Hardangervidda and is very stable between the single years of the study period (2001 to 2006). Even though it has been discussed that natural barriers might explain this clustering to some extent (see chapter 2.4), results from large-scale summer selection models gave clear indications that human disturbance is a major contributing factor for this clustering (see chapter 5.3) and results from disturbance simulation models during summer could illustrate the impact (see chapter 5.3).

In this study land cover was classified into eight different classes (compare chapter 3), some of which (RIDGE) are associated with winter pastures, some as summer pastures (SNOWBED), but no classification results based on the same method exist for other reindeer areas, yet. A comparative study with other reindeer areas within southern Norway characterizes Hardangervidda to yield a relative abundance on summer pastures (Jordhøy *et al.* 1996). According to this study, Hardangervidda demonstrates a well above average percentage of summer pastures (app. 38%), while areas like Rondane or Snøhetta reached significantly lower values (app. 27%). In contrast, (potential) winter pastures within Hardangervidda have been described as relatively scares (app. 15% vs. 35% in Forollhogna and Rondane or even 40% in Knutshø). Even though the results from the comparative study differ (app. 15% winter pastures vs. app. 23% RIDGE in this study), it might thereby be argued that summer pastures are unlikely to be the limiting factor for Hardangervidda’s carrying capacity.

Nevertheless, clustering during summer could be problematic, as the proportion of summer pastures cited above only reflects potential habitats. If, as both, distribution results and model findings, suggest (see chapters 2.3 and 5.3 respectively), only a small percentage of the potential summer pastures is actually utilized, two possible conclusions can be derived: Summer pastures could be so abundant that clustering within the south-central part of the study area could be sufficient for reindeer’s gain in body mass during summer and hence be sustainable at the current population level. Alternatively, reindeer could already compromise on energy intake during summer due to a suboptimal trade-off with avoidance of disturbance[94]. To conclude between these two possibilities, slaughter weight of animals during hunt can deliver further insights: Data suggest Hardangervidda reindeer to yield relatively low (yet improving) sex and age specific values when compared to other reindeer areas like Knutshø and Rondane (Solberg *et al.* 2010). On the other hand, data does not give an indication whether this is due to a relative shortage of winter pastures or a lower gain during summer month, possibly triggered by cumulated human disturbance.

Concluding these findings, clustering during summer clearly is remarkable, but it should also be considered that reindeer's functional response to human disturbance was detected by the models at a low-density situation (see also McLoughlin *et al.* 2010) and should be repeated at a high-density level or be compared to other reindeer areas (see below). It is therefore argued, that clustering during summer is unlikely to constitute a serious threat for the conservation of

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[94] Also note that Gill, Norris & Sutherland (2001) have shown that avoidance of disturbance need not reflect the population-level consequences as the number of animals within a habitat is not only dependent on the fitness costs of human disturbance but also on the availability of alternative habitats.

reindeer in Hardangervidda at the current stage. However, further research is needed in order to increase the knowledge about the contributions of relatively low proportions of winter pastures and avoidance of potential summer pastures for the below average body conditions of Hardangervidda reindeer, indicated by slaughter weight.

Fragmentation/migration barriers and climate change are long-term threats for conservation of wild reindeer in Hardangervidda and Norway

Even though a targeted population size of 10,000 animals seems sustainable at present, two long-term threats for conservation of wild reindeer in Hardangervidda can be derived from seasonal distributions and model results: First, clear indications on both, fragmentation within habitat and reduced connectivity between habitats, can be derived from the data. Second, snow conditions do play a significant role in winter habitat selection with potential effects of climate change currently not fully understood (Turunen *et al.* 2009; Stien *et al.* 2010; Aanes *et al.* 2002; Weladji & Holand 2006; Weladji *et al.* 2002; Arctic Climate Impact Assessment 2004).

Indications for habitat fragmentation caused by anthropogenic factors were presented in chapter 2.3 (no migration to neighboring reindeer areas found in GPS-data) and in chapter 5.3 (strong negative functional response to human during summer). While the lichen biomass model predicted the highest values within the eastern edges of Hardangervidda (especially within the north eastern habitat islands) (see Map 4-2), and the relative selection probabilities within the small- and large-scale models increased significantly with higher lichen biomass (see Figure 5-14), the observed reindeer distributions during winter did not include the eastern most areas (see Figure 2-7). Furthermore, the predicted habitat preferences of these areas where reduced (see Map 5-4), even though they yielded the highest predicted lichen volumes. When disturbance related factors were eliminated within the simulation models, a significant eastward shift of potential winter habitats became apparent (see Map 5-6).

