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Spatiotemporal variation in resource utilisation by a large herbivore, the moose

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Preface

The first year as a PhD student I smiled every day when biking home from work, being a PhD was fun. That was probably the most "boring" year. Since then I have learned a lot about moose, science and myself, taken part in interesting events and meetings and got to know many great people. Of course this is only a part of the story, but I will remember my time as a PhD as a good time.

I thank my supervisors for their advices and support in both good and tough days. Bernt-Erik Sæther for being the one trying to make me realise that there were essential things in biology I still had to learn. You even tried to explain one of these things to me by using an example about kids wanting to eat ice cream. I think I was so surprised about your pedagogical example that I did not understand anything. I thank Erling Johan Solberg for being the nicest supervisor ever. When I did not understand these essential things Bernt-Erik tried to tell me about, you would patiently explain it to me. Last, but maybe most important, I thank Ivar Herfindal for literally being behind my back all these year. Without you, I would have been far more frustrated when analysing the data, and finishing my PhD would have required a lot more time and effort.

When starting my PhD I apparently looked like someone that needed a lot of help: originally, I had four supervisors! However, when Reidar Andersen got the job as the director of SNO there was little time left to supervise a PhD-student. Still, I appreciate being a part of the project "Hjortevilt 2030". You also introduced me to many kind people at DN. I am grateful for getting to know all of you at Viltseksjonen and its associated members. You have a unique atmosphere and I always feel welcome when dropping by your offices. A particular thanks to Erik Lund for being my mentor at DN.

I also thank my co-authors for a nice collaboration. Christina and Jean-Pierre for long daytrips in the field collecting vegetation data. I remember being a bit worried when Jean-Pierre eagerly told me stories and explained things with his hands above the head – while driving the car. Moreover, I thank Rune Eriksen and Rasmus Astrup at The Norwegian Forest and Landscape Institute for collecting even more vegetation data. I especially thank Christer for providing me with data every time I ask for it, and Bram for kindly giving educational help when I am stuck in R. I am also very grateful for the help from both of you when finishing my thesis. I will continue to thank Brage, Aline, Irja and Snorre for advices about spelling and grammar, how to write this thesis, and how to survive the dissertation.

Ivar taught me to drink coffee by introducing me to the social life at NTNU. I got to know friends and colleges over many cups of coffee at Sito. I think these breaks will be what I miss the most when I look back at my years as a PhD. I also want to thank all my friends from my earliest years as a student. We have had a lot of fun!

I have never felt taller than the months I shared office with Eirin and Yngvild, but I remember nice days with Advent calendar approaching Christmas. I want to thank Ivar for patiently being my officemate the following years. And Christer for refusing to be my officemate – I couldn't have preformed my analyses without using your computer, which is far better than mine.

Not to forget, a family, and a family in law, that let me know every time they see a moose so I can count it. That is my PhD: counting moose in the forest. It nice to have all of you around, both here in Trondheim and down south. Alf and Ida, I want to thank you for every day reminding me that the most important part of my day is after four o'clock.

Although I just wrote a doctoral thesis about moose, my interest in this large animal will never exceed my father's. If he had been around, I know he would have read every word in this thesis (maybe as the only one except the committee?). Thus, nothing seems more right than to dedicate this thesis to him.

Trondheim, November 2011

Kari Bjørneraas

Table of contents

The thesis is based on the following papers

I. **Bjørneraas K,** van Moorter B, Rolandsen CM and Herfindal I (2010) Screening GPS location data for errors using animal movement characteristics. Journal of Wildlife Management 74 (6): 1361–1366.[1]

II. **Bjørneraas K**, Solberg EJ, Herfindal I, van Moorter B, Rolandsen CM, Tremblay J-P, Skarpe C, Sæther B-E, Eriksen R and Astrup R (2011) Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology 17 (1): 44–54.[2]

III. **Bjørneraas K**, Herfindal I, Solberg EJ, Sæther B-E, van Moorter B and Rolandsen CM (2011) Habitat quality, space use and functional response in summer habitat selection by moose (*Alces alces*). Oecologia: online early.[3]

IV. **Bjørneraas K**, Rolandsen CM, Herfindal I, Solberg EJ and Sæther B-E (manuscript) Large-scale tracking of plant phenology in a northern ungulate: the effects of sex.[4]

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[1] CMR and KB initiated the project. KB, CMR, BVM and IH developed the method. BVM programmed the screening method. KB wrote the manuscript with input from BVM, CMR and IH. *Used with permission of The Wildlife Society.*

[2] KB, EJS, IH, CMR, JPT, CS and BES contributed to the conception and design of the study. CMR, BES and EJS provided GPS data. RE and RA provided and organised the vegetation data. CMR, KB, EJS, JPT and CS conducted vegetation analysis included in an earlier version of the paper, but this was not included in the final version. CMR, KB and EJS collected reproduction data for some of the moose. KB performed all statistical analyses. IH and BVM contributed with GIS and statistical expertise. KB wrote the manuscript with input from EJS, BVM, CMR, JPT, CS, BES, RE and RA. *Used with permission of Wildlife Biology.*

[3] KB, IH, BES, EJS and CMR contributed to the conception and design of the study. CMR, BES and EJS provided GPS data. CMR, KB and EJS conducted fieldwork. KB performed statistical analyses. IH and BVM contributed with GIS and statistical expertise. KB wrote the manuscript with input from IH, EJS, BES, BVM and CMR. *Used with kind permission from Springer Science + Business Media.*

[4] IH, KB, CMR, EJS and BES contributed to the conception and design of the study. CMR, BES and EJS provided GPS data. CMR, KB and EJS conducted fieldwork. KB estimated phenological tracking based on a method developed by IH. KB performed statistical analyses and wrote the manuscript with contributions from CMR, IH and EJS, and with comments from BES.

INTRODUCTION

Sometimes it is all about being in the right place at the right time. For wild animals, the right time is when high-quality food is plentiful (e.g. Perrins 1970). The right place, however, varies a lot because environmental heterogeneity creates spatiotemporal variation in the abundance of plants and prey. Accordingly, many species adjust their behaviour over time in order to optimally utilise the heterogeneity in food resources (Milner-Gulland et al. 2011). Some animals may change their preference for a resource as abundance changes, some will leave a resource patch when the payoff-rate falls below a certain threshold, whereas others track the spatial relocation of a resource (MacArthur and Pianka 1966, Krebs et al. 1974, Charnov 1976, Fryxell and Sinclair 1988, Fryxell 1997). In theory, such behavioural adjustments to variations in the resource base can lead to an optimal foraging behaviour, which maximises intake of energy and nutrients, and in turn fitness returns (Stephens and Krebs 1986). Although distribution of food is an important component shaping animal behaviour and distribution, the benefits of access to food can be traded against other factors such as habitat heterogeneity, predation risk and intra- or interspecific competition (Sih 1980, Pimm and Rosenzweig 1981, Fryxell and Sinclair 1988, Houston et al. 1993, Rettie and Messier 2000, Alerstam et al. 2003, McKinnon et al. 2010). With a heterogeneous environment in mind, and references to optimal foraging and potential trade-offs, I will use the moose (*Alces alces*) as a model-species to examine how large herbivores, in particular ungulates, adjust their behaviour in order to cope with spatiotemporal variation in resources.

The optimal foraging theory suggests that food selectivity and energy intake rate is a function of resource availability (Emlen 1966, MacArthur and Pianka 1966). Extending this theory, fitness is a function of foraging efficiency (Schoener 1971, Pyke et al. 1977). This relationship was originally modelled for predators with a change in prey density (Emlen 1966, MacArthur and Pianka 1966), but similar principles applies to optimal foraging for herbivores, as preference and utilisation of a plant should vary according to its abundance (Owen-Smith and Novellie 1982, Belovsky 1984). However, herbivores face food resources that are highly variable in quality and widely spread throughout the landscape, thus there is more to herbivore diet selection than the optimal foraging theory alone (Hanley 1982, Pyke 1984, Senft et al. 1987, Hanley 1997). Senft and co-authors (1987) therefore suggested that one view herbivore foraging as a behavioural process instead of a process favoured by natural selection, and they found it useful to look at foraging decisions at a hierarchy of 'ecological scales'. A herbivore has to make multiple decisions, ranging from where in the landscape it is

beneficial to be located to which part of the plant to eat (Senft et al. 1987). Over the years, it has become widely recognised that resources such as cover, water location and plant nutritive quality can vary in their importance at different ecological scales, emphasising the relevance of a multiscale approach when examining herbivore behaviour, distribution and resource selection (Senft et al. 1987, Hobbs 2003).

Although it has been suggested that herbivores seldom are food-limited, at least in the presence of predation (Hairston et al. 1960, Slobodkin et al. 1967), it is widely recognised that plant availability and quality may influence fitness components, population dynamics, movement and distribution (Caughley 1970, Klein 1970a, White 1983, Fryxell and Sinclair 1988, Sæther 1997, Gaillard et al. 2000, Cook et al. 2004). For instance, even minor changes in the intake rate of high-quality plants may lead to substantial differences in body growth and reproductive output (the multiplier effect; White 1983). When intake rate is not constrained by forage abundance (Spalinger and Hobbs 1992, Wilmshurst et al. 1995), ruminants thus typically trade-off plant biomass for quality (Fryxell 1991). Studies of large herbivore behaviour at a fine spatial scale have shown that they feed selectively on highly digestible forage of high nutritional quality (Klein 1970b, Klein 1970a), which reduces the time needed for rumination and thereby increases the net energy intake and/or releases more time for other fitness-related activities (Belovsky 1981, Owen-Smith and Novellie 1982, Belovsky 1984). The digestibility and nutritive value of forage varies among plant species and plant parts (Mattson 1980, Van Soest 1994) as well as in time and space (Albon and Langvatn 1992, Hebblewhite et al. 2008). For instance, as plants mature, poorly digestible components accumulate, and selective tracking of new plant growth during the growing season is beneficial (White 1983, Van Soest 1994), particularly late in the growing-season, when food is generally abundant and digestion time rather than feeding time is the main constraint on energy intake (Van Soest 1994). Accordingly, spatial and temporal heterogeneity in food resources, and plant quality in particular, explains the movement and aggregation of many large herbivores, and also represents the driver of migratory patterns (McNaughton 1985, Fryxell and Sinclair 1988, Fryxell 1991, Albon and Langvatn 1992, Wilmshurst et al. 1995, Fryxell et al. 2005, Hebblewhite et al. 2008).

Availability of high-quality forage is only one of a set of biotic and abiotic factors constituting a species' fundamental niche (sensu Hutchinson 1957). Indeed, all factors that are actually or potentially important for a species' persistence can be viewed as one of many dimensions in a species' niche space (Hutchinson 1957). Describing a niche and identifying which factors to measure can be challenging (Polechová and Storch 2008). In ungulates in

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particular, it is recognised that the quality, the quantity and the accessibility of food are important determinants of the foraging niche (Sæther and Andersen 1990, Andersen and Sæther 1992). Still, there are other components important to ungulates, such as cover for protection from thermal stress, predators or humans (Mysterud and Østbye 1999), which all are parts of the multidimensional ecological space of an ungulate (i.e. niche Hutchinson 1957).