GPS-data suggested a clear boundary effect of both, Rv7 within the north and Rv55 in the south of Hardangervidda. During the entire study period (2001 to 2006), only one short crossing of Rv7 could be observed for one of the radio collard reindeer. No migration could be observed to either Setesdal-Ryfylke or Nordfjella reindeer area, while historic evidence from pitfall systems clearly suggests former connectivity of these areas (Wildhagen 1954; Vaa 2002; Jordhøy, Binns & Hoem 2005; Jordhøy 2007, 2008). As noted initially (compare chapter 1.1), hindered migration is critical in a long-term perspective for two reasons: First, a reduction in genetic diversity within smaller populations can lead to reduced survival rates (Fahrig 1997, 2003). Second, and more fundamental within the Hardangervidda context, inability to migrate as a strategy to optimize for seasonal differences in resource availability (Berger 2004; Berger, Cain & Berger 2006; Sawyer *et al.* 2009) can increase mortality rates within reindeer populations in stochastic events like surface icing (Skogland 1978; Kohler & Aanes 2004; Chan *et al.* 2005; Hansen, Aanes & Sæther 2010; Stien *et al.* 2010).

In addition to increased habitat fragmentation and/or migration barriers, alterations in snow conditions can pose a long-term threat for the conservation of wild reindeer, not only in Hardangervidda but probably equally or even more important also for other reindeer populations in southern Norway. As shown in chapter 5.3, winter distribution of reindeer is dependent on snow depth. Model results confirm this selection for lower snow depth by significantly reduced selection probabilities as snow depth increases (see Figure 5-23). It can thereby be derived that potential increases in snow depth triggered by climate change (Roald *et al.* 2003) could yield substantial consequences for reindeer's forage availability within the study area, since cratering can become more difficult (Skogland 1978; Fancy & White 1985; Collins & Smith 1991). A potential increase in surface icing due to more frequent thawing/freezing in early winter as expected by climate change (Klein 1999; Arctic Climate Impact Assessment 2004) could be even more critical for reindeer during winter, as large proportions of pastures can be locked (Skogland 1978; Kohler & Aanes 2004; Chan *et al.* 2005; Hansen, Aanes & Sæther 2010; Stien *et al.* 2010).

Finally, it has to be noted that the two long-term threats for reindeer conservation (piecemeal development of infrastructure and climate change) are likely to multiply in their consequences when induced simultaneously on a reindeer population. While both single effects can be threatening within themselves, a situation of increased stochastic risk of locked winter pastures due to altered snow conditions (snow depth, icing) together with blocked migration corridors to compensate for this increasing risk is surely even more severe.

Management implications

Results from distributions, movement patterns and habitat selection models can not only increase our theoretical knowledge of wild reindeer, but also have direct implications for management: First, potentially valuable information for population management (hunting quotas) can be derived both, from the lichen biomass model and reindeer's functional response to human disturbance. Second, a better alignment of human interferences with reindeer's needs can be suggested through more efficient mitigation measures (spatial distribution of recreational use[95], reduction of barrier effect by roads[96]).

As discussed above, the management aim to stabilize the Hardangervidda reindeer population at app. 10,000 animals can be strengthened by the study results. At present hunting quotas first and foremost are based on airborne minimum counts together with assessment of body condition (slaughter weight, jawbone measurements) of killed animals (Skogland 1990a; Strand et al. 2004; Strand, O., Andersen, R. & Jordhøy, P. 2006; Solberg *et al.* 2010). While this method can be shown to yield sufficient results within other (smaller) reindeer areas (e.g. Knutshø or Forollhogna), reindeer management within Hardangervidda suffered considerable problems due to large fluctuations (Strand, O., Andersen, R. & Jordhøy, P. 2006; Solberg *et al.* 2010). These can partially be traced back to larger uncertainties within minimum counts[97] as habitat size increases (and the chance for encountering a sufficient proportion of reindeer population decreases). More fundamentally, analysis of body weight can be skewed (due to positive selection by hunters for larger animals) (Skogland 1989a, 1990a) and be a too slow management indicator, as (winter) pastures might be significantly degenerated before the body condition is affected (Skogland 1983a, 1985a, 1986b). Against this background, monitoring of lichen volume can add valuable information for management decisions, given sufficient accuracies and timely, easy to use applications (see future prospects below).