The net gain of utilising a resource or a habitat type may be limited by intra- or interspecific competition (Pimm et al. 1985). In an ideal free distribution (IFD) animal space use should be related to the heterogeneous distribution of habitats (Fretwell and Lucas 1969). Consequently, each individual should settle in the habitat best suited for survival and reproduction, and density within a habitat type should be related to its suitability. Similarly, individuals with a high availability of suitable habitat types need smaller areas to fulfil their requirements, whereas the opposite is predicted when habitat productivity is low (the habitat-productivity-hypothesis; Harestad and Bunnell 1979). Several studies of ungulates support the latter relationship (Table 1 in van Beest et al. 2011). Still, ungulate populations do not always conform to the IFD model (Mysterud et al. 2001, Pettorelli et al. 2003, Jones et al. 2006, McLoughlin et al. 2007), partly because the assumptions of IFD limit the environment to which the theory applies (Tyler and Hargrove 1997). For instance, it may be inapplicable in areas where intermittent rather than continuous production of forage causes aggregation of animals in regions with the best forage available at a given time (Owen-Smith et al. 2010). Modelling results also suggest that IFD predicts animal distribution most successfully at a spatial scale limited by the daily movement of the animals under study, although this was dependent on the degree of small-scale environmental heterogeneity (Tyler and Hargrove 1997). Another explanation for populations not conforming to an IFD is that herbivory alters plant morphology, biomass and composition (Bergström and Danell 1995, Mathisen et al. 2010), causing a dynamic resource base, which makes the IFD model unsuitable (Jones et al. 2006). Hence, several factors may lead to deviations from an IFD and must be accounted for in order to understand how and why density, habitat selection and home range size vary with local resource distribution.

Individual characteristics such as reproductive status or sex can influence the trade-offs between access to high-quality forage versus other important and limiting niche components (Miquelle et al. 1992, Dussault et al. 2005b). Components that influence ungulate space use are, for instance, predation, environmental conditions or topography (Houston et al. 1993, Dussault et al. 2005b, Kittle et al. 2008), and trade-offs between such factors and food

can be reflected in different habitat selection by males and females (Miquelle et al. 1992, Kie and Bowyer 1999). The reproductive strategy hypothesis (RSH) explains differences in habitat selection between sexes from an evolutionary perspective (Main 2008). It predicts that habitat choice by females is influenced by factors affecting offspring survival; however, when barren or not influenced by predation, females should select the best forage available to them (Main et al. 1996, Main 2008). Further, males are predicted to maximize their energy intake in preparation for rut. The forage selection hypothesis (FSH) provides another explanation, and is based on the difference in dietary requirements between males and females in sexual size dimorphic ungulates (Ruckstuhl and Neuhaus 2002). This hypothesis suggests that males are physiologically better able to digest food with high fibre content due to their larger rumens (Demment and Van Soest 1985). Although several similar hypotheses have been suggested (e.g. sexual dimorphism body size hypothesis; Main and Coblentz 1996, the gastrocentric hypothesis; Barboza and Bowyer 2000, the nutritional needs hypotesis; Mysterud 2000), they are all in accordance with the Jarman-Bell principle (Bell 1971, Jarman 1974), which states that larger ruminants should be able to tolerate a lower quality diet than smaller ruminants. The FSH extends this principle to differences in habitat choice in sexual dimorphic ungulates, where the smaller females should use higher-quality food habitats and males should select more strongly for high food quantity (Ruckstuhl and Neuhaus 2002).

Habitat selection is commonly described as disproportional use of a habitat type in relation to its availability, and selection for a habitat type reflects an animal's preference for one or several resources within that type (Manly et al. 2002). Knowledge about the relationship between animals and their habitat with its associated resources is important for our understanding of animal behaviour and space use (Rosenzweig 1981, Kie et al. 2002). For some species or populations, this is particularly essential because habitat loss or degradation threatens their existence (Venter et al. 2006). To fully understand animal habitat use and selection, measuring selection at one scale is often insufficient (Levin 1992, Mayor et al. 2009). Therefore, similar to the forage selection process predicted by optimal foraging theory, the resource selection process can be expressed at a hierarchy of spatial scales, ranging from an individual's selection of a food item to the geographical range of a species (Johnson 1980). The selection hierarchy should reflect the ecological scale at which fitness limiting factors act (Rettie and Messier 2000). For instance, at the landscape scale, ungulates may select habitat types minimising the predation risk, whereas they often are predicted to select for habitat types providing high-quality forage at finer scales (Rettie and Messier 2000, Dussault et al. 2005b, but see e.g. Kittle et al. 2008). Habitat heterogeneity can influence the degree to which

habitat selection differs across spatial scales. Variation among scales will typically be lower in homogeneous landscapes (Schaefer and Messier 1995) compared to more heterogeneous environments (Boyce et al. 2003).

In resource selection studies, choosing the proper temporal scales to consider can be equally or even more important than the choice of spatial scales (Fahrig 1992). Temporal dynamics in the environment may lead to variation in costs and benefits associated with a habitat type during a given period. A typical example is variation in habitat selection among seasons because regular environmental changes cause variations in food supply (Godvik et al. 2009, Zweifel-Schielly et al. 2009). At a shorter temporal scale, ungulates commonly forage in open, food-rich areas during nighttime and select habitat types providing cover during daylight (Godvik et al. 2009). Contradictory to optimal foraging theory predicting maximisation of long-term energy gain, ungulates have also been found to maximise the short-term gain of a food resource (Fortin et al. 2002). Accordingly, a correct reflection of ungulate resource selection will often depend on a multiscale approach.

The way in which utilisation of a resource changes with its availability is termed functional response, and was first described for predation and parasitism (Solomon 1949, Holling 1959a). For herbivores, a dietary functional response can be described based on the quality, quantity and accessibility of food (Andersen and Sæther 1992, Spalinger and Hobbs 1992). The concept has also been extended to include larger ecological scales. In habitat selection, functional response can be observed if selection for a habitat type changes with a change in its availability (Mysterud and Ims 1998), and has been identified in a number of studies of ungulates (Boyce et al. 2003, Osko et al. 2004, Godvik et al. 2009, Hansen et al. 2009, Herfindal et al. 2009). In heterogeneous environments, individuals will be located areas that differ in their habitat composition, and if these individuals vary in their relative use of a habitat type, functional response in habitat selection can be detected (e.g. Herfindal et al. 2009). This can for instance be related to the fact that one habitat type seldom contains the optimal combination of resources required for survival and reproduction, or that a substantial change in habitat availability can lead to a switching response (i.e. a type III functional response curve; Holling 1959b).

Understanding how animals with different individual characteristics utilise resource heterogeneity at multiple scales is essential for an adaptive management (Hobbs 2003). To obtain this knowledge, scientists have studied animal resource use and habitat selection for decades (e.g. Lack 1933). However, since observers were sent into the field in the study of Lack in 1933, technology has developed. In the 1960s, the first radio-collars were used to

track animals (Craighead and Craighead 1965), and today millions of animal locations are collected using Global Positioning Systems (GPS). During the same period, new challenges have emerged with respect to the handling of data quantity and quality (Frair et al. 2010, Hebblewhite and Haydon 2010, Urbano et al. 2010). A demand for new methods has arisen, both with respect to modelling and statistical approaches but also in order to correct imprecise GPS locations or detect sampling bias (Fieberg et al. 2010, Frair et al. 2010, Kie et al. 2010). Without correction of GPS data, we might come to the wrong conclusions in science or management (Frair et al. 2010). However, with the proper choice of methods and a sufficient sample size, GPS technology offers a unique tool for understanding patterns of animal behaviour and distribution (Cagnacci et al. 2010). Still, it should not be forgotten that the best insight is obtained when we combine this technology with a field-based understanding of the study species and its environment (Hebblewhite and Haydon 2010).

STUDY AIMS

An important question in ecology and management is how wild herbivores utilise resources in a changing environment, and whether the utilisation differs among individuals with different characteristics. A better understanding of these topics is important because climate change may affect the distribution of resources and because large herbivores living in human dominated landscapes experience continuous or sudden alterations of the environment, and thus their living conditions. The aim of this thesis is to examine spatiotemporal and demographic variation in resource utilisation by a large ungulate, the moose, in a human dominated landscape. Moreover, to investigate how ungulates adjust to changes in the resource base, I examine functional responses in resource selection. More specifically, by using data from GPS collared moose I aim at answering the following questions:

1) How can the quality of animal GPS data be improved without trading data accuracy for data quantity (paper I)?
1) How does moose habitat selection in a human modified landscape vary temporally (paper II, III)?
2) Is animal distribution and individual space use related to the abundance of selected or avoided habitat types (paper III)?
3) What is the functional response in moose habitat selection (paper III)?
4) Is large-scale movement related to spatiotemporal variation in plant phenology (paper IV)?
5) How and why does resource utilisation differ among males and females of different reproductive status (paper II–IV)?