A better (spatial) alignment of human interferences with reindeer needs has been proposed as second management implication within this thesis. Two perspectives seem relevant: First, a better alignment of recreational use with reindeer needs within Hardangervidda is essential (number and location of summer and winter trails, tourist and private cabins)[98]. Second, reestablishment of (large-scale) habitat connectivity between Hardangervidda and its neighboring reindeer areas seems desirable.

Habitat preference maps point at the western and south central areas as the best summer habitats (compare Map 5-3) and eastern areas as winter habitats (compare Map 5-4). These findings were even more profound, when human disturbance related factors were eliminated: The predicted suitable summer habitats enlarged significantly within west and north direction,

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[95] See also Whittaker & Knight (1998); Knight & Cole (1995); Boyle & Samson (1985) and Helle & Särkelä (1993) for factors that influence wildlife responses to recreationists.

[96] E.g. Spellerberg 1998 and references therein; Holschuh & Otter 2000; Iuell *et al.* 2003; Cain *et al.* 2003; McDonald & Clair 2004; Ng *et al.* 2004; Clevenger & Waltho 2005

[97] See also Strand, Solberg & Jordhøy (2003) on the potential of radio-marking as an alternative for minimum counts.

[98] See also Hagen (2002) and e.g. Duchesne, Côté & Barrette (2000) for an assessment of caribou’s response to winter ecotourism in Canada.

while winter habitats significantly shifted eastwards (compare Map 5-6). Negative functional responses to human disturbance related factors could be identified as relevant drivers of these spatial deviations (see chapter 5.3). Given the current overall level, it can thereby be derived, that human use within the study area during summer should focus more on the eastern parts of Hardangervidda, while, in contrary, winter use should preferably utilize the more western areas. In addition, the overall level of recreational use and building activity within the study area should not exceed current levels and even be reduced, especially within areas sensitive for either winter pastures (e.g. Dagali) and/or migration corridors to neighboring habitats (e.g. Imingfjell).

The lack of connectivity with adjacent reindeer areas has been identified as a major potential threat to long-term conservation of wild reindeer in Hardangervidda and southern Norway in general (see above) and, as also noted earlier, negative functional response to existing mountain road stretches (Rv7 and Rv55) is a driver for this. Management should therefore be concerned to reestablish former migration corridors between neighboring reindeer habitats and the Hardangervidda population. Sub-seasonal distributions as depicted within chapter 2.3 (compare also Figure 2-7) give strong indications on possible, efficient strategies: Clustering during summer within the south central parts of the study area make obvious to focus on migration corridors facing south (Setesdal-Ryfylke) during this time of year, while efforts reducing barrier effects of Rv7 do not seem beneficial as long as clustering remains. On the other hand, both findings from seasonal distributions during winter (compare Figure 2-7) and availability of lichen biomass (compare Map 4-2) suggest that habitat connectivity to northern and western areas should be prioritized during winter.

However, large-scale mitigation through tunnels and/or wildlife over-crossings are both, costly and uncertain in their effects (see e.g. Johnson & Todd 1977; Jordhøy & Strand 1999a/b or Ng *et al.* 2004). Even though the findings presented within this thesis support the idea of strengthening habitat connectivity through reducing barrier effects, they do not seem sufficient for (small-scale) planning and evaluation of mitigation measures. Further research is therefore needed (see below).

6.3 Future prospects

Better knowledge on small-scale effects of cumulated human disturbance needed

A discussed within chapter 5.4, reindeer's large- and small-scale functional responses to human disturbance related factors (distance to roads, trails, cabins) are similar during summer (avoidance), yet the relative factor importance is significantly lower within the small-scale model. At the same time, clustering during summer has been discussed to at least be partially explained by cumulated human disturbance within chapter 2.4, even though natural barrier effects are likely to contribute to the observed clustering during EARLY SUMMER and SUMMER. However, no significant indications were found for unique habitat qualities of selected summer ranges apart from low levels of disturbance (compare chapter 5.4).