METHODS

Study area

The study area is located in central Norway (64º30'N, 12º50'E) and covers Nord-Trøndelag county as well as Rissa municipality in Sør-Trøndelag county, Bindal municipality in Nordland county and parts of central Sweden (Fig. 1). It ranges from coastal areas with a boreonemoral character to alpine zones (Moen 1999, Karlsen et al. 2006). Altitude increases gently from coast to inland. The vegetation consists mainly of coniferous forest with Norway spruce (*Picea abies*) and smaller parts of Scots pine (*Pinus sylvestris*) (Larsson and Hylen 2007). Mixed and deciduous forests cover parts of the study area. Birch (*Betula pubescens* L.) dominates at higher elevations, whereas grey alder (*Alnus incana*), aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and several species of willow (*Salix*) spp. are common in the middle boreal zone (Moen 1999). Commercial forestry is intensive throughout the study area, but takes place predominantly in high-productive coniferous forest. Systematically, smaller parts of the forest are clear cut or cleaned followed by reforestation (Rolstad et al. 2002). This creates variation in forest age, vegetation characteristics and species composition, particularly within coniferous forest. Bogs with sparse or no tree vegetation are scattered throughout the area creating a heterogeneous landscape. Cultivated land is an important landscape element in some coastal areas, but is also found in several inland municipalities (Moen 1999). These areas are typically used for grass or grain production. The plant growing season lasts approximately from May until the end of September, but its length decreases from the coast inland and with increasing altitude (Karlsen et al. 2006). The study area is covered by snow in winter. The number of large carnivores is low (< 30 bears (*Ursus arctos*) and < 5 wolves (*Canis lupus*); Wabakken et al. 2007, Wartiainen et al. 2009), but occurs in a higher density at the borders of Sweden than in the coastal areas.
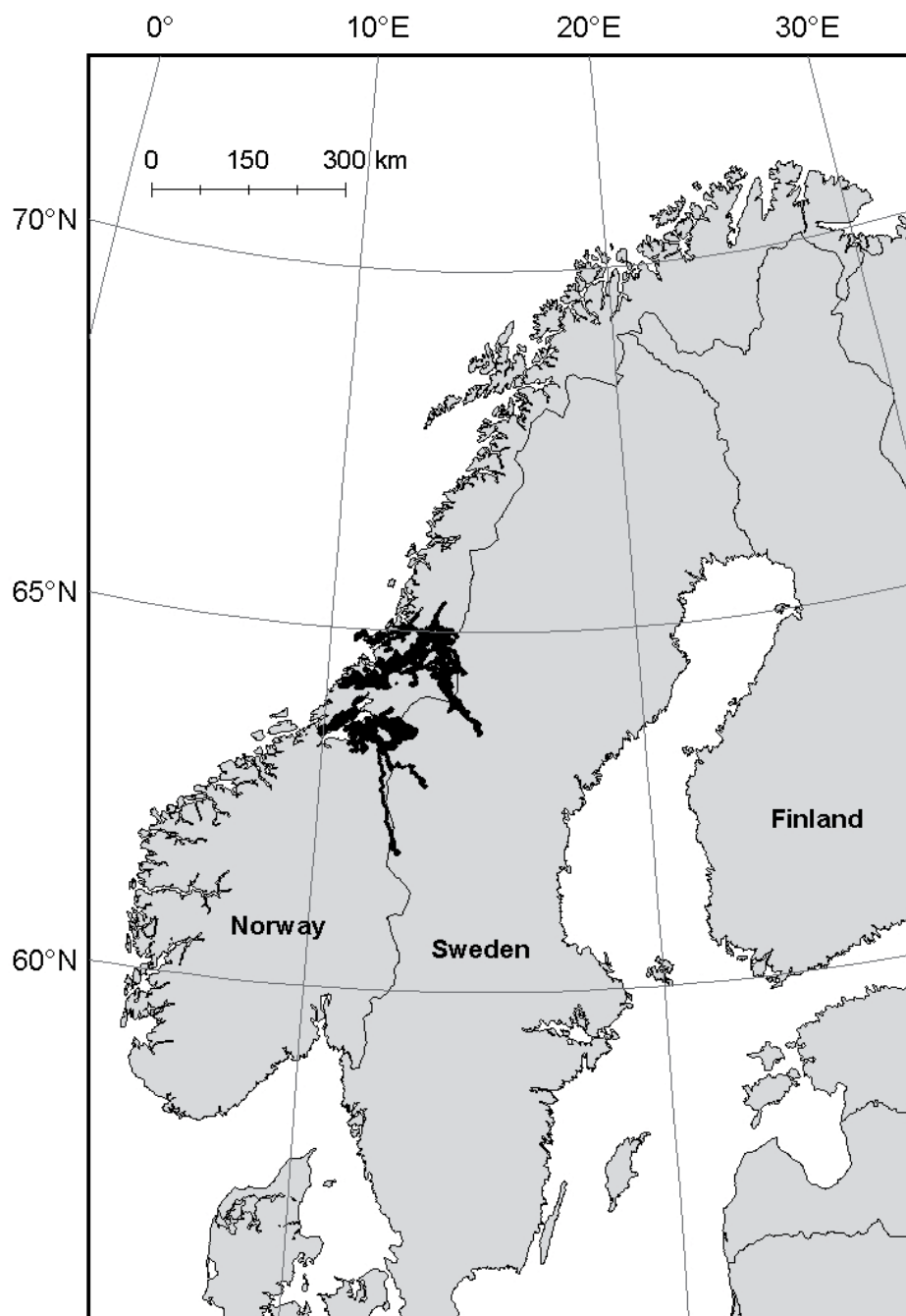
Figure 1. GPS locations (black dots) registered from GPS collared moose that were marked within central Norway.

Study species

Moose is the largest browsing animal in Scandinavia. It is a sexual size dimorphic species, where males weigh around 500 kg, whereas females are approximately 25% lighter (Solberg and Sæther 1994, Andersen and Sæther 1996). Moose have a polygynous mating system, and mating occurs in autumn. The probability of ovulation is higher for prime aged females than for yearlings, and depends on body condition (Sæther and Heim 1993, Garel et al. 2009). Females commonly give birth to one or two offspring in spring or early summer.

Moose are ruminants, and because rumination time is dependent on the quality of the forage (Hanley 1982, Van Soest 1994), moose benefit from being selective foragers. Most commonly, moose forage on deciduous trees like birch, rowan, aspen and willow in both winter and summer (Månsson et al. 2007, Wam and Hjeljord 2010). In winter, pine also becomes an important food plant (Månsson 2009). Spruce is rarely browsed by moose and can be regarded as unimportant as moose forage (Månsson et al. 2007). Moose also feed extensively on bilberry bushes (*Vaccinium myrtillus*), particularly towards the end of the growing season (Hjeljord et al. 1990, Wam and Hjeljord 2010), and on several grasses, tall forbs and ferns during summer (Hjeljord et al. 1990, Sæther and Heim 1993, Wam and Hjeljord 2010). Scandinavian moose show a large variation in movement behaviour; while some moose are year-round residents, others migrate large distances between summer and winter ranges (Sæther et al. 1992, Ball et al. 2001, Hjeljord 2001, Bunnefeld et al. 2011).

Data collection

Moose data

During 2006–2008, 171 moose were collared in the study area. Of these 38 were adult males, 107 were adult females, whereas 14 males and 12 females were marked as calves (approximately 8 months old). Seven moose were fitted with Tellus GPS collars and 164 moose with GPS PLUS/GPS PRO Light collars. Capture, handling, and anesthetizing of moose was approved by the Norwegian Directorate for Nature Management and the Research Animal Committee in Norway. The GPS collars were programmed to obtain a fix every one or every second hour. The fix rate success was generally high, around 99%, and during the project period, more than two million GPS locations were collected. Although the proportion of three-dimensional fixes was high, there were still evident location errors in the data set. All

collars were equipped with very high frequency (VHF) transmitters. Using the VHF-signals, females were tracked once or several times a year to monitor reproductive status. The main period for calving was at the end of May and beginning of June (Rolandsen et al. 2010). In the different analyses, data from a selection of animals that fitted specific criteria for the respective study were used.

Harvest data was used as a measure of moose density. In Norway, there is a relatively close relationship between fluctuations in population density and number of moose harvested, and a reasonable density index can therefore be estimated from harvest data (Solberg and Sæther 1999, Solberg et al. 2006). Additionally, predation has only a small effect on population growth due to few large predators being present (Wabakken et al. 2007, Wartiainen et al. 2009), and mortality not related to hunting is low (Stubsjøen et al. 2000, Solberg et al. 2003). The moose density index was estimated as the number of harvested moose per km^2 of suitable moose habitat (undeveloped areas below the tree line). The hunting season is from 25 September to 31 October.

Vegetation data

Information about the distribution of habitat types in the study area was derived from digital land cover maps. A satellite-based vegetation map, provided by the Northern Research Institute (Johansen et al. 2009) was used to identify habitat types in the analyses in *paper II*. This map is a generalized and consistent vegetation map covering the whole Norwegian mainland (Johansen et al. 2009). A forestry map provided by the Norwegian Forest and Landscape Institute gave more detailed information about the forest stand age and tree species composition (*paper II*) (Gjertsen 2007). This map was made based on a multi-source forest inventory method, combining satellite data, land cover maps and data from field plots (Gjertsen 2005, Gjertsen 2007). In *paper III* habitat types were derived from a digital land cover map provided by the Norwegian Forest and Landscape Institute (Bjørdal and Bjørkelo 2006). This map describes land resources, with emphasis on capability for agriculture and natural plant production.

Vegetation data collected by the National Forest Inventory in Norway (NFI) was used to gain information about the vegetation within different habitat types (*paper II-III)*. The NFI is based on a network of permanent sample plots distributed over the forested part of Norway (Larsson and Hylen 2007, Landsskogtakseringen 2008). The plots are circular with an area of 250 m^2. Variables such as tree species, age, height and tree volume are recorded, as well as

information about browsing pressure from ungulates, coverage of deciduous scrubs, dominant vegetation types, and coverage of bilberry bushes (Larsson and Hylen 2007, Landsskogtakseringen 2008). One fifth of the plots are measured each year, such that each plot is visited every five years (Gjertsen 2007). NFI-data from 1995–2008 was used in the thesis.

The Normalised Difference Vegetation Index (NDVI), derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) data set, was used as an approximation of photosynthetic activity and plant biomass (Huete et al. 2002) (*paper IV*). The data has a spatial resolution of approximately 250*250 m and a temporal resolution of 16 days. NDVI is the relationship between reflected near-infrared (NIR) and red (RED) radiation from the ground, and is computed as: (NIR - RED)/(NIR + RED) (Huete et al. 2002). NDVI is related to vegetation characteristics such as chlorophyll abundance, canopy leaf area, above ground biomass and net primary production (Myneni et al. 1995, Veroustraete et al. 1996, Schloss et al. 1999, Boelman et al. 2003).

Analyses

To increase the quality of GPS location data, a screening method that identifies locations arising from unrealistic movement patterns was developed (*paper I*). The method consists of two main steps: First, it identifies fixes that are further away than a preset threshold from surrounding fixes. Second, it identifies locations forming a spike in the trajectory. The identified locations are likely measurement errors and should be excluded from any data set prior to further analysis. To evaluate the screening method, I applied it to locations collected from GPS collared moose. Among other factors, I examined whether the method detected all obvious outliers and whether its performance changed during the year. Its overall performance was also compared to the performance of four commonly used methods of GPS screening (Moen et al. 1996, Edenius 1997, D'eon et al. 2002, D'eon and Delparte 2005, Lewis et al. 2007).

The large amount of moose GPS locations and the detailed vegetation maps gave a unique opportunity to examine the relationship between the moose and its environment. Finding appropriate methods for examining these data was challenging due to the many methods available, but also because methods that have been developed for VHF-telemetry data are not necessarily suitable for analysing the more detailed and voluminous GPS location

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data (Kie et al. 2010). When examining different levels of moose resource selection (Fig. 2), several methods were used in some of the analyses to make sure that the qualitative conclusions were not a result of the method applied. For each of the different levels of the resource selection process, we applied methods assumed suitable for examining that level.

First-order selection	→	geographical range
Second-order selection	→	home range
Third-order selection	→	habitat components
Fourth-order selection	→	food items

Figure 2. Johnsons (1980) hierarchical ordering of the resource selection processes. In the thesis, the focus is on second- and third-order selection.

At the largest spatial scale (first-order selection, Fig. 2), I analysed the distribution of moose in the study area in relation to the distribution of different habitat types using a linear model (*paper III*). This model related the moose density index to the proportion of different habitat types within a municipality.

At the second level (second-order selection, Fig. 2), I estimated individual home ranges by applying two home range estimators to the data (*paper III*). One method was the non-parametric local convex hull (LCH) method (Getz and Wilmers 2004). An LCH constructs a home range based on a union of local minimum convex polygons associated with the data (Getz and Wilmers 2004). The other was the Brownian Bridge Movement Model (BB) (Horne et al. 2007). A BB is based on a Brownian motion that depends on a start and an ending location as well as time and distance between locations (Horne et al. 2007). Both approaches are statistical models creating a utilisation distribution (UD) for each individual, assumed suitable for studying home ranges (Kie et al. 2010). I used the 90% volume contour, which has been suggested in order to avoid the inclusion of areas unfamiliar and unused by the animal (Börger et al. 2006). Another problem may occur if a disjoint UD creates a split home range, which may exclude corridors used for travel among habitats providing important resources at different times (Kie et al. 2010). However, as I was mainly interested in the variation among individuals and not the home range size *per se*, the methods should be appropriate for further analyses.

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The UD estimated by the BB was also used to examine habitat selection within the home range (third-order resource selection, Fig. 2) (*paper III*). The UD tells us the probability of finding a moose within a given area of its home range (Marzluff et al. 2004). Another method used to examine moose habitat selection was the Step Selection Function (SSF) (*paper II,III*). An SSF estimates selection by comparing characteristics of used areas with characteristics of the available landscape (Fortin et al. 2005). Lastly, it was tested whether moose tracked photosynthetic activity by relating moose movement to NDVI (*paper IV*). This was examined using an environmental tracking model. The model estimated phenological tracking by utilising information about the spatiotemporal dynamics in plant phenology along the trajectory of a moose during the growing season.

The above methods were used to examine spatiotemporal variation in moose resource use, resource selection and tracking of plant phenology. First, circadian variation in habitat use during the whole year gave an indication of where moose are to be found. Next, circadian variation in habitat selection was examined to see how the importance of different habitat types varied throughout the day in four different seasons. Likewise, I looked at seasonal variation in habitat selection. I also examined functional response in summer habitat selection, which can be defined as changes in selection for a habitat type with changes in availability (i.e. non-proportional use) (*sensu* Mysterud and Ims 1998). Additive models were used in order to detect potential non-linear functional responses (Wood 2006, Aarts et al. 2008). Finally, I examined if moose that moved long distances or upwards in the terrain, i.e. moose with a large horizontal or vertical displacement, tracked changes in plant growth better than individuals with a small displacement did. In most of the analyses, information on individual characteristics was used to test for differences in resource utilisation among males and females of different reproductive status.

MAIN RESULTS AND DISCUSSION

How can the quality of animal GPS data be improved without trading data accuracy for data quantity (paper I)?

GPS tracking systems can record enormous amounts of data, providing unique opportunities to examine animal movement and behaviour, such as resource selection (Godvik et al. 2009, Beyer et al. 2010, Leblond et al. 2010). The first step when analysing GPS data should be exclusion or correction of location errors, as inclusion of inaccurate locations can introduce

systematic biases and wrong conclusions (Visscher 2006, Hurford 2009). By using animal movement characteristics, a method that effectively identified erroneous GPS locations was developed. The method was designed to detect two types of erroneous locations: locations that are unlikely given the movements before and after, and locations that form an out-and-back geometry. In partially migratory populations, one challenge is the large variation in movement between successive locations among individuals. To allow for different movement strategies, we evaluated the accuracy of each GPS fix in relation to a limited number of prior and subsequent locations.

A well known problem for methods screening animal GPS locations for errors is that data accuracy is increased in exchange for a large loss of data, and sometimes without eliminating all obvious outliers (D'eon and Delparte 2005, Lewis et al. 2007). However, we found our method to handle the trade-off between data accuracy and data reduction well. The screening method also outperformed four previous suggested GPS screening methods (Moen et al. 1996, Edenius 1997, D'eon et al. 2002, D'eon and Delparte 2005, Lewis et al. 2007), both with respect to detection of obvious errors and the trade-off between increased accuracy and data loss. The method works well for screening of moose GPS locations (e.g. van Beest et al. 2011), but can also be applied to other species by adjusting the criteria determining what is likely and unlikely movement behaviour. However, one assumption is that the underlying behaviour of the focal species is similar to moose, e.g., exclusion of locations forming an out-and-back geometry will be wrong for central-place foragers.

By examining the movements of moose in our study area, the criteria for identifying a moose GPS location as erroneous were determined at an accuracy acceptable for further analyses. Thus, with knowledge about the general movement of a study species it is possible to determine unlikely movement behaviour, and by applying the method presented in paper I, the quality of the GPS location data can be improved without suffering a large loss of data.

How does moose habitat selection in a human modified landscape vary temporally (paper II, III)?

Moose in central Norway were selective in their choice of habitat, and took advantage of the habitat heterogeneity caused by forestry and agriculture. Overall, moose selected forested habitat types, but the selection pattern varied during the day and among seasons. During nighttime in the vegetation growing season, moose selected open, agricultural land and young forest, whereas old forest was selected during daytime. Such a circadian selection pattern is

also found in other ungulate populations (Godvik et al. 2009, Leblond et al. 2010). Ungulates are often relatively active during twilight and darkness, whereas they may rest or forage in areas providing cover during daylight hours (Ager et al. 2003, Godvik et al. 2009). Increased use of forest during daytime can minimise the exposure to potential predators, but also to humans. The latter can be particularly relevant for moose in central Norway because they are heavily harvested by humans and found to retreat to areas further from settlement during daytime (Lykkja et al. 2009).

Moose showed a pronounced variation in habitat selection among seasons. With respect to the selection of different forest types, selection in winter was clearly distinct from the rest of the year. In winter, moose showed an overall high selection for mature and old forest. These forest types can be beneficial as they can reduce snow depth due to a closed canopy, increasing the accessibility to field layer vegetation and reducing the cost of movement (Parker et al. 1984). Although there was an evident increase in the selection for pine forest, which is an important winter browse for moose (Månsson 2009), it was no clear selection for this habitat type or any other habitat type during winter. Thus, the overall habitat selection pattern was weaker in winter compared to the rest of the year. Another study found moose to be very selective in their choice of food items in this season (Wam and Hjeljord 2010). This suggests an increased selectivity at a fine scale in winter, while relaxing the selectivity at the habitat level. The findings of a more pronounced habitat selection by moose in the vegetation growing season can be due to a large advantage of selecting patches providing high-quality forage at that time of the year. In fact, summer foraging conditions has been proposed as the more important than winter severity for growth and reproduction of moose (Herfindal et al. 2006, Brown 2011).

Moose often forage on deciduous browse (Månsson et al. 2007, Wam and Hjeljord 2010), and their population growth rate is found to be positively related to the abundance of mixed deciduous habitats (Brown 2011). Thus, the high selection for deciduous forest, but also agricultural land, in summer and autumn found in paper II was expected. However, when dividing spruce forest into age classes, moose in central Norway also showed a high selection for young spruce forest during the growing season. Here, the results from paper II and III are slightly contradictory with respect to summer habitat selection. Although both papers showed that forest was the most selected habitat type, females with young showed strongest selection for high-productive coniferous forest in paper III, but clearly selected deciduous forest in paper II. One plausible explanation is that the habitat types were derived from different maps in the two studies, and that the sample sizes differed. Moreover, because moose seldom

forage on spruce (Månsson et al. 2007), a closer look at the resources found within spruce forest was necessary. A habitat type will seldom contain a perfect mixture of resources, and we can therefore expect ungulates to avoid and select different habitat types depending on the resources they require at a given time. Within the study area, young spruce forest was often located in high-productivity areas, and had a relatively high abundance of vegetation characterised as preferred moose forage. This can explain the high selection for this habitat type. Indeed, successional forest has for a long time been recognized as important for moose because of their high cover of attractive forbs and high density of deciduous trees within reach of moose (Peek 1997, Rempel et al. 1997, Wam et al. 2010). Moreover, spruce forest dominated the study area, whereas deciduous forest and agricultural land, which provided good moose forage during the vegetation-growing season, constituted a smaller part. Thus, moose seem to select habitat types based on a combination of forage quality and habitat abundance, as found in other studies (Herfindal et al. 2009).

Cover is another component important to ungulates, being provided by tall trees with dense canopy (Mysterud and Østbye 1999). Selection for habitat types providing cover is usually interpreted as a behavioural response to avoid predation (Mysterud and Østbye 1999, Dussault et al. 2005b) or to reduce heat or cold stress (Schwab and Pitt 1991, Mysterud and Østbye 1999, Dussault et al. 2004). Due to logging activity in the study area, moose experience a heterogeneous environment with respect to cover. However, because moose selected high-productivity forests over low-productivity forests, it seems that food governs the choice of habitat type more than cover.

Temporal variation in habitat selection was present at multiple scales, and the results clearly demonstrate the importance of spatial scale in ungulate resource selection studies. If I had examined habitat selection at one long temporal scale only, e.g. a year, I would not have identified the changing importance of different habitat types across seasons. Similarly, I would have failed to detect the variation in relative importance of food and cover during the day without examining circadian variation in habitat selection. In addition, there are differences between daily and seasonal decisions. For instance, by analysing the variation in selection for forest stages among seasons only, the importance of mature forest during daytime in summer would not have been observed. This highlights the importance of multiscale analysis of habitat selection in order to understand ungulate responses to a heterogeneous environment.

Is animal distribution and individual space use related to the abundance of selected or avoided habitat types (paper III)?

The moose habitat selection studies (see above) provided an important basis for examining whether the availability of selected and avoided habitat types was linked to individual variation in home range size or moose distribution within the study area. Space use by ungulates depends on the interaction between energetic requirements (McNab 1963, Harestad and Bunnell 1979) and the spatial distribution of limiting resources (Mitchell and Powell 2004). Among the factors influencing variation in home range size are weather conditions (Rivrud et al. 2010), food supply (Dussault et al. 2005a, van Beest et al. 2011) and habitat heterogeneity (Kie et al. 2002). In accordance with the habitat-productivity-hypothesis, which states that animals need larger areas to fulfil their requirement when productivity is low (Harestad and Bunnell 1979), we found moose to have larger home ranges when the proportion of unproductive areas was high within their home range. Home ranges containing a high proportion of the most selected habitat type were thus smaller. As this habitat type provides both forage preferred by moose and cover, it probably provides a sufficient resource base over a relatively small area.

The moose density, indexed by harvest data at the municipality level, was lower in areas with high cover of the three least selected habitat types during summer. Density was also higher in areas with high availability of agricultural land, a productive habitat type that potentially supports a large number of animals. However, there was no support for higher density in forested habitat types providing abundant, good forage. Thus, despite the first mentioned relationships, the overall relationship between the abundance of different habitat types and the local moose density index departed from an ideal free distribution (IFD; Fretwell and Lucas 1969). Plausible explanations for the partial mismatch between the assumed habitat suitability and animal density is that (1) individuals are not free to occupy the most suitable habitat (i.e. competitive interference), (2) the value of resources within a habitat type is not fully known, and that (3) this value is not similar to all individuals (Tyler and Hargrove 1997). Although the IFD-model has proven useful when examining the distribution of some ungulates (Wahlström and Liberg 1995), it may be inappropriate for ungulates living in highly heterogeneous and dynamic environments (Jones et al. 2006). Moreover, the IFD-model may be unsuitable for the moose study because density was estimated at a large spatial scale (Tyler and Hargrove 1997, Mysterud et al. 2001), or because the variation in moose harvest does not reflect the variation in moose density precisely enough. Whatever the reasons

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for the density not fully conforming to an IFD, the results suggest that the quality of habitat types is important for space use and distribution of moose, at least to some degree.