Against this background, getting a better understanding of the impact of disturbance on reindeer's small-scale behavior is crucial for two reasons: First, such knowledge can enhance the understanding of the current seasonal habitat selection during summer and possibly foster mitigation measures to reduce summer clustering. Second, planning of large-scale mitigation measures (environmental tunnels, wildlife over-crossings) is dependent on a better understanding of small-scale movement decisions by animals, rather than large-scale reactions.

Habitat clustering during summer has been discussed as remarkable (see chapter 6.2). Uncertainty remains in a midterm perspective, to which extent the body condition of the animals (and thereby overall carrying capacity of the study area) is negatively affected by this. Possible mitigation measures to counteract human disturbance induced clustering during summer foremost include the displacement of trails and/or (private/) tourist cabins or a less frequent use of those facilities (see e.g. Nellemann *et al.* 2010). Whether or not such recommendations should be given (and whether mitigation measurements can successfully be implemented), is very much dependent on reindeer’s (small-scale) functional responses to those potential barriers. It is therefore important to enhance our knowledge about how disturbance related factors are perceived by reindeer on a small-scale level and how these factors potentially alter reindeer's behavior.

The same holds true for planning and localization of large-scale mitigation measures with the intention to restore former migration corridors between currently separated reindeer areas within southern Norway. Again, a successful planning of such mitigation measures (e.g. environmental tunnels and/or wildlife over-crossings of roads (Rv7, Rv55) or potential closing/less frequent use of mountain road stretches) is dependent on reindeer’s perception[99] on potential barriers at a small-scale level.

Data collected within this study only delivers limited information on such potential small-scale behavior alterations. Two factors are responsible for this: First, the chosen fix rate of

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[99] See also Olden *et al.* (2004) for context dependent perception of animals and the relevance to movement.

GPS radio collars (3h interval) was not intended for such a scale (patch level), as argued above (compare 2.2). Little can therefore be said on a change in behavior/movement patterns when reindeer encounter potential barriers such as roads, trails or cabins. Second, the actual number of such encounters with barriers is overall limited within the dataset. This seems plausible, assuming reindeer's large-scale selection of seasonal habitats with low overall disturbance levels (as could be shown within chapters 2.3 and 5.3). Further research is therefore needed and proposed within the following.

Large-scale mitigation requires further research

As discussed above, mitigation measures to reduce habitat fragmentation and enhance connectivity between populations are costly (economically and politically) and successful implementations are difficult to predict. Acceptance of environmental tunnels or wildlife overcrossings is thereby very much dependent on exact location and behavioral response by animals (Holschuh & Otter 2000; Iuell *et al.* 2003; Cain *et al.* 2003; McDonald & Clair 2004; Ng *et al.* 2004; Clevenger & Waltho 2005). Within the Hardangervidda context barrier effects of both, Rv7 and Rv55, (potentially) hindering migration to adjacent habitats (Nordfjella and Setesdal-Ryfylke respectively) have to be assessed in close-up before final recommendations on mitigation measures can be given (see also Strand, Bevanger & Falldorf 2006 and Bevanger, Falldorf & Strand 2005).

It is therefore proposed to collect high frequency data using reprogrammable GPS radio collars via GSM-network (e.g. 5 min intervals). To ensure feasibility (battery life), collars should be programmed to automatically switch to high frequency mode, whenever potential barriers (Rv7, Rv55) are encountered by the reindeer. Whenever possible, location data should be backed-up by behavioral observations within the vicinity of the areas of interest (see e.g. Colman *et al.* 2001, 2004; also Sutherland 1998). Based on both data types, changes in movement patterns should be investigated to analyze working mechanisms of potential barriers. Likewise, suitable migration corridors should be identified from the data, in order to allow for an appropriate consideration of reindeer conservation needs within planning and management decisions in the future.

Two strategies to follow up on the dynamic properties of the models: comparison with high-density situation vs. comparative analysis between different areas

Within the discussions of the single chapters (compare 2.3 and 5.3) it has frequently been noted, that the presented results probably are depending on the current reindeer density within

Hardangervidda. Both, seasonal habitat distributions and functional responses to external factors, are likely to (at least partially) have dynamic and density dependent properties (McLoughlin *et al.* 2010). Especially the clustering during summer, the avoidance of the lichen-rich outer boundaries of eastern Hardangervidda and the observed barrier effects of both, Rv7 and Rv55, are assumed to depend on the current population level. The dynamical properties of the models thus warrants further research. Two ways forward are proposed: (i) A comparison of the model findings presented in this study should be carried out at a high-density situation. (ii) The results should be related to other reindeer areas.

(i) It has been shown in chapter 1.3, that the current population numbers of reindeer within the study area (app. 8,000) represent lower bound values in a timeline comparison of the last 30 years (compare Figure 1-2). For higher density periods during the 1970ties and early 1980ties Hardangervidda reindeer flocks have frequently been observed within Nordfjella area during winter (Strand, Jordhøy & Solberg 2001). Likewise, crossings of reindeer to Setesdal-Ryfylke have been reported on a more regular level (Strand, Jordhøy & Solberg 2001) and eastern habitat islands (e.g. Dagali) and appendices of the study area (e.g. Imingfjell) were utilized during winter, frequently. This could supports the hypothesis that the spatial behavior of reindeer indeed is density dependent.

Human disturbance related factors have without a doubt been increasing significantly in Hardangervidda within the last 20 years (Taugbøl *et al.* 2001; Jordhøy & Strand 2009; Strand *et al.* 2010). Behavioral observations made during high-density periods in the past can therefore not be directly transferred to the present, even when assuming higher tolerance levels to human disturbance related factors at a high-density situation. Hence, a better understanding of density dependent effects on reindeer habitat selection is necessary. It is therefore proposed, that the findings presented within this study should be compared with a high density situation within the study area in the future (see also McLoughlin 2010).

(ii) Comparing the findings presented in this thesis with other reindeer populations in southern Norway is also assumed to yield valuable information for a better understanding of the habitat use of the species. A better calibration of results could substantially contribute to answer decisive questions: What is a “normal” behavior? What are the differences between populations? Are those differences due to habitat or induced by human disturbance? What is critical? And: Where is mitigation needed? Four areas of interest seem obvious for comparisons between reindeer areas: Habitat qualities (distribution of land cover types, lichen biomass, level of human disturbance), seasonal distributions, movement patterns and factor response, including human disturbance.

Comparative assessment of habitat qualities is a necessary baseline analysis for a better understanding of reindeer habitat use (seasonal distributions, movement patterns and factor response). Spatial distribution of land cover types (e.g. summer vs. winter pastures), lichen biomass and other external factors (especially absolute level and spatial distribution of human disturbance) constitute the environment, in which reindeer behave and make decisions. In order to evaluate this behavior, differences in factor distributions hence have to be known. The methods presented for land cover classification and biomass assessment within this thesis (see chapters 3 and 4) are proposed as a baseline.

Differences in seasonal distributions between reindeer areas can deliver crucial insights on both, habitat use and habitat fragmentation. Decisive research questions are: Does the annual cycle follow the same (empirical) seasons? Where are seasonal habitats located? What is the relative size of those areas? Is (large-scale) migration between seasonal habitats visible? What can be derived for habitat fragmentation? And: Do exchanges occur with neighboring reindeer populations?

Comparative analysis of (seasonal) movement patterns can contribute to an enhanced understanding of reindeer's strategy to optimize for spatially uneven distributed resources. Results from other reindeer areas (and potentially other species) can help to answer fundamental questions on how reindeer make spatially relevant decisions: To which extent are seasonal search patterns of reindeer genetically preset? What is the influence of habitat qualities? How flexible are the detected movement patterns within a changing environment? What can be derived for human disturbance related factors and possible mitigation measures?

Finally, comparative analysis of reindeer's (large and small-scale) functional responses to external factors can likewise deliver valuable insights to theoretical knowledge of habitat use and contribute to relevant management decisions on the long-term conservation of this (and other) species. Questions in focus should be: Is reindeer's functional response to external factors comparable between reindeer areas? What are the relevant differences? And why do they exist? What is the explanatory power of differences in habitat qualities compared to density? What can be learned for sensitivity to human disturbance? What can be tolerated? And what are the decisive factors for this tolerance level?

A new method for monitoring lichen biomass

It has been argued above, that the monitoring of lichen volume can significantly enhance the quality of management decisions (see chapter 6.2). The lichen biomass model presented within this thesis (see chapter 4) is seen as a promising contribution to such a lichen-monitoring scheme. On this basis, two focus directions for implementing a feasible management tool are proposed: an enhanced ease-of-use (index stability for non-ridge vegetation, enhanced absolute calibration) and an increase both, in spatial and temporal resolution (more continuous timeline).