What is the functional response in moose habitat selection (paper III)?

Moose in the study area had home ranges that differed greatly in composition, i.e. they contained different proportions of the different habitat types. I found that individuals with contrasting habitat availabilities showed different habitat selection, and interpreted this non-proportional relationship between selection and availability as a functional response in habitat selection (Mysterud and Ims 1998). Interestingly, there was no evidence of functional response for habitat types assumed to not provide beneficial resources, whereas the selection for habitat types providing food and/or cover increased with availability. A possible explanation is that when a high-quality habitat type becomes scarce, the costs of searching for it exceeds the benefits and selection will decline with decreasing abundance (i.e. a switching response, type III; Holling 1959b). Furthermore, the shape of the functional response differed from several other studies, where selection for favourable resources increased as their availability declined (Godvik et al. 2009, Herfindal et al. 2009, Wam and Hjeljord 2010). However, not only will the abundance of the focal resource be important (Shipley et al. 1998), but also the abundance of surrounding resources (Wam and Hjeljord 2010). The contrasting results may therefore be an effect of what is defined as available, which differs among studies and home range estimators (Laver and Kelly 2008).

Is large-scale movement related to spatiotemporal variation in plant phenology (paper IV)?

Large-scale movements by ungulates are often related to selective foraging for new plant growth (Fryxell and Sinclair 1988, Milner-Gulland et al. 2011). Newly emerged plants are rich in nutrients and highly digestible (Van Soest 1996), thus tracking of the phenological development of plants is considered favourable for ungulate growth and performance (Pettorelli et al. 2005, Hebblewhite et al. 2008, Post et al. 2008). In temperate ecosystems, ungulates can take advantage of a successively delayed vegetation green-up with altitude, a coast-inland gradient or other landscape characteristics (Albon and Langvatn 1992, Mysterud et al. 2001, Hebblewhite et al. 2008). Accordingly, I found moose with a large horizontal or vertical displacement to track phenological development better than individuals with a short net displacement did, i.e. moose seem to gain better access to high-quality forage when

moving long distances or using a diversity of altitudes. It is therefore likely that migration between seasonal ranges is positively influencing energy gain, and possibly factors such as body growth or reproduction for moose in the study area. Previous studies of ungulates have shown a positive relationship between a diverse plant phenology and growth or reproduction (Mysterud et al. 2001, Post et al. 2008).

Due to a coarse spatial- and temporal resolution of the environmental data, we may have failed to detect fine-scale tracking of plant phenology. Because the NDVI-data measures the canopy and not the productivity in the field layer (Chen et al. 2004), this can limit the use of NDVI in high productive forests (Pettorelli et al. 2006). Accordingly, we may have failed to detect utilisation of variation in plant development caused by canopy shading, found in previous studies of moose (Hjeljord et al. 1990). Still, due to forest heterogeneity vegetation green-up is probably less asynchronous in smaller areas than at a large scale within the study area (Karlsen et al. 2006). The conclusion was clear: individuals that exhibited long-distance movements or used a diverse range of altitudes experienced a prolonged period with access to new plant growth of presumably high quality.

How and why does resource utilisation differ among males and females of different reproductive status (paper II–IV)?

When the costs and benefits of selecting for resources differ among individuals depending on their sex or stage in life, demographic differences in habitat selection can be observed (Miquelle et al. 1992, Kie and Bowyer 1999, Dussault et al. 2005b, Main 2008). For instance, reproducing females will often show a higher selection for habitats providing protection for offspring than males or females without young (White and Berger 2001, Ciuti et al. 2006, Main 2008). In central Norway, females overall selected habitat types providing good foraging opportunities. However, in spring and summer, i.e. when the calves were born, habitat selection of reproducing females differed from males and non-reproducing females. Females giving birth avoided habitat types with no or little cover even though they provided very abundant and high quality forage. In contrast, barren females showed highest selection for these habitat types. This is in accordance with the reproductive strategy hypothesis (Main 2008) and confirms previous studies where habitat selection by reproducing females reflected the need to protect young from predators (White and Berger 2001, Dussault et al. 2005b). Predation risk is relevant in the interior part of our study area, but most of the moose in the present studies experience little or no predation (Rolandsen et al. 2010). However, some

degree of anti-predator behaviour can be retained following several decades of predator absence (Berger et al. 2001). Moose cows may also perceive anthropogenic disturbances as a potential predation risk (Tremblay et al. 2007, Lykkja et al. 2009), which can contribute to explaining their selection for cover when calves are young.

For male moose, food was evidently the main driving force in habitat selection as habitat types providing a high abundance of preferred forage was selected more than habitats providing mainly cover. This result is in accordance with other studies where male moose quickly moved into food-rich areas and avoided habitat types providing cover but scarce food in spring and summer (Leblond et al. 2010). It is also expected that males select for abundant food more than females due to their larger body size and thus higher energy requirements (McNab 1963).

Males also tracked plant development better than females. Similar to habitat selection, this may reflect that females trade access to new plant growth of high-quality for protection of calves. Because females give birth early in the growing season (Rolandsen et al. 2010), the presence of young may limit their ability to follow the vegetation green-up. While males seem to follow the phenological development of plants for a longer period, females possibly strive to arrive to their summer ranges before the calving period. They can then benefit from the emergence of nutritious plants during the lactation period, which is energetically costly (Robbins and Robbins 1979, White 1983). Interestingly, females without calves showed the same tracking of plant phenology as reproducing females.

Overall, resource selection by females with calves reflected their need to balance foraging and protection of young. The lack of difference among barren and reproducing females with respect to tracking of new plant growth suggests that they have an underlying adaptive strategy favourable for reproduction. However, without the presence of young females can relax the trade-off between high-quality food and cover, which was reflected in their habitat selection. Still, due to the low sample size of barren females, these results should be interpreted with some caution. It was more evident that male moose are adapted to maximise energy intake, as all results showed that they selected for areas proving abundant, high-quality forage.

Relevance for wildlife management and future prospects

A thorough understanding of the relationship between harvested populations and their resources is important when management decisions are to be made (Fryxell et al. 2010). Especially when facing changes in resource abundance e.g. due to human-caused habitat alterations, knowledge about the ecological interaction between populations and their habitat becomes useful (Morris 2003, Fryxell et al. 2010). It has for a long time been recognised that the introduction of clear-cutting forestry in the 1960s provided Scandinavian moose with prime habitats that probably contributed to increase the moose carrying capacity (Lavsund et al. 2003). This thesis confirms the importance of successional forest as an important habitat type for moose. However, it has also been shown that moose more often are located in older forest stands than young forest stands, although these stands were generally less selected than young forest. Consequently, basing management or habitat preservation solely on the most preferred habitat can lead to decisions unfavourable for the species in focus. As noted by Shipley (1998), a mixture of resources can be important as different resources provide different benefits.

A mismatch between the scales at which a study is performed and the scales of management can be problematic (Hobbs 2003). I have shown that the relative importance of different habitat types and their associated resources depends on the scale of investigation. For instance, resources found to be important at a small scale may be less important at larger scales. This means that it is not always suitable to extend findings to larger areas or longer times than what have been investigated (Hobbs 2003). Changes in selection with changing habitat availabilities contribute to an even more complex picture of how ungulates can utilise the landscape, and emphasise the importance of thorough analyses of animal space use and resource utilisation. The use of GPS technology together with proper data on environmental factors has made ecologists well equipped for such challenges and has offered a unique opportunity to understand animal resource use and selection at a variety of spatial and temporal scales. However, as emphasised by Gaillard and co-authors (2010), it is first when we manage to link this knowledge to life-history traits that we come closer to understanding how the performance of a population will change with altered environmental conditions. Examining how resource availability, habitat selection and environmental tracking influence body condition, reproduction and survival is therefore a natural next step to better understand the relationship between moose and their environment.

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Paper I

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Paper II

Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape

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Habitat alteration by humans may change the supply of food and cover for wild ungulates, but few studies have examined how these resources are utilised over time by individuals of different sex and reproductive status. We examined circadian and seasonal variation in habitat utilisation within a moose *Alces alces* population in central Norway. Our study area covers forests and open habitats, both influenced by human alterations (e.g. forestry and agriculture). We expected moose to select habitats with good forage and cover in all seasons, but to select open foraging habitats mainly during night-time. Moose selected good foraging habitats, such as young forest stands and cultivated land during night, whereas the utilisation of older forest stands providing cover increased during daytime. This circadian pattern changed throughout the year, seemingly related to variation in hours of daylight and provision of forage. Young forest stands provided higher density of preferred food plants compared to older stands and were highly selected from spring until autumn. Relative to young forest, the selection for older forest stands increased towards winter, likely due to provision of higher plant quality late in the growing season, and to reduced accumulation of movement-impeding snow during winter. Selection of cultivated land varied among seasons, being highest when crop biomass was high. We also found some indications of state-dependent habitat selection as reproducing females avoided open, food rich areas in the first months after their calves were born, whereas males and females without young selected these areas in spring and summer. Our results clearly show that moose exploit the variations in cover and food caused by forestry and agriculture. This is particularly relevant for moose in Norway as current changes in forestry practice lead to a reduction in young, food-rich forest stands, possibly aggravating the already declining body conditions and recruitment rates of moose.

Key words: Alces alces, forest stage, habitat selection, moose, Norway, reproductive status, step selection function, ungulates

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For herbivores, plasticity in foraging behaviour is important in order to cope with variation in resource availability (Hanley 1997) and herbivores may, as a result, show temporal variation in habitat selection (Godvik et al. 2009, Zweifel-Schielly et al. 2009). Habitat selection may be viewed as a complex of scale-dependent behavioural decisions concerning environmental factors, intra- and interspecific interactions, and the state of the individual animal (Senft et al. 1987, Rettie & Messier 2000, Boyce et al. 2003, Ciuti et al. 2006, Kittle et al. 2008). For instance, at the landscape scale herbivores often select habitat types in order to minimize predation risk (Rettie & Messier 2000, Dussault et al. 2005), while for forage maximisation smaller scale variations in diversity, abundance and spatial distribution of food plants are important (Belovsky 1978, Andersen & Sæther 1992, Månsson et al. 2007a). Herbivores may optimise their foraging by tracking spatiotemporal variation in quality and quantity of food caused by variation in weather and site productivity (Fryxell et al. 2005). Indeed, variation in forage quality may have feedback effects for herbivore population dynamics and life history characteristics (Gaillard et al. 2000) as even minor changes in ingestion rates of high-quality forage can have substantial effect on growth and reproduction (White 1983).

Not all habitat types contain an adequate mixture of complementary resources, such as abundant high-quality forage and shelter. Consequently, during a given day ungulates can benefit from utilising habitat types of different qualities resulting in time-dependent habitat selection (Demarchi & Bunnell 1995, Godvik et al. 2009). The choice of habitat type at a particular time is governed by trade-offs between associated costs and benefits (Rettie & Messier 2000). For example, ungulates commonly forage in open habitat types where food plants are abundant and of high nutritional quality (Hebblewhite et al. 2008, Godvik et al. 2009). However, in open areas, animals can be more exposed to thermal stress (Demarchi & Bunnell 1995, Dussault et al. 2004), predators and humans, which they generally try to avoid (Nikula et al. 2004, Dussault et al. 2005, Lykkja et al. 2009). To optimise the cost-benefit relationship on a circadian basis (i.e. during the 24-hour period), ungulates may therefore increase their use of forest stands providing cover and thermal shelters during daytime (Demarchi & Bunnell 1995, Dussault et al. 2004) and use more open forage-rich habitat types during darkness when they

are less visible to predators and humans (Godvik et al. 2009, Lykkja et al. 2009).

Environmental factors such as snow cover and plant production and phenology can generate variation in habitat selection at a longer temporal scale (Poole & Stuart-Smith 2006, Godvik et al. 2009, Zweifel-Schielly et al. 2009). This applies to forested areas where ungulates utilise young forest stands early in the growing season (Hjeljord et al. 1990, Boyce et al. 2003), likely due to the newly sprouting plants of high nutritional quality (Hjeljord al. 1990, Hebblewhite et al. 2008) and higher density of forage (Hjeljord et al. 1990, Månsson 2009). In contrast, older forest stands, that may also provide cover, seem to be more used during autumn when the forage quality of shade-living plants is relatively higher (Bø & Hjeljord 1991, Hebblewhite et al. 2008). Old forest stands can also be important during winter as they generally have lower snow depth and thus allow better access to food plants in the dwarf shrub layer and reduces movement costs (Parker et al. 1984). Moreover, once the deciduous leaves have fallen, the selection of conifers as forage increase (Nikula et al. 2004). To optimise the energetic balance, habitat selection by ungulates should track these seasonal variations.

The costs and benefits associated with different habitat types are also likely to vary according to age, sex or reproductive status of the animal (Nikula et al. 2004, Dussault et al. 2005). Predation risk may be higher for females with young, which may respond by seeking habitat types providing protective cover (Dussault et al. 2005, Ciuti et al. 2006). Conversely, males are more likely to choose habitat types that maximize energy gains (Main 2008). Such differences in habitat use may be stronger in some seasons than in others, causing state-dependent seasonal variation in habitat selection (Nikula et al. 2004).

In this study, we examined whether moose *Alces alces* in central Norway showed temporal variation in habitat selection, and whether variation in selection differed among moose of different sex and reproductive status. We expected (i) moose to show circadian variation in habitat selection, reflecting a trade-off between food and cover with variation in light. Moreover, because of seasonal variation in phenology and snow cover, we predicted (ii) moose to select farmland and young forest stands, with rich supply of deciduous browse, during the growing season, and (iii) more closed habitat types in winter due to less snow and better access to field-layer vegetation. Lastly, we expected

(iv) reproducing females to avoid open areas more often than other categories of moose, particularly during the first months after birth.

Material and methods

Study area

The study area (approximately 29,000 km²) is located in central Norway (64°30'N, 12°50'E) and ranges from coastal areas in the boreonemoral zone to alpine zones (Moen 1999). Large parts are covered by coniferous forest, mostly used for commercial forestry. The main tree species are Norway spruce *Picea abies*, Scots pine *Pinus sylvestris* and downy birch *Betula pubescens*. Bogs with sparse or no tree vegetation are scattered throughout the area, creating a heterogeneous forest landscape. Cultivated land is mostly found at lower altitudes (Moen 1999) and is typically used for grass or grain production.

To assess the foraging value of different forest types and succession stages, we analysed vegetation data from 567 circular sample plots of 250 m², collected by the Norwegian National Forest Inventory during 2005-2008 (Landsskogtakseringen 2008). We estimated density of trees within moose browsing height (0.5-3.0 m) of rowan *Sorbus aucuparia*, aspen *Populus tremula* and goat willow *Salix caprea*, which are all highly preferred browse species for moose (Månsson et al. 2007b). Similarly,

we estimated the density of other accessible deciduous tree species pooled. These included mainly downy birch, an important but less preferred browse (Månsson et al. 2007b), and grey alder *Alnus incana*, which is rarely eaten. Additionally, we estimated availability of Scots pine, an important winter browse (Månsson 2009). We also recorded the proportion of plots with field-layer vegetation (i.e. vegetation < 0.5 m, but excluding trees and bushes that can normally exceed this height), categorised as good, intermediate and poor forage. Good forage was defined as vegetation types with tall forbs and ferns, of which many are eaten by moose during summer (e.g. Hjeljord et al. 1990, Sæther & Heim 1993). Intermediate forage was defined as vegetation types with bilberry *Vaccinium myrtillus*, and low forbs and grasses, whereas poor forage vegetation types were dominated by bog bilberry *Vaccinium uliginosum*, various mosses and lichens. To quantify availability of cover for moose, we estimated the density of trees with a trunk diameter of > 20 cm at 1.3 m above ground. Trees of this size typically form a closed canopy, reducing the ground snow cover and providing protection from weather and visual exposure to humans. Results are shown in Table 1, and provide the background for dividing the area into different habitat types relevant to moose (see below).

In central Norway, the vegetation growing season usually starts in May and peaks in July (Karlsen et al. 2006). From late November to late April, the

Table 1. Proportion of plots (250 m², N = 567) with field-layer vegetation of different moose forage quality, density of trees within moose browsing height (i.e. 0.5-3.0 m) and proportion of trees with a diameter of > 20 cm at 1.3 m above ground in six different forest types. Good forage plots are mainly covered with tall forbs and ferns, intermediate forage plots with bilberry, whereas poor forage plots are mainly covered with bog bilberry and other poor quality plants. Data were collected during 2005-2008. The cover types O = open, I = intermediate and C = dense forest, and the forage quality types P = poor, F = fair and G = good of the different habitat types were estimated for moose in spring (Sp), summer (Su), autumn (Au) and winter (Wi).

| Forest type | Proportion of field-layer quality | | | Number of trees/ha (± 1 SE) | | | | Forage quality | Cover |
	Good	Intermediate	Poor	Rowan-aspen-willow	Other deciduous	Pine	Large trees	Sp,Su,Au,Wi	Sp,Su,Au,Wi
Young spruce	0.29	0.71	0.00	1074 (236)	1952 (260)	7 (4)	76 (21)	G,G,G,F	I,I,I,I*
Mature spruce	0.17	0.77	0.06	840 (84)	1524 (108)	32 (12)	112 (11)	F,F,F,F	C,C,C,C
Old spruce	0.12	0.71	0.17	559 (55)	874 (60)	62 (13)	154 (10)	P,P,P,F	C,C,C,C
Mixed	0.08	0.55	0.37	559 (105)	1733 (142)	179 (35)	66 (9)	F,F,F,G	C,C,C,C/I
Pine	0.00	0.45	0.55	416 (174)	914 (186)	246 (70)	138 (38)	P,P,P,G	C,C,C,C
Deciduous	0.35	0.55	0.10	1566 (277)	2409 (243)	3 (2)	15 (10)	G,G,G,F	I,I,I,I/O
Bog								P,P,P,P	O,O,O,O
Cultivated land								F,G,G,P	O,O,O,O
Open vegetation								F,F,F,F	O,O,O,O

* Estimate of the average provision of cover by young forest in the study area. The actual provision of cover depends on the age of the respective forest stand, varying among O, I and C.

study area is normally covered by snow, but with large spatial variation in average monthly snow depth (approximately 2-100 cm). Large carnivores are present at low abundance (< 30 bears *Ursus arctos* and < 5 wolves *Canis lupus* in the entire study area; Wartiainen et al. 2009, Wabakken et al. 2007). Moose are hunted in September and October, which coincides with the rutting season. Moose give birth in late May and early June. Based on the biology of moose, weather conditions and plant productivity, we defined four seasons for use in the analyses: i) spring (May and June), ii) summer (July and August), iii) autumn (September-November) and iv) winter (December-April).

Habitat types

Habitat types were derived from two digital land cover maps with a resolution of 30 x 30 m. From a satellite-based vegetation map, provided by the Northern Research Institute (Johansen et al. 2009), we defined four coarse land cover types: forests, agricultural land, bog (mainly peat bog) and open vegetation, which we assumed to differ in provision of food and cover for moose (see Table 1). Open vegetation included moors, sparsely vegetated areas, as well as meadows. As the land cover map did not include forest age, we also used a forestry map with data on forest stand age and tree species composition provided by the Norwegian Forest and Landscape Institute (Gjertsen 2007). We defined four forest types: pine-dominated forest, deciduous forest, mixed forest and spruce-dominated forest. We had no detailed data on species composition for mixed forest, but this typically is a mixture of coniferous and deciduous species with no species constituting more than 50% (Gjertsen 2005). We also defined three forest development stages: young forest (< 40 years), mature forest (40-80 years) and old forest (> 80 years).

Based on the forest inventory plots (Landsskogtakseringen 2008; see Table 1) and information on moose diet from literature (Hjeljord et al. 1990, Nikula et al. 2004, Månsson et al. 2007b, Månsson 2009), we allocated a qualitative cover and forage value to each habitat type (see Table 1).

Moose data

We used data from 64 GPS-collared moose for which the GPS attempted to acquire one position (or fix) at two hour intervals. For each hour of the day we recorded between 38,151 and 38,413 fixes during the study period, 2006-2009. The analysis was divided in two parts: analysis of land cover utilisation and analysis of forest type and forest stage utilisation. In the analysis of land cover utilisation, we included 11 males and 53 females for which >10 GPS-fixes were available every second hour of the day per month during one or several years (May-April). We tracked 10 males and 27 females for more than one year. We knew the reproductive status (calf/calves: N = 81, or no calf: N = 12) for all females each year.

In the analysis of forest type and forest stage utilisation, we used maps covering forested areas only, reducing the available number of fixes per moose. We included seven males and 35 females, for which a minimum of five GPS-locations in forest were available every second hour of the day per month. All males and 15 females were tracked for more than one year. Presence of calf/calves was recorded in 43 breeding attempts, whereas no calf was recorded in seven breeding attempts. Each moose provided between 2,675 and 12,454 GPS-locations. Data were screened for positional errors following Bjørneraas et al. (2010).