Successful monitoring methods have to be sufficiently accurate and easy to use for management (Rönnbäck *et al.* 2003; Coppin *et al.* 2004). Two major obstacles should be solved: First, lichen biomass assessment as proposed within chapter 4.2 requires an existing land cover map as the functional relationship between index values and lichen volume from field samples might only hold true within the reflectance profile of ridge vegetation. While having a land cover map was imperative for the definition of spatial habitat models within this thesis, monitoring of lichen biomass in other settings does not necessarily depend on such a detailed map. Further assessment of the valid definition interval for lichen volume prediction utilizing multiple index values is therefore desirable. In addition, it should be asked to which extend reflectance values from collected field sample points can be reutilized within other areas, in order to minimize fieldwork requirements. Second, absolute calibrations between images, necessary for change detection and timeline comparisons in the future, are both, essential for reliable monitoring schemes and difficult to obtain. Requirements for lichen monitoring are high, as monitoring intervals are short and small differences have to be detected. Further research on accurate, yet easy to use calibration methods between images is therefore essential. To enhance absolute calibration, it is proposed to include ground truth sample points as reference values to improve calibration models.

As noted above, an increase in resolution should be the second area of focus for developing a feasible lichen-monitoring scheme. It has been argued repeatedly that vegetation/lichen biomass mapping within a mountainous environment in Scandinavia is rather small-scale due to the heterogeneity of the landscape (compare chapters 3.2 and 4.2). In the same chapters it has likewise been argued that, given the advantages and disadvantages of the current satellite systems, Landsat can be seen as a satisfactory compromise between spatial resolution and other factors. For comparative reasons, nevertheless, it is proposed to test for possible uplifts in lichen prediction accuracies through enhancing the spatial resolution by using other satellite systems (e.g. SPOT 5). Even more important within a functioning monitoring scheme contributing to management decisions within a tight timeline, image availability is a crucial success factor. At present, no feasible satellite system is available granting for both, high spatial resolution and short image acquisition cycles (compare Table 3-3).

Better understanding of snow conditions is needed for risk assessment of climate change

Finally, as noted above, altered snow conditions triggered by climate change have been identified as a major threat for the long-term conservation of wild reindeer, not only in Hardangervidda but also in southern Norway (see chapter 6.2). The results of this study indicate three areas of further research to enhance the understanding of this process: (i) Predictions of climate change and its local impact on Hardangervidda (temperature, precipitation), (ii) improved description of snow surface condition/spatial resolution of data and (iii) research on alterations in seasonal habitat use triggered by changes in snow conditions, including possible mitigation measures (e.g. restoration of migration corridors).

(i) While climate change has been widely accepted as a fact within the scientific community and numerous prediction models have been presented (see IPCC 2007 and references therein), less is known about small-scale spatial changes in temperature and participation within single areas like Hardangervidda. Assumptions currently include both, increase in precipitation and higher variability in temperatures (Roald *et al.* 2003). It can thereby be followed, that snow conditions within the study area are likely to experience significant changes within the future with respect to snow depth and surface condition. It has been shown within this work (see chapters 2.4 and 5.3) that reindeer’s seasonal habitat selection is indeed dependent on snow conditions (here snow depth). In order to assess these changes further, small-scale prediction models on altered spatial distribution of snow condition parameters are necessary.

(ii) Second, in order to enhance impact assessment of snow conditions on reindeer’s seasonal habitat selection and functional responses, better data on snow depth (resolution and quality) as well as a better description of surface conditions are essential. Given the limited data availability within the study area, a feasible research direction could be to test the application of the snow-pack model developed by Kohler & Aanes (2004).

(iii) More fundamentally, given both, better knowledge on climate change and enhanced data quality/resolution, more research is needed on possible alterations in reindeer's seasonal habitat use within a changing environment. Focus should be on the question of how reindeer’s stochastic mortality rate develops within an environment altered by climate change depending on habitat fragmentation and connectivity. It will be essential to conclude whether potential measures like restoration of migration corridors will be able to mitigate negative climate change effects in the future and thereby ensure the long-term conservation of wild reindeer in southern Norway and elsewhere.

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Declaration on oath

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

Hamburg, May 18, 2012

Tobias Falldorf

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NINA Report

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