Statistical analyses

We analysed the circadian use of land cover types and forest stages by examining proportion of locations within the different habitat types. We applied a generalised additive mixed effect model (GAMM) with cyclic regression splines and binomial family with log-link (mgcv package in R; Wood 2006) for each habitat type. Proportion of positions within the respective habitat was the only explanatory variable included. To reduce heteroscedasticity and account for repeated measurements from the same individual, we added moose-id as a random factor. To account for temporal dependency among observations, we used a continuous correlation structure (corARMA; Pinheiro & Bates 2000). We compared models with different time lags for each habitat type. We selected the models with the best approximating correlation structure, i.e. the best time lag, based on Akaike Information Criterion (AIC; Pinheiro & Bates 2000).

To analyse the circadian and seasonal variation in habitat selection we used Step Selection Functions (SSFs; Fortin et al. 2005). The SSF compares characteristics of the area used by moose with characteristics of the available landscape by generating random locations (Fortin et al. 2005). We paired each animal location with two random locations that were located in a random direction
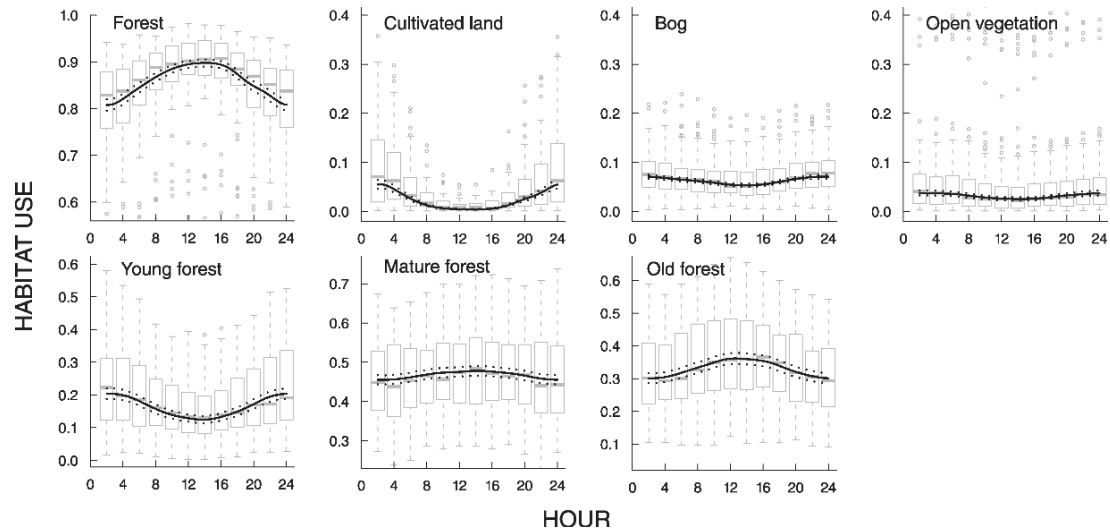
Figure 1. Circadian variation in moose habitat use for different land cover types (upper four panels) and forest stages (lower three panels). The curves were estimated by GAMMs and dashed lines indicate ± 1 SE. The box plots show the distribution of the GPS-observations.

and distance within two km (the 99% quantile of the observed step lengths) from the GPS-location. The GPS-locations represent areas used by moose, whereas the random locations represent the available areas. Given the high total number of locations (1,590,799 for the land cover analysis and 634,668 for the forest analysis), the random and the animal locations should provide a representative measure of used and available habitat types within the study area.
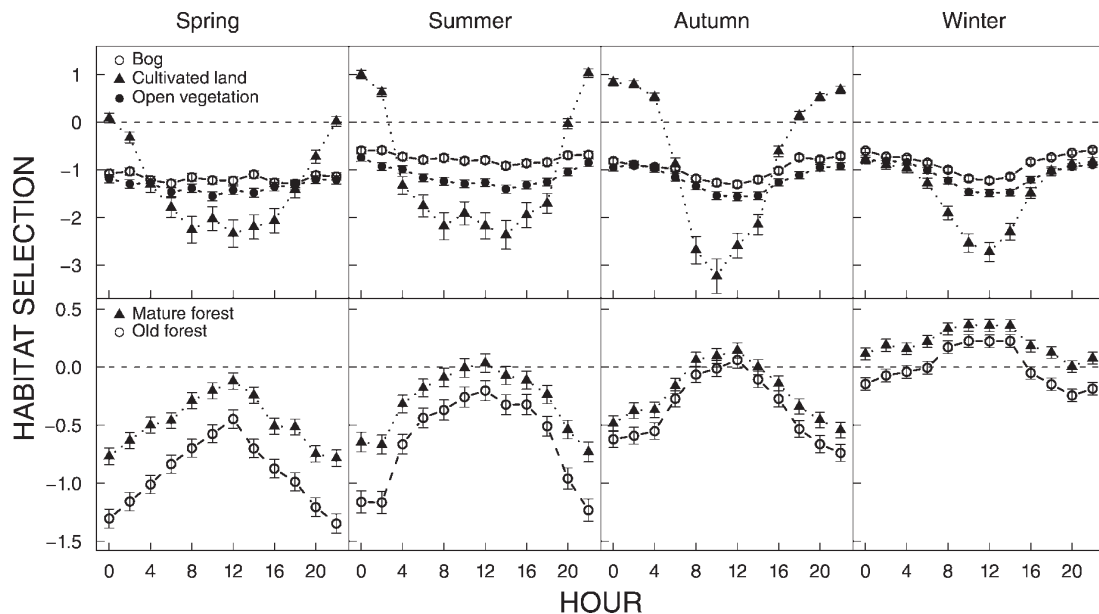
Figure 2. Step Selection Function-scores showing circadian habitat selection in four seasons by moose in central Norway. The upper panels show land cover selection with forest as reference land cover whereas the lower panels show selection of different forest stages with young forest (< 40 years old) as reference stage. The highest values indicate the selected habitat type at a given hour. The reference habitat type is selected when other habitat types have values below zero. Bars show robust standard errors.

To compare habitat types of used and available locations, we used conditional logistic regression from the R-package survival (Therneau 2009). The β-coefficients estimated by the conditional logistic regression are associated with the different habitat types, and indicate the log odds for that habitat type being chosen by the animals relative to a reference habitat type. The habitat type with the highest β-value is selected. Accordingly, selection for the reference habitat occurs when the other habitat types have $\beta < 0$. We analysed the selection of land cover types, forest types (pine, mixed, deciduous, and spruce forest) and forest development stages (young, mature and old; see Table 1). For the combined analysis of forest types and development stages, only spruce forest was stratified into development stages due to low abundances of deciduous, pine and mixed forest. To test for state-dependent habitat selection, we performed the analyses of seasonal habitat selection separately for males and females with and without young.

Availability and use of water and urban areas ($< 1\%$) were eliminated from the analyses. We accounted for possible temporal autocorrelation in the data by estimating robust standard errors as precision estimates for the β-values (Fortin et al. 2005). All analyses were conducted in R for Windows version 2.10.1 (R Development Core Team 2009).

Results

Moose showed a non-linear circadian variation in habitat use (effective degrees of freedom, edf > 1; Fig. 1). Open land cover types were used more at night (cultivated land: edf = 7.3, P < 0.001, bog: edf = 5.7, P < 0.001, open vegetation: edf = 6.3, P < 0.001; see Fig. 1), whereas forest was used more during the day (edf = 7.5, P < 0.001; see Fig. 1). Within forested areas, moose used young forest stands more during night than day (edf = 6.9, P < 0.001), whereas the opposite was found for mature (edf = 4.0, P < 0.001) and old forest stands (edf = 6.1, P < 0.001; see Fig. 1). All GAMMs examining circadian variation in habitat use were significantly improved by inclusion of a continuous correlation structure (Δ AIC > 2).

The habitat selection patterns were similar to the circadian variation in habitat use (Fig. 2). In summer and autumn, moose selected cultivated land at night, and showed equal selection for forest

Figure 3. Step Selection Function-scores showing seasonal land cover selection by moose in central Norway, forest being the reference land cover. The land cover with the highest values is the selected land cover at a given season. The reference land cover is selected when other land cover types have values below zero. Bars show robust standard errors.
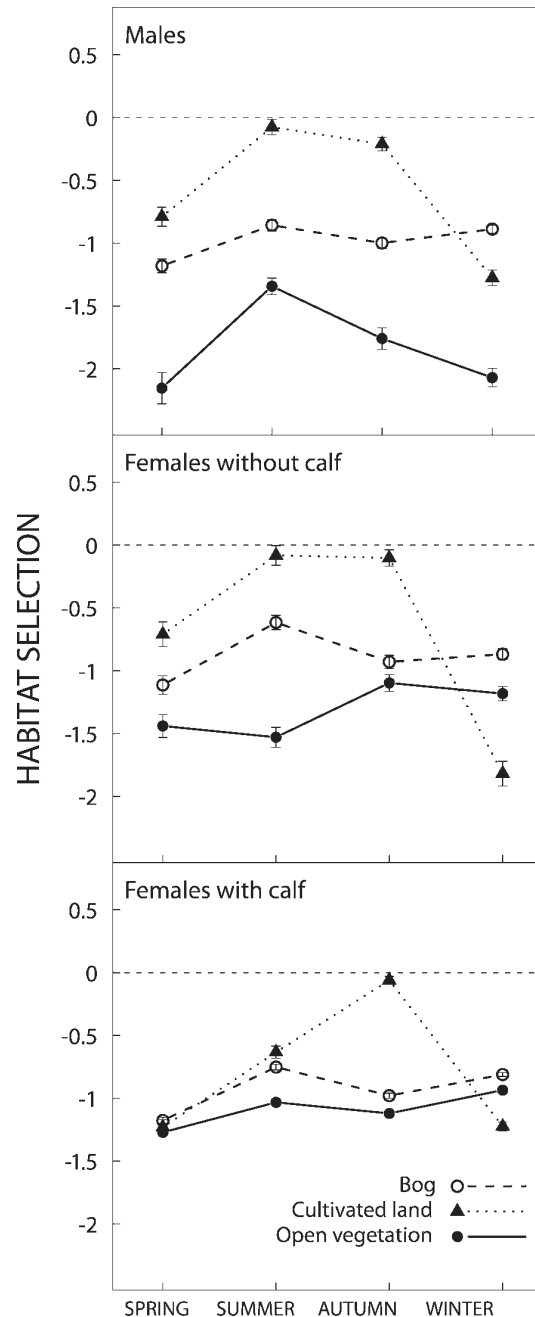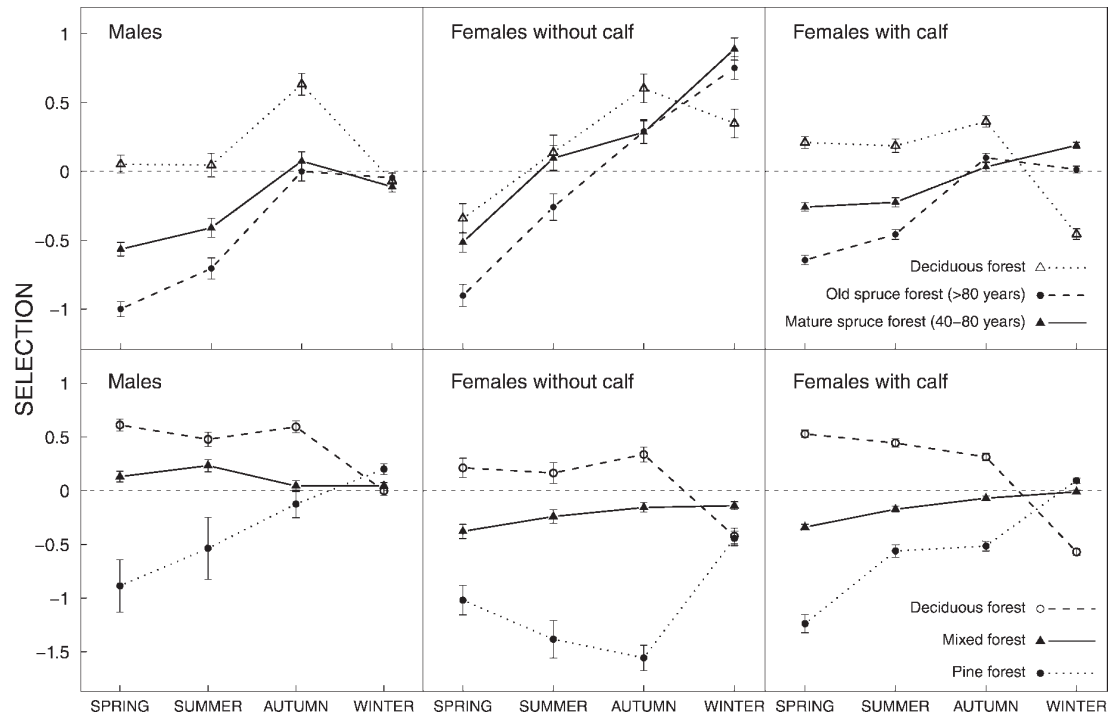
Figure 4. Step Selection Function-scores showing seasonal selection of forest type and forest stage by moose in central Norway. The forests with the highest values are the selected forest type or stage at a given season. Values below zero indicate that this forest type or stage is less selected than the reference forest, i.e. young spruce forest in the upper panels and spruce forest in the lower panels. The reference forest is selected when other forest types and stages have values below zero. Bars show robust standard errors.

and cultivated land around midnight in spring. In forested areas, moose selected young forest stands during night in spring, summer and autumn, but selected mature and old forest stands at an increasingly larger part of the day from spring to winter.

Overall, moose selected forest in all seasons, as well as cultivated land during the growing season (Fig. 3). In summer, males (β = -0.08, P = 0.21) and females without calf (β = -0.08, P = 0.29) showed equal selection for forest and cultivated land, whereas reproducing females clearly selected forest to all other land cover types (β < -0.63, P < 0.001). In autumn, females with (β = -0.06, P = 0.06) and without calves (β = -0.10, P = 0.11) showed a high selection for cultivated land (see Fig. 3).

When examining the selection of forest stands with different tree species compositions, all moose categories selected deciduous forest stands in spring, summer and autumn (β > 0.21, P < 0.02). Females without young showed a similar selection for spruce forest in summer (β=0.16, P=0.09; Fig. 4 lower panels). Moreover, when splitting spruce

forest into different stages, we found males to show equal selection for young spruce forest stands and deciduous forest stands in spring (β=0.05, P=0.43) and summer (β = 0.04, P = 0.60). Also females without young showed equal selection for young spruce forest and deciduous forest stands in summer (β = 0.13, P = 0.28), and even higher selection for young spruce forest stands in spring (deciduous forest: β = -0.34, P = 0.002).

Moose showed decreasing selection for deciduous forest and increasing selection for pine forest from spring to winter. The latter pattern was particularly prominent for males and females with calf (see Fig. 4). Females also showed a higher selection for mixed forest towards winter (see Fig. 4).

Discussion

Ungulate habitat use is often found to be a product of trade-offs between the need of forage and protection from predators, humans and weather.

However, as the relative magnitude of the different factors, as well as the animal requirements may change over time, habitat use and selection may vary during the year (e.g. Godvik et al. 2009). Accordingly, we found habitat utilisation to vary temporally at the scale of days and seasons, where moose seemed to select habitat types with abundant, good forage, but also trade food for cover during periods of high perceived predation risk (Lykkja et al. 2009).

Open habitat types may provide good access to high-quality forage, but also increase the exposure to predators, humans and weather (Demarchi & Bunnell 1995, Godvik et al. 2009, Herfindal et al. 2009). The selection for open habitat types with good forage during night-time and for closed forests during day-time in spring, summer and autumn (see Fig. 2) support prediction (i) that moose try to optimise the relationship between food and cover, as found for other ungulates (e.g. Godvik et al. 2009). In our study system, the abundance of large predators is low (Wabakken et al. 2007, Wartiainen et al. 2009); therefore the variation in short-term utilisation of habitat types providing cover and forage is more likely a behavioural response to perceived predation by humans (Lykkja et al. 2009). The high utilisation of habitat types providing cover during daytime (see Figs. 1 and 2) may also to some extent be a response to heat stress. Moose may experience heat stress at ambient air temperatures above 14°C in summer and -5°C in winter (Renecker & Hudson 1986), thresholds that are regularly exceeded in our study area (Karlsen et al. 2006). However, a recent study detected no differences in habitat use relative to thermoregulation thresholds for moose (Lowe et al. 2010).

During the growing season, ungulates may benefit from feeding on newly emerged plants of high nutritional quality (White 1983, Hebblewhite et al. 2008). In our study area, habitat selection by moose in this part of the year (see Figs. 3 and 4) was clearly related to the provision of food as they selected cultivated land, deciduous forest and young spruce forest, which all provide good forage (see Table 1), in accordance with prediction (ii). The increased selection of older forest stages in autumn (see Figs. 2 and 4) may be due to higher quality of shade-living plants (Hjeljord et al. 1990, Bø & Hjeljord 1991) late in the growing season, or because hunting increases moose selection for cover.

Snow increases the energetic costs of movement (Parker et al. 1984), which is a likely explanation for the observed increase in selection of older forests (> 40 years) in winter (see Fig. 4, prediction (iii)). Old forest stands have high density of large trees (see Table 1) and a well-developed canopy that restricts accumulation of snow (Peek 1998). Moreover, these forest types commonly provide rich cover of bilberry (i.e. intermediate forage quality; see Table 1), which is found to constitute an increasing part of the moose diet in autumn (Hjeljord et al. 1990). However, following less access to plants in the field-layer and lack of deciduous leaves in winter, moose may also increase their browsing on pine (Månsson 2009). This is consistent with our findings that moose selected pine forest stands in winter (see Fig. 4). Mixed forests also provide fair amounts of pine (see Table 1), explaining the relatively high selection for mixed forest stands in this season (see Fig. 4). Hence, we suggest that habitat selection by moose in winter is a compromise between movement constraints and the feeding values of the different habitat types.

Ungulates accompanied by young are generally expected to select areas with low predation risk (Dussault et al. 2005, Ciuti et al. 2006, but see Theuerkauf & Rouys 2008). Moose in Norway experience relatively low natural calf mortality (average survival rate above 0.8; Stubsjøen et al. 2000), but are heavily harvested and tend to avoid humans (Lykkja et al. 2009). Thus, also in our study area reproducing females were expected to avoid open areas more than other moose (prediction iv). Concordantly, we found that females with young clearly avoided cultivated land during summer, in contrast to males and females without young (see Fig. 3). At this time of the year cultivated land commonly provide good forage, but no cover. Thus, the optimal trade-off between forage and cover, when these resources are spatially segregated, appears to depend on reproductive status. Protection of young can also explain why reproducing females selected deciduous forest during the growing season (see Fig. 4), whereas males and females without calf showed equal or even higher selection for young and presumably more open spruce forest.

Moose exploit the variations in foraging opportunities and cover created by human land transformation. Indeed, modern forestry and agriculture seem to enhance foraging opportunities for ungulates (i.e. high density of preferred food plants in young forest; see Table 1), and high clear-cutting frequency has been suggested to be important for the persistent high densities of moose in Fenno-

scandia (Lavsund et al. 2003). However, the current trend in Norwegian forestry is less clear-cutting (Rolstad et al. 2002), leading to declining proportions of prime habitats for moose. This can have negative consequences for the moose condition in areas where high moose density has already resulted in a high browsing pressure, deteriorating forage quality, declining body mass, and lower recruitment rates (Hjeljord & Histøl 1999, Lavsund et al. 2003). It is therefore essential to learn if preferred food species can tolerate increasing browsing pressure, or if selective browsing may lead to recruitment failure of heavily browsed species (Tremblay et al. 2007). It will also be important to know the relationship between moose condition and the utilisation of different forest and land cover types, if we are to evaluate the cost and benefits associated with different habitat types. This may increase our ability to predict if current high densities of moose can be sustained without further decline in body condition and fecundity when facing changing forestry practices.

Conclusion

Our study demonstrates that habitat selection by moose is governed by a trade-off between good forage and protection from predators and humans, a trade-off that varies with the reproductive status of moose. The preference for cover and high-quality food generates changes in habitat selection throughout the year, as the availability of these resources varies among seasons and habitats. Human land use has contributed to form habitat types with abundant moose forage, in addition to create a heterogeneous landscape which provides a mix of habitat types providing cover and high-quality food. This heterogeneity is utilised by moose, suggesting that human habitat alteration has contributed to better conditions for moose in our study area, particularly when it comes to access to food.

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Paper III

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Paper IV

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two symparic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*

1987 Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988 Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988 Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988 Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988 Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989 John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989 Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989 Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989 Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990 Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990 Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990 Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990 Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990 Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990 Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991 Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991 Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991 Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991 Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991 Trond Nordtug	Dr. scient Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods
1991 Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991 Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism

1991 Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991 Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992 Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992 Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992 Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992 Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992 Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993 Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993 Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993 Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993 Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993 Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993 Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993 Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993 Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994 Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994 Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994 Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994 Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994 Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply

1994 Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995 Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995 Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995 Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995 Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996 Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996 Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996 Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996 Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997 Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997 Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors
1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway

1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997 Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997 Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997 Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998 Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach
1998 Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999 Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999 Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)

1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts

2002 Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002 Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002 Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002 Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002 Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002 Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002 Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002 Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002 Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002 Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003 Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003 Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003 Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003 Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003 Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003 Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003 Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003 David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003 Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003 Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004 Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004 Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004 Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004 Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities

2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds
			Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates

2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod (*Gadus morhua* L.) Focus on formulated diets and early weaning

2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009 Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009 Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009 Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010 Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010 Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010 Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010 Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010 Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010 Anders Lyngstad	ph.d Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010 Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010 Ingerid Brænne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010 Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010 Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011 Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011 Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011 Ann-Iren Kittang	ph.d Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011 Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011 Christopher Gravningen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in *Arabidopsis thaliana*
2011 Grethe Robertsen	ph.d Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011 Line-Kristin Larsen	ph.d Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011 Maxim A. K. Teichert	ph.d Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density

2011	Torunn Beate Hancke	ph.d Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology
2011	Sajeda Begum	ph.d Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	ph.d Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	ph.d Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	ph.d Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	ph.d Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